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A unique specimen of gopher snake (*Pituophis melanoleucus catenifer*) lacking dorsal and lateral body scales was used to evaluate the physiological importance of reptilian scales. Its dorsal integument totally lacked the outer "superficial" dermal layer and possessed a keratin layer much thinner than that of normal scales. In tests of rates of pulmocutaneous water loss and heat transfer, no difference was observed between the scaleless animal and a normal individual of comparable age and size. These data cast doubts upon the assertions that scales are an adaptation to retard water loss or that their presence is significant in convective heat transfer.

INTRODUCTION

A scaly, keratinized integument is one of the distinctive features of the Reptilia, and has classically been interpreted as an important morphological characteristic in the adaptation to terrestrial existence. Considerable information is available on the morphogenesis and morphology of the integument, especially the epidermis (e.g., Maderson 1964, 1965; Maderson and Licht, 1967), but evidence for the physiological importance of scales is sparse and based largely on indirect observations. For example, correlations between variations in the size and form of scales and several climatic conditions have been used to suggest that scales may be important in the regulation of water loss or heat transfer (Soulé, 1966; Soulé and Kerfoot, 1972). Direct physiological tests of such hypotheses have been hindered by the inability to manipulate the structure of the scales.

A unique opportunity to study the physiological function of reptilian scales was presented by the capture of a hatchling gopher snake (*Pituophis melanoleucus catenifer*) that was scaleless over most of the body surface. The present paper reports a comparative study of evaporative water loss and convective heat transfer in this scaleless snake and a normal specimen of the same species.

MATERIALS AND METHODS

The scaleless specimen was collected by Mr. Mike DeSmidt and Mr. Rick Carvelo in an area near Oakland, California, on September 25, 1971. It was kept in captivity at room temperature for about a month before this study. For comparative purposes we obtained

a normal hatchling *P. m. catenifer* of almost identical proportions (Table 1), collected from the same area.

Evaporative Water Loss and Metabolism.—In the first series of experiments, simultaneous measurements were made of total-pulmocutaneous—evaporative water loss and oxygen consumption at 28 ± 0.3 C in a darkened chamber. This temperature was chosen because it is within the range of active body temperatures of *Pituophis* (Brattstrom, 1965; Greenwald, 1971). The snake was suspended and immobilized in an extended position in a fine mesh plastic screening within a glass tube (50 cm \times 2.5 cm diameter). Dry air was metered at 50 cm³/min through this tube (air velocity approximately 1 cm/min). Total water loss was measured gravimetrically by absorption of water vapor from the excurrent line with Drierite (anhydrous CaSO₄). Water loss was also verified by measuring relative humidity with a HygroDynamics humidity sensor interposed in the excurrent air line between the animal chamber and drying tube. Good agreement was obtained between the two methods. To monitor oxygen consumption of the snake, the dried air was passed through a Beckman paramagnetic oxygen analyzer with a flow-through system. Both oxygen consumption and water loss were monitored continuously from 0900 to 1600 PDT. Stable minimal values were obtained within 3 hours after introduction of the animal into the chamber. RH remained at about 13% and O₂ above 20.6% in the animal's chamber. Both animals were fed a small mouse 48 hours before measurement and had access to water up to the time of experimentation.



Fig. 1. Photograph of "scaleless" hatchling gopher snake, *Pituophis melanoleucus catenifer*. (Photographed by Dr. Nathan W. Cohen, University Extension, University of California, Berkeley, California.)

Convective heat transfer.—Rates of convective heating and cooling were measured by immobilizing snakes in the extended position in a "jacket" of fine mesh plastic screening similar to that used in the above tests. In heating experiments, snakes were cooled to 15 C and transferred immediately to a cabinet equilibrated at 33 ± 0.1 C, 39% RH. In cooling experiments, snakes were first warmed to 32 C and then transferred to the same cabinet after it was equilibrated to 15 C, 48% RH. Wind speed was held at 0.2 m/sec in both tests, and animals were oriented perpendicular to the direction of air flow on a wire platform above the substrate. Body temperatures were monitored continuously with a 30-gauge thermocouple connected to a Honeywell Elektronik I6 recorder inserted into the intestine through the cloaca.

Histology of the skin.—At the termination of the above physiological tests, a sample of skin was taken from the dorsolateral region of the body immediately posterior to the vent. Separate tissue samples were fixed in either Bouin's solution or neutral buffered formalin and then imbedded in Paraplast, sectioned

at 7 micra and stained with Erlich's hematoxylin and eosin or by van Gieson's method. The latter staining method tended to color the outer keratin layers more than did the former method.

An attempt was made to approximate the surface area of each snake by enlarging photomicrographs of the skin (see Figs. 2a and 3a) and using planimetry to estimate the total distance included in the width of the photograph. Photographs of equal width from the two snakes were assumed to represent equal "straight-line" distances along the animals' bodies.

RESULTS AND DISCUSSION

General description of scaleless specimen.—The color pattern of the scaleless hatchling was essentially normal, but the body lacked the glossy appearance normally associated with reptilian scales. Ventral scales (scutes) were present, although they were split into two or four sections. The animal also possessed a single row of ventrolateral scales and scattered facial scales (five upper labials, a rostral, and a supra-ocular) (see Fig. 1); other-

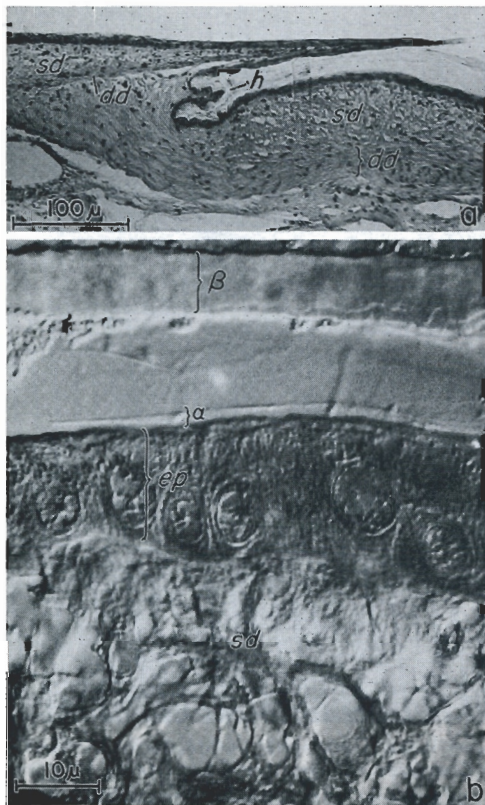


Fig. 2. Photomicrographs of the dorsolateral integument of a normal gopher snake: skin was fixed in Bouin's and stained with hematoxylin and eosin.

(a) low magnification of surface layers showing portions of two scales and a hinge region (*h*). The "superficial" dermis (*sd*) and deep dermis (*dd*) are both evident in each scale. A band of deep dermis can be seen penetrating into the top of the scale.

(b) enlargement of part of the surface of one of the normal scales shown above viewed with a Nomarski interference microscope to help discriminate the two keratin layers (α - and β -). The space between the two layers is probably an artifact of fixation. The epidermis (*ep*) is in the resting (non-sloughing) condition; it appears compressed and has a flat surface. The outer, superficial, dermis (*sd*) is seen as being highly structured.

wise, the body had the superficial appearance and texture of a naked, newborn mouse. This snake behaved normally: it moved normally, fed voluntarily and showed normal digestion and defecation immediately before study.

Histology.—Histologically, the few scales present on the "scaleless" specimen resembled those of the normal animal; but the



Fig. 3. Photomicrographs of the dorsolateral integument of a scaleless gopher snake (skin was prepared in the same way and corresponds to the same region as shown for the normal snake in Fig. 2).

(a) the outer, superficial, dermal layer (*dd*) is absent and the epidermis is irregular; the epidermis rests directly on a layer of deep dermis.

(b) enlargement of a portion of the integument shown above viewed by Nomarski interference microscopy. Note the two thin keratin layers (α - and β -) on the surface of the skin (top) and the irregular surface of the epidermal layer (*ep*).

unscaled portion of the body differed from the normal condition in several major respects. Instead of having the typical folded (scaled) surface, covered with a flat, compact epidermis (Fig. 2a), the body surface was wrinkled, the epidermal layer was thin, and the contour of the surface layer was highly irregular (Fig. 3a). In the resting (non-sloughing) condition, the outer surface of the normal scale has a thin α -keratin layer overlaid by a relatively thick β -keratin layer (Fig. 2b). Two distinct keratin layers were also visible on the surface of the scaleless animal; the width of α -keratin layer was

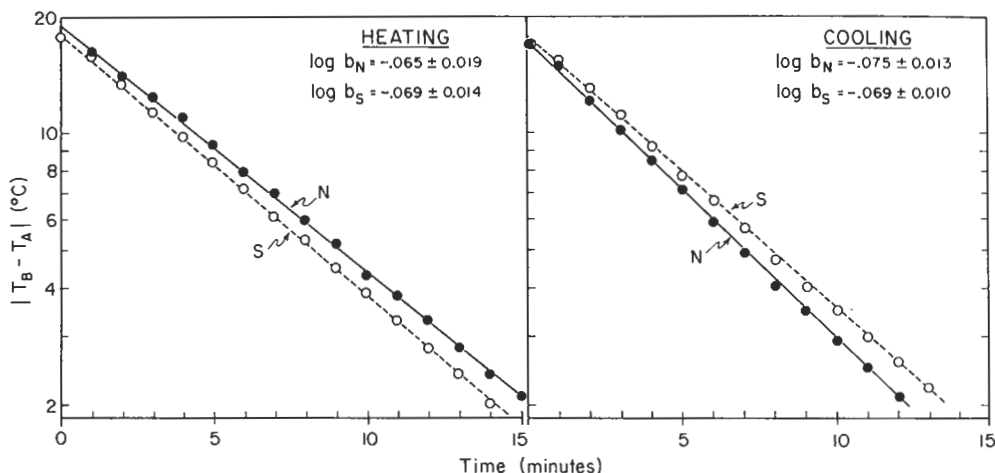


Fig. 4. Rates of heating and cooling of a normal (N) and scaleless (S) gopher snake. The points and curves represent the average of five separate trials with each animal. The average of the 5 individually determined rates of heat transfer (b) with 95% confidence limits for each snake are also shown.

essentially normal but the outer (presumably β -) keratin layer was extremely thin (Fig. 3b). Although the reptilian scale is generally referred to as an epidermal structure as distinct from the "dermal" scales of fish (Carter, 1967; Romer, 1970; Goin and Goin, 1971), it is clear from the histology of the gopher snake (Fig. 2a) that the dermis constitutes the major morphological element of the scale. In fact, a thick layer of "superficial" dermis (the outermost dermal element) appears to be the principal supportive element. This superficial dermal layer was completely lacking in the scaleless specimen; the subepidermal tissue resembled the deep dermis of the normal animal. In general, the body surface of the scaleless snake seemed most like the flexible hinged region that exists between the scales of the normal animal (Fig. 2a).

Planimetric measures of the surface of the skin shown in Figs. 2a and 3a yielded values of 914 and 760 μ for the normal and scaleless animals, respectively. However, 54% of the surface of this distance in the normal animal is under the overlapping region of the scales. Thus, the effective area for water loss in the normal animal is probably overestimated by this method. Evidently the increased area due to folding is compensated by the more irregular topography of the epidermis and, hence, the overall surface areas of the animals do not appear to differ greatly.

Convective Heat Transfer.—Five consecutive heating tests were performed on each snake, followed by five cooling tests. The average rates of heating and cooling in the five trials is shown for each snake in Figure 4. In contrast to reports for several other reptiles, mostly relatively large lizards (Bartholomew and Tucker, 1963, 1964; Bartholomew and Lasiewski, 1965; Weathers, 1970), there was not a significant difference between the rates of heating and cooling for either individual. Furthermore, no significant difference was evident in the rate of heating or in rate of cooling between the normal and scaleless individual.

Metabolism and Evaporative Water Loss.—Oxygen consumption and total water loss were virtually identical in the two specimens (Table 1). The values obtained for these measurements in the resting snakes compare favorably with data collected for many other reptiles, including snakes (Claussen, 1967; Gans et al., 1968; Prange and Schmidt-Nielsen, 1968; Templeton, 1970). Rates of water loss for the scaleless specimen were about 40% lower than those reported for adult *P. m. affinis* in dry air at 25 C on the basis of surface area (Prange and Schmidt-Nielsen, 1969). Gans et al. (1968) found that rates of evaporative water loss in snakes correlated with the aridity of their environment; inter-specific variations of 100-fold were observed in total water loss. Our values for the scale-

TABLE 1. RATES OF METABOLISM AND WATER LOSS IN NORMAL AND SCALELESS HATCHLING *Pituophis* at 28 C.

Specimen	Weight (gm)	Length* (cm)	O ₂ Consumption (cc O ₂ /g X hr)	Water Loss (mg/hr)
Normal	11.1	34	0.215	11.2
Scaleless	11.5	30	0.214	10.8

* Snout-to-vent length of living specimen. Values are only approximations due to difficulty in stretching the animal. Both animals had a maximum girth of about 8.5 mm.

less snake are the same as their measurement for the same subspecies, and compare favorably with the lowest values for water loss obtained for xeric-adapted species of the same body size.

Studies in a variety of squamate reptiles have shown that cutaneous water loss accounts for approximately half of the total water loss of the animal (Dawson et al., 1966; Bentley and Schmidt-Nielsen, 1966; Claussen, 1967). Prange and Schmidt-Nielsen (1969) showed that the skin is the major route of water loss, accounting for 64% of the total, in *P. m. affinis*. While we did not measure directly the relative contributions of pulmonary and cutaneous water loss, the similarity of the metabolic values for the two snakes suggest that the pulmonary component was the same for both. Accordingly, it seems reasonable to conclude that their rates of cutaneous losses were also very similar.

CONCLUDING REMARKS

The present study suggests that the commonly held views regarding the physiological role of the scales of reptiles may be incorrect. The complete absence of scales over most of the body appears to have little effect on the convective heat exchange of the snake. However, our experiments do not rule out the possibility that scales may be significant in some other mode of heat exchange (e.g., radiation). Despite the gross differences in the morphology of the integument—epidermis and dermis—of the two snakes, no difference was apparent in rates of water loss. Caution should, therefore, be used in the interpretation of certain morphological features of reptilian scales as adaptations to the restriction of water loss. It is noteworthy in this regard that there is no apparent correlation between scale form and the pronounced interspecific differences in cutaneous evapo-

ration among reptiles (cf. Dawson, et al., 1966; Bentley and Schmidt-Nielsen, 1966; Claussen, 1967). The similarity between the morphology of the dorsum of the scaleless snake and the hinge region between the scales of the normal animal suggests that there is probably no differential water loss between the outer scale region and the hinge portions of the integument in normal animals. The several characteristic features of the scale itself (i.e., the thick β -keratin on the scale surface, the compact epidermis and the underlying supportive superficial dermis) cannot, therefore, be regarded as adaptations to restrict water loss, and other functions (perhaps mechanical protection) must be considered for the scale. Alternatively, the comparatively low rates of cutaneous water loss characteristic of reptiles relative to other terrestrial vertebrates must be viewed as a function of some aspect of the integument other than scales *per se*.

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