

EVAPORATIVE WATER LOSS IN SCALELESS SNAKES

ALBERT F. BENNETT* AND PAUL LICHT

Department of Zoology, University of California, Berkeley,
CA 94720, U.S.A.

(Received 19 June 1974)

Abstract—1. Rates of water loss were measured in two aberrant scaleless water snakes, *Natrix sipedon*, and in six normal animals.

2. Pulmocutaneous water loss of the scaleless animals was equal to or less than that of the controls at 20, 27, and 34°C.

3. The thermal dependence of pulmocutaneous water loss in all snakes was low ($Q_{10} = 1.31-1.89$).

4. The proportion of total water loss due to cutaneous evaporation (86.5%) in a scaleless animal at 20°C was similar to that previously reported for normal *Natrix*.

5. Thus, reptilian scales and their associated features (e.g. thick keratin layers, superficial dermal layer) cannot be considered adaptations for the curtailment of integumentary water loss.

INTRODUCTION

REPTILIAN skin is characterized by a low water permeability: cutaneous water loss in this group is low in comparison to all other vertebrates. However, the morphological and physiological bases of this low cutaneous permeability are poorly understood. The fact that a scaly integument is one of the most conspicuous features of the reptiles has led to the common hypothesis that scales may be important for retarding water loss. However, our recent observations (Licht & Bennett, 1972) on an aberrant scaleless gopher snake, *Pituophis catenifer*, have cast doubts on this view. Despite gross morphological abnormalities in its integument, the rate of pulmocutaneous evaporative water loss in this scaleless animal was identical to that in a normal specimen. We concluded that reptilian scales and their associated features (e.g. thickened beta-keratin and superficial dermis) cannot be considered adaptations to restrict water loss.

Unfortunately, it is difficult to generalize on the basis of a single specimen. Further we did not partition water loss into pulmonary and cutaneous components; it is possible that the scaleless individual might have had a lower pulmonary water loss and hence a higher cutaneous loss than the control animals. However, such differences seemed unlikely since rates of oxygen consumption were the same in both animals. Also, water loss was measured only at a single body temperature and the contribution of scales to water retention may vary with temperature.

The subsequent acquisition of two more scaleless snakes of another species, the water snake *Natrix sipedon*, members of a different subfamilial group and ecological type, allowed further examination of the importance of scales in water loss. In particular, we took this opportunity to examine the thermal effects and compartmentalization of water loss in relation to scale structure.

MATERIALS AND METHODS

Two scaleless specimens of the common water snake *Natrix sipedon* were collected by David Roudebush in Harford County, Maryland, and were sent to us by Dr. George Zug of the U.S. National Museum. One of the specimens was a small juvenile (approximately 30 cm and 9.6 g) and the other (65 cm and 82.6 g) had been in captivity for several years. Both animals were similar in appearance; they possessed ventral scutes but completely lacked all dorsal and lateral scales. In this regard, they had even fewer scales than the *Pituophis* examined previously (Licht & Bennett, 1972). The body surface had a superficially smooth texture and lacked the characteristic luster of the normal snake; their color patterns were essentially normal. For comparison, a series of three juvenile (7–11.5 g) and three adult (84.8–125.8 g) *Natrix* were utilized as control animals.

For determination of total pulmocutaneous water loss, animals were placed individually in a darkened air-tight glass tube (1.0 m × 2.5 cm. diameter) containing a thermocouple to monitor temperature. Dry air was metered through this chamber at a rate sufficient to maintain an internal water vapor pressure of 3–8 mm Hg (10–30% r.h.) The relative humidity of the excurrent air line was monitored with a Hygrodynamics narrow range humidity sensor connected to a Varian strip chart recorder. Water loss values were also checked gravimetrically by the collection of water vapor with Drierite (anhydrous CaSO_4); values were identical to those obtained from the humidity sensor. The animal and sensing apparatus were placed in a controlled temperature cabinet set at 20, 27, or 34°C ($\pm 0.5^\circ\text{C}$). The animal was left at each temperature for 1 hr to equilibrate and humidity readings were then recorded continuously for 2–3 hr. Animals remained quiet and inactive during measurement. The 15-min period during which relative humidity readings were lowest was utilized to estimate minimum rates of water loss. The humidity readings never varied more than 1% during the minimum measurement period.

Attempts to partition pulmonary and cutaneous water loss were generally unsuccessful because the skin of the scaleless animals was extremely delicate and tore easily. However, one successful experiment in which the head was isolated from the body by use of a rubber membrane allowed estimation of the cutaneous component at 20°C in the smaller scaleless individual.

* Present address: School of Biological Sciences, University of California, Irvine, CA 92664, U.S.A.

Table 1. Minimal rates of pulmocutaneous water loss in scaleless and normal *Natrix*. Water loss is reported as mg H₂O per g body wt/hr

Specimen	Wt. g	Temperature		
		20°C	27°C	34°C
Small				
Scaleless	9.6	2.35	2.84	3.74
Normal	11.5	4.17	7.30	11.3
Normal	11.4	8.53	12.3	18.1
Normal	7.0	9.37	15.0	20.9
Large				
Scaleless	82.6	1.84	2.50	3.68
Normal	84.8	1.92	3.30	4.84
Normal	125.8	2.40	1.74	2.54
Normal	106.3	1.84	2.80	4.62

RESULTS

The rates of pulmocutaneous water loss for all snakes at three different temperatures are reported in Table 1. The water loss of the larger scaleless snake is in every case encompassed by the range of rates of the control animals of similar size. The smaller scaleless animals, however, lost much less water than the control snakes of similar size. Its rate of water loss was only 22–32% of that of the controls.

The thermal dependence of pulmocutaneous water loss is given in Table 2. There is no appreciable rise in the rate of water loss with increasing body temperature over the thermal range investigated. Likewise, there is no difference between the thermal dependence of water loss in the scaleless and control animals.

In the experiment to partition pulmonary and cutaneous water loss, the rate of total pulmocutaneous water loss of the small scaleless snake was 2.83 mg H₂O/g × hr. Cutaneous water loss was 2.45 mg H₂O/g × hr, or 86.5% of the total water loss.

DISCUSSION

The absence of scales and their associated structures does not affect the rate of water loss in *Natrix*. If anything, the rate of pulmocutaneous water loss in the smaller animal is significantly less than that of the control snakes. The values of pulmocutaneous water loss measured for our control *Natrix* are very similar to those reported for semi-aquatic and forest-dwelling snakes of equal size (Gans *et al.*, 1968). There is a marked correlation between habitat and water loss in reptiles: species living in dry areas have much lower rates of water loss than those inhabiting wetter

Table 2. Thermal dependence of the rates of water loss in scaleless and normal *Natrix*

Specimen	Q ₁₀	
	20–27°C	27–34°C
Small scaleless	1.31	1.48
Small normal	1.81	1.72
Large scaleless	1.55	1.74
Large normal	1.41	1.84

areas (Dawson *et al.*, 1966; Bentley & Schmidt-Nielsen, 1966; Claussen, 1967; Gans *et al.*, 1968; Prange & Schmidt-Nielsen, 1969). For example, pulmocutaneous water loss is 1.9 to 3.4 times greater in *Natrix*, a semi-aquatic group, than in *Pituophis*, a terrestrial, arid-inhabiting genus (Gans *et al.*, 1968; Prange & Schmidt-Nielsen, 1969). Prange and Schmidt-Nielsen (1969) have demonstrated that these interspecific differences are due to a greater cutaneous water loss in *Natrix* than in *Pituophis*, respiratory water losses being identical. Whatever the basis of interspecific differences in water loss, it is also evident in scaleless animals. Pulmocutaneous water loss in the small scaleless *Natrix* is 2.8 times as great as that of the scaleless *Pituophis* (Licht & Bennett, 1972).

The cutaneous portion (86.5%) of pulmocutaneous water loss in the small scaleless *Natrix* is identical to the value measured for *Natrix taxispilota* (88% at 25°C) by Prange & Schmidt-Nielsen (1969). The cutaneous water loss of our scaleless snake on the basis of surface area (0.42 mg H₂O/cm² × hr) is less than that measured in the normally-scaled *Natrix* (0.70 mg H₂O/cm² × hr) (Prange & Schmidt-Nielsen, 1969) (surface area calculated according to Benedict's relation (1932) of $A = 12.5 W^{2/3}$, in which A is surface area in cm² and W is body weight in g). It appears, therefore, that cutaneous water loss is no greater in scaleless than in normal reptiles.

The thermal preferendum of *Natrix* is approximately 27°C (Brattstrom, 1965); these animals would rarely encounter a body temperature of 34°C in nature. The latter temperature provides a degree of heat stress without eliciting hyperventilation, with its consequent large increment in respiratory water loss. The Q₁₀ values for pulmocutaneous water loss (Table 2) are intermediate to the values (1.2–2.6) reported for lizards by Dawson *et al.* (1966). There is no suggestion in the data that the scaleless animals lose a proportionately greater amount of water at higher temperatures than do the control snakes.

These experiments substantiate our earlier conclusion (Licht & Bennett, 1972) regarding the role of the reptilian integument in water conservation. It is difficult to see how variations in scale morphology can be considered adaptations to retard water loss since animals which lack them have properties of water loss identical to animals which possess them. The thermal dependence, the rate of pulmocutaneous water loss, and the proportion accounted for by cutaneous evaporation are all similar in scaleless and normal animals. The fragility of the skin of the scaleless animals suggests that mechanical protection may be a principal function of a scaly integument. The differential in water loss between the scaleless *Natrix* and scaleless *Pituophis* also demonstrates that the pronounced interspecific differences in water loss observed among the reptiles are not functions of differences in scale size or morphology but rather reflect more fundamental properties of the reptilian integument.

Acknowledgements—This investigation was supported by a Miller Postdoctoral Research Fellowship to AFB and NSF Grant 22642 to PL. We wish to thank Mr. David Roudebush and Dr. George Zug of the United States National Museum for supplying the scaleless animals.

REFERENCES

- BENEDICT F. G. (1932) The physiology of large reptiles. *Carnegie Inst. Wash. Pub.* **425**.
- BENTLEY P. J. & SCHMIDT-NIELSEN K. (1966) Cutaneous water loss in reptiles. *Science, Wash.* **151**, 1547-1549.
- BRATTSTROM B. H. (1965) Body temperatures of reptiles. *Am. Midl. Nat.* **73**, 376-422.
- CLAUSSEN D. L. (1967) Studies of water loss in two species of lizards. *Comp. Biochem. Physiol.* **20**, 115-130.
- DAWSON W. R., SHOEMAKER V. H. & LICHT P. (1966) Evaporative water losses of some small Australian lizards. *Ecology* **43**, 589-594.
- GANS C., KRAKAUER T. & PAGGANELLI C. V. (1968) Water loss in snakes: Interspecific and intraspecific variability. *Comp. Biochem. Physiol.* **27**, 747-761.
- LICHT P. & BENNETT A. F. (1972) A scaleless snake: Tests of the role of reptilian scales in water loss and heat transfer. *Copeia* **1972**, 702-707.
- PRANGE H. D. & SCHMIDT-NIELSEN K. (1969) Evaporative water loss in snakes. *Comp. Biochem. Physiol.* **28**, 973-975.

Key Word Index—Evaporation; integument; *Natrix*; reptile; scales; skin, snake; water loss.