

Mechanical behaviour of snake skin

BRUCE C. JAYNE

Developmental and Cell Biology, University of California, Irvine, CA 92717, USA

(Accepted 28 April 1987)

(With 6 figures in the text)

Forty-nine samples of skin from the mid-ventral, ventrolateral and mid-dorsal regions of six species of snakes were mechanically tested in uniaxial extension at 0.05 strain/sec. The species of snakes studied ranged from generalists to specialists for arboreal or aquatic habitats. Analysis of the loading curves revealed substantial variation in loads and maximum stiffnesses among samples from different dorsoventral regions within an individual and among homologous samples from different species. Skin thickness varied by a factor of more than five, but this only partially accounts for the differences in the force per width of sample at a given extension. Qualitative differences in the dermal collagen fibres are implied by the shapes of the loading curves and the terminal elastic modulus which varied from about 15 to 585 MN/m². The strain at beginning of failure ranged from 0.12 to 0.60. The size of the scales within a skin sample was not a reliable predictor of the loading behaviour of the sample. Correlations between the mechanical behaviour of skin and specializations in locomotion and associated musculature are discussed.

Contents

	Page
Introduction	125
Materials and methods	126
Results	129
Species accounts	129
Effects of skin thickness	130
Effect of scale size	134
Discussion	135
Comparison with skin of other vertebrates	135
Mode of failure	136
Anatomical and functional correlations	136
Summary	139
References	139

Introduction

The mechanical properties of skin are of interest to a wide variety of disciplines such as engineering, pathology, surgery and functional morphology. Although some mechanical testing of skin has been performed *in vivo* (Finlay, 1970), most knowledge is from *in vitro* testing (e.g. Lanir & Fung, 1974; Vogel & Hilgner, 1979). Such tests have provided the basis for current theories and models which assert that the mechanical behaviour of skin is primarily determined by the network of collagen and elastin fibres in the dermis (Lanir, 1979). Because of the importance of the mechanical properties of skin to medicine, most information is available for mammalian skin which is usually from humans or from common laboratory animals such as rats, rabbits and cats.

Recent studies have examined the morphology and mechanical properties of the skin from other vertebrate classes. Motta (1977) described the arrangement of collagen fibres in the stratum compactum of sharks as forming layers of alternately oriented sheets that form helical paths around the body of the shark. After performing stress-strain tests on shark skin, Wainwright, Vosburgh & Hebrank (1978) suggested that shark skin functions as an extensor for transmitting locomotor forces and also provides re-enforcement to resist the pressures encountered during lateral flexion. Methodology similar to that of Wainwright *et al.* (1978) has also been used to study the mechanics of teleost skin. Hebrank (1980) found that eel skin was stiffer than shark skin and suggested similar functions; however, the skin of the Norfolk spot and skipjack tuna does not appear capable of transmitting locomotor forces (Hebrank & Hebrank, 1986).

Most studies of the skin of squamate reptiles have dealt with the shedding cycle or the physiological importance of the integument (for recent review see Lillywhite & Maderson, 1982). Consequently, anatomical descriptions have primarily concentrated on the epidermis and superficial layers of the dermis. The limited information available for the collagen fibres in the deep dermis of snakes suggests an organized, cross helical pattern of layering (Pockrandt, 1936; Licht & Bennett, 1972). Gross differences in the scalation of snakes have long been used in taxonomic studies, but the functional consequences of this variation are unclear. Discussions of functional morphology of snake epidermis have generally emphasized interactions of skin and substrata such as frictional resistance and adhesive properties (Gans, 1974; Gans & Baic, 1977). The role of the distensibility of skin in accommodating the large objects swallowed by snakes has also been discussed (Gans, 1974), but the relevance of mechanical behaviour of skin to locomotion has received scant attention.

Because snakes occupy a wide variety of habitats, it is not surprising that they have diverse skin morphology and utilize many different locomotor modes to cope with the resistive forces imposed by various substrata. With the exception of the rectilinear mode of locomotion, snakes use various patterns of vertebral flexion to generate propulsive forces (Gray & Lissmann, 1950; Gans, 1974, 1984; Jayne, 1986).

The internal mechanical properties of skin may be most important for the rectilinear mode of snake locomotion. As described by Lissmann (1950), this unique locomotor mode uses activity of the cutaneous and costocutaneous muscles to contract the skin and move the skin relative to the skeleton in order to propel the animal. Hence, the skin undergoes successive extension and contraction. The sites of insertion and masses of the cutaneous and costocutaneous musculature vary widely among snakes and in some cases this variation is correlated with specializations in habitat and locomotion (Buffa, 1905; Gasc, 1974; Voris & Jayne, 1976). Because of the variations in the gross morphology of the skin and associated musculature, it is desirable to know if there may be correlated differences in the stiffness of the skin.

This study investigates the mechanical properties of snake skin during uniaxial tensile loading. Skin stiffness was evaluated using the following comparisons: 1) locomotor specialists vs. generalists, 2) species with vestigial vs. robust costocutaneous muscles, 3) anatomical regions containing the costocutaneous muscles vs. those without, 4) wide vs. narrow ventral scale morphology and 5) large- vs. small-scale size.

Materials and methods

The snake species studied are all about the same size (adult length of approximately 1 m), but they differ greatly in the gross morphology of the skin and associated musculature, as well as in their habitats and modes

of locomotion. With respect to skin and costocutaneous musculature, *Nerodia fasciata pictiventris* (Florida banded water snake) is an anatomically generalized colubrid occupying semi-aquatic to terrestrial habitats. *Ahaetulla prasina* (vine snake) is an extremely slender colubrid that is highly arboreal. Completely aquatic snakes were represented by the booid *Acrochordus granulatus* (file snake) and the hydrophiids (sea snakes) *Hydrophis melanosoma* and *Enhydrina schistosa*. These 3 aquatic species can only move on land with great difficulty and the speeds attained during terrestrial locomotion are generally very slow (Smith, 1943). Unlike other hydrophiid genera, *Laticauda* (sea krait) frequently leaves the water, although it is primarily aquatic.

Nerodia, *Ahaetulla* and *Laticauda* all have a 1:1 correspondence between the numbers of vertebrae and ventral scales (Alexander & Gans, 1966). Their ventral scales are much wider than the dorsal scales and are of sufficient width that they are the only (or primary) surface of the snake that normally contacts a flat substratum. *Acrochordus*, *Hydrophis* and *Enhydrina* have lost the 1:1 correspondence between vertebrae and ventral scales (Alexander & Gans, 1966; Voris, 1975), and in these snakes the ventral scales are no wider than the dorsal scales. In *Ahaetulla*, *Hydrophis* and *Enhydrina*, the mass of the costocutaneous musculature is extremely reduced compared to the other taxa studied (Voris & Jayne, 1976).

Table I lists the species studied and the method of storage of the specimens before the preparation of the skin samples. All snakes had been kept in captivity for a minimum of 3 weeks before dying from unknown causes or being killed by an intracardial injection of sodium pentobarbital solution. No samples were used if gross examination revealed scars or infected areas. All strips of skin removed from snakes were approximately 110 × 15 mm with the long axis of each sample oriented longitudinally. Within each snake, samples were removed from 3 different dorsoventral positions: mid-ventral, mid-dorsal and ventrolateral. The mid-ventral and mid-dorsal samples always included the midline. The mid-ventral samples usually included a substantial portion of the region of insertion of the M. costocutaneous inferior. The position of the ventrolateral samples varied among species because this sample included the region of insertion of the M. costocutaneous superior, the location of which varies widely among species. Table I lists the position of the ventrolateral samples by indicating the dorsal scale rows included. Dorsal scale rows were counted starting with the ventral scale as zero and proceeding dorsally. Ventrolateral samples were removed from the left and right sides at the same anteroposterior position to provide replication of a particular anatomical region. The samples were removed from 1 of 4 different anterior-posterior positions. Sites 1 and 2 were located about 240 to 120 mm and 120 to 0 mm anterior to midbody, respectively. Sites 3 and 4 were 0 to 120 mm and 120 to 240 mm posterior to midbody, respectively. Table II uses the following abbreviation scheme for each sample. The first 3 letters of a sample indicate the species and individual (Table I). The numeral indicates the anterior-posterior position of the sample and the last letter designates the dorsal-ventral position (V, mid-ventral; D, mid-dorsal; R or L, right or left ventrolateral). For example, ApB2L indicates skin from *Ahaetulla prasina* B at site 2 in the left ventrolateral region.

After each strip of skin had been removed from the snake, I used my fingers to remove excess adhering musculature. Each strip of skin was trimmed to resemble an hour glass. The ends of the sample tapered towards the middle to form a central rectangular portion approximately 70 × 7 mm. The expanded ends of the samples were gripped with emery cloth glued to a clamp that was tightened with screws. The clamps were oriented so that the sample was vertical during the loading test. Ringer's solution kept the samples wet during preparation and testing. Before testing each sample, Vernier calipers were used to measure the width to the nearest 0.1 mm and minimum and maximum thickness to the nearest 0.05 mm.

Skin samples were loaded uniaxially in the longitudinal direction using an Instron servo-hydraulic materials testing machine with a 443 N load cell. A Nicolet digital oscilloscope was used to store the load and extension of each sample as digital data with a density of 200 load-extension data points/sec. Load was measured to the nearest 0.044 N and extension was measured to the nearest 0.032 mm. Data were transferred to a PDP 11 computer for analysis and plotting. The initiation of loading of a sample was determined after examining a plot of the digital data on an oscilloscope. Strain was calculated by the formula $\Delta L/L_0$, where L_0 equals the sample length at load initiation and ΔL equals the sample extension. Because of the difficulty in determining the thickness of the skin, load per unit width was used for primary comparison of different samples. Stresses (load per minimum cross-sectional area) in the samples were calculated primarily to

TABLE I

Specimens used for uniaxial loading of skin. SVL = snout-vent length in mm. Ventrolateral = dorsal scale rows included in right and left ventrolateral samples of skin. * = killed with injection of sodium pentobarbitol, whereas other snakes died of unknown causes while in captivity. All refrigeration (R) was 1 °C and frozen storage (F) was -5 °C. T_{pres} = maximum time between death and storage and T_{test} = maximum time between death and end of tests

Species (Individual)	Sex	SVL	Ventrolateral	Storage	T_{pres}	T_{test}
<i>Nerodia f. pictiventris*</i> (NfA)	F	750	1-3	none	0	5 h
<i>N. f. pictiventris*</i> (NfB)	F	710	1-3	none	0	5 h
<i>Ahaetulla prasina</i> (ApA)	F	1000	0-2	none	0	8 h
<i>A. prasina</i> (ApB)	F	1050	0-2	R	2 h	24 h
<i>Laticauda colubrina</i> (LcA)	F	1100	4-6	R	12 h	3 d
<i>Hydrophis melanosoma</i> (HmA)	F	820	5-9	F	8 h	1 wk
<i>Enhydrina schistosa</i> (EsA)	M	720	6-10	F	8 h	2 wk
<i>Acrochordus granulatus</i> (AgA)	F	560	24-37	F	8 h	1 wk

TABLE II

Summary of select tests of uniaxial loading of snake skin samples based on load per unit width of sample (N/mm). Maximum slope of loading curves is in N/mm and this occurred at the strain during beginning of failure. See **Materials and methods** for explanation of sample labels and calculations

Sample	Range skin thickness (mm)	Load at strain of		Begin fail load and (strain)	Max. slope	Max. load	Strain at failure
		0.10	0.15				
NfB2V	0.30-1.55	0.17	0.25	1.25 (0.24)	12.6	1.36	0.26
NfB2L	0.25-0.80	0.08	0.24	1.83 (0.30)	15.9	1.96	0.32
NfB1D	0.20-0.50	1.01	2.34	5.61 (0.24)	41.9	5.65	0.26
ApB1V	0.15-0.40	0.69	1.35	0.97 (0.12)	14.2	1.48	0.17
ApB2L	0.15-0.25	0.19	0.41	0.55 (0.18)	5.2	0.77	0.28
ApB4L	0.10-0.25	0.17	0.42	1.29 (0.28)	7.0	1.39	0.31
ApB3D	0.10-0.15	0.20	0.30	1.32 (0.35)	7.5	1.53	0.38
LcA2V	0.60-1.05	1.00	3.36	28.04 (0.35)	153.0	33.51	0.43
LcA1L	0.55-1.05	0.23	0.68	21.30 (0.35)	176.9	24.69	0.37
LcA2D	0.40-1.20	2.52	8.88	24.30 (0.23)	233.8	33.18	0.29
HmA1V	0.25-0.50	0.06	0.19	8.17 (0.51)	43.0	9.32	0.54
HmA2L	0.15-0.50	0.03	0.07	4.26 (0.60)	20.0	4.26	0.60
HmA1D	0.20-0.35	0.07	0.19	6.55 (0.43)	37.2	6.55	0.43
EsA2V	0.35-0.60	0.04	0.10	1.66 (0.45)	8.2	3.17	0.69
EsA2R	0.25-0.50	0.03	0.06	0.78 (0.41)	3.7	0.88	0.49
EsA3D	0.15-0.50	0.04	0.08	1.04 (0.46)	4.2	1.18	0.60
AgA1V	0.25-0.70	0.06	0.17	2.67 (0.42)	12.6	3.17	0.49
AgA2R	0.25-0.45	0.02	0.04	2.47 (0.51)	12.3	2.62	0.57
AgA1D	0.15-0.30	0.04	0.10	0.93 (0.53)	3.8	0.98	0.59

facilitate comparisons with other studies and to supplement certain interspecific comparisons.

In order to compare the overall similarities among different tests, plots were made of load/width versus strain. Laterally flexing a freshly killed *Nerodia fasciata* revealed the skin of an intact snake may undergo a maximum longitudinal strain of about 0.10 to 0.15. Thus, for each plot, the load/width was determined at 0.10 and 0.15 strain to estimate loading at physiologically encountered values. A computer algorithm was used to find the maximum slope of each plot by determining the least squares regressions for successive windows of 75 data points which included the last 0.02 strain for that sample. Maximum slope was used as an indicator of the maximum stiffness of the material and the strain at each region of maximum stiffness was recorded to the nearest 0.01. The beginning of failure was defined as the point after which the slope continuously decreased, and this occurred at the same strain as maximum stiffness. The end of failure was indicated by a load of zero. Because strain rate is known to affect the stiffness of skin (Lanir & Fung, 1974), all tests were performed at 0.05 strain/sec as a representative physiological value.

Results

Table II summarizes the results of the uniaxial loading for only one representative skin sample for each species. Results from all 49 samples tested can be found in Jayne (1985). Compared to the variation observed in the loading behaviour of samples either from different species or from different dorsoventral locations, only slight variation was attributable either to individuals within a species (*Nerodia fasciata* and *Ahaetulla prasina*) or to anteroposterior location within an individual. Between species, substantial differences are apparent for the loads at 0.10 and 0.15 strain, beginning of failure and the end of failure. For all 49 samples, the strain at the end of failure varied from 0.17 to 0.69 and maximum slope varied from 3 to 234 N/mm.

Species accounts

Figure 1 illustrates representative loading curves for the skin of *Nerodia fasciata*. At 0.10 and 0.15 strain, average loads of the four ventral samples (0.12, 0.30 N/mm) were nearly identical to the values from the five ventrolateral samples (0.11, 0.37 N/mm), whereas the average values from the two dorsal samples (0.90, 2.22 N/mm) were much higher. Dorsal skin samples also had a greater average maximum slope (43.3 N/mm) than either the ventral (13.0 N/mm) or ventrolateral (19.7 N/mm) samples. Skin from all three dorsoventral sample areas failed at about 0.30 strain.

For *Ahaetulla prasina* (Fig. 2), the average loads at 0.10 and 0.15 strain for the five ventrolateral (0.15, 0.36 N/mm) and three dorsal (0.21, 0.36 N/mm) samples were quite similar and only about one-half those of the three ventral samples (0.38 and 0.79 N/mm). The ventral skin also had an average maximum slope (12.4 N/mm) about twice that of the ventrolateral and dorsal samples (5.8, 6.1 N/mm). For *A. prasina* B, ventrolateral samples from the more posterior position did not fail until strains greater than those of the more anterior samples, and as a result they attained greater maximum slope and maximum load (Fig. 2 and Table II). Skin from *A. prasina* generally failed near 0.30 strain.

Figure 3 illustrates loading curves for skin from *Laticauda colubrina*. The dorsal skin of *L. colubrina* had the highest loads at 0.10 and 0.15 strain (2.52 and 8.88 N/mm) observed for any sample (Table II). *Laticauda colubrina* also had skin much stiffer than any other species in this study, with maximum slopes ranging from 153 to 234 N/mm. Failure began near 0.30 strain.

Representative loading curves for the skin of *Hydrophis melanosoma* are illustrated in Fig. 4. At 0.10 and 0.15 strain, the average loads of the four ventrolateral samples (0.04, 0.8 N/mm) were less

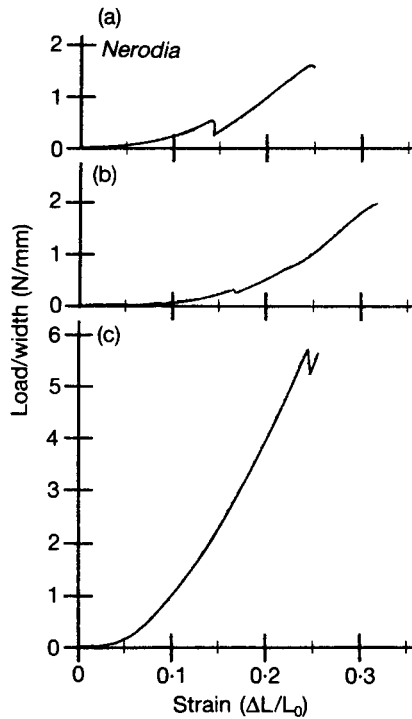


FIG. 1. Loading curves for skin from *Nerodia fasciata pictiventris*. (a) Ventral sample NfB2V; (b) ventrolateral sample NfB2L; and (c) dorsal sample NfB1D.

than half those of the three dorsal (0.09, 0.24 N/mm) and three ventral (0.10, 0.31 N/mm) samples. Loads measured for the ventral region were more variable than those of the ventrolateral region. For example, the load of the ventral skin at 0.10 strain ranged from 0.04 to 0.16 N/mm, whereas that of the ventrolateral region ranged only from 0.03 to 0.04 N/mm. The average maximum slope ranged from 22.9 N/mm for the ventrolateral region to 44.0 N/mm for dorsal skin. Half of the samples of the skin from *H. melanosoma* did not begin to fail until strains greater than 0.50.

Figure 5 shows representative loading curves for the skin of *Enhydrina schistosa*. The average loads of the skin of *E. schistosa* at 0.10 and 0.15 strain were very low (< 0.08 N/mm) for all regions. The skin of this species attained the greatest observed strain, with five of the nine samples exceeding strains of 0.60 before the end of failure.

Figure 6 illustrates loading curves for the skin of *Acrochordus granulatus*. All skin of this species had small loads at 0.10 and 0.15 strain (Table II). The dorsal sample had the smallest maximum slope compared to similar values for the ventral and ventrolateral samples (Table II). The beginning of failure occurred at strains greater than 0.45 for three of the four samples.

Effects of skin thickness

For snakes of similar size, load/width of skin is a convenient measure to compare both the resistance generated by skin during lateral flexion and the ability of the skin to transmit locomotor

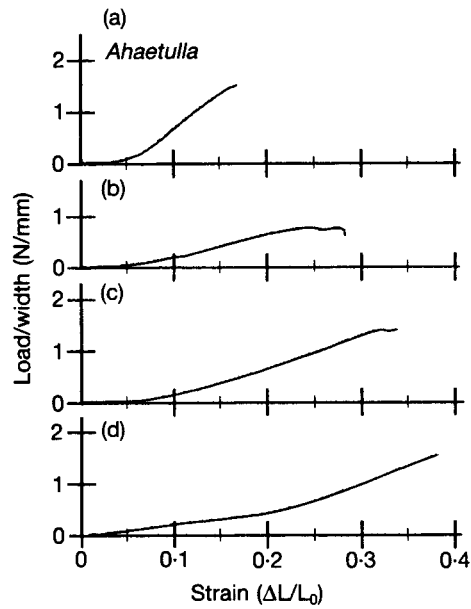


FIG. 2. Loading curves for skin from *Ahaetulla prasina*. (a) Ventral sample ApB1V; (b) ventrolateral sample ApB2L; (c) ventrolateral sample ApB4L; and (d) dorsal sample ApB3D.

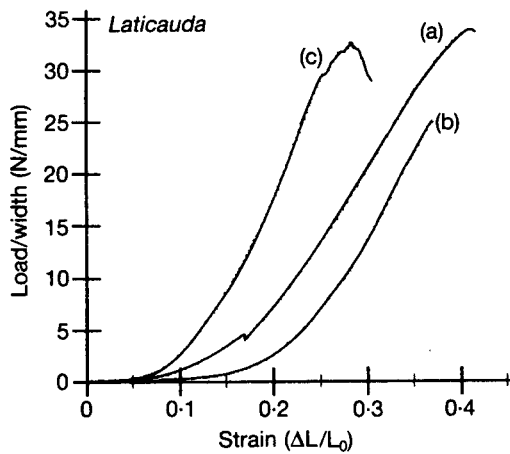


FIG. 3. Loading curves for skin from *Laticauda colubrina*. (a) Ventral sample LcA2V; (b) ventrolateral sample LcA1L; and (c) dorsal sample LcA2D. (Note vertical scale is different from all other figures.)

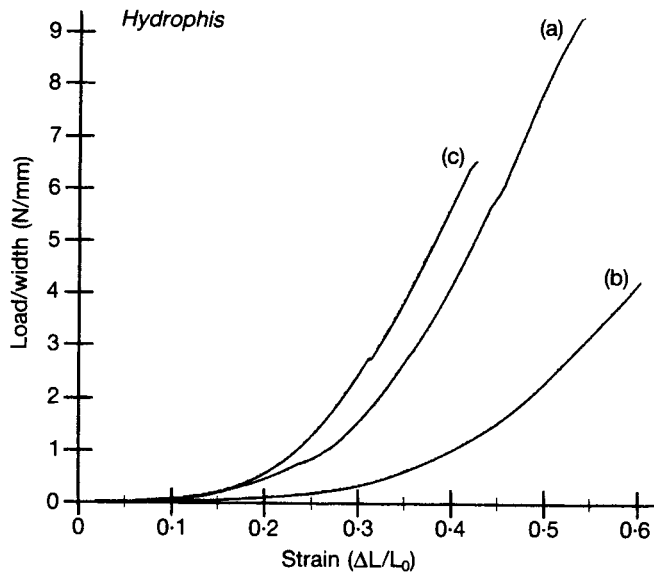


FIG. 4. Loading curves for skin from *Hydrophis melanosoma*. (a) Ventral sample HmA1V; (b) ventrolateral sample HmA2L; and (c) dorsal sample HmA1D.

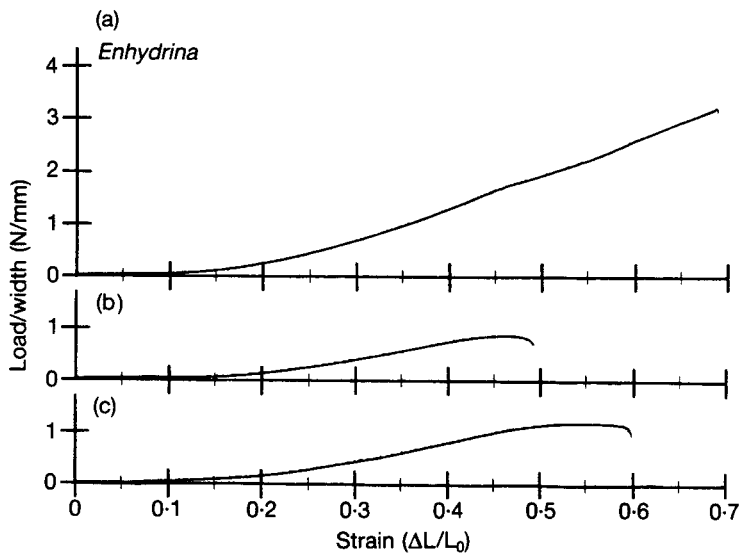


FIG. 5. Loading curves for skin from *Enhydrina schistosa*. (a) Ventral sample EsA2V; (b) ventrolateral sample EsA2R; and (c) dorsal sample EsA3D.

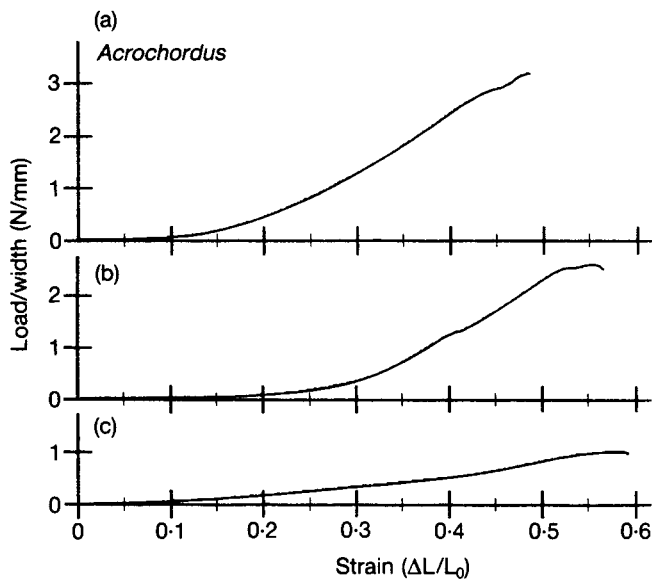


FIG. 6. Loading curves for skin from *Acrochordus granulatus*. (a) Ventral sample AgA1V; (b) ventrolateral sample AgA2R; and (c) dorsal sample AgA1D.

forces. For a given width of skin, the rate of loading during a constant strain rate may differ from two primary causes. Differences in either the structure of the individual collagen fibres or in the overall thickness of the collagen fibre matrix will alter the resistance of the skin to stretching. Although the scales of snake skin cause heterogeneity in thickness, dividing load/width by minimum thickness approximates stress. Different stresses of samples at a given strain should indicate qualitative differences in the structure of the collagen fibres.

Minimum thickness of the skin samples varied considerably both among and within species (Table II). However, the variation in thickness does not by itself account for differences in skin parameters (compare Tables II and III). For example, in *Nerodia fasciata*, the load/width and slope of the loading curve were much larger for the dorsal compared to the ventral skin (Table II). Furthermore, the minimum thickness of the ventral skin was about 50% greater than that of the dorsal skin. Consequently, adjusting for minimal cross-sectional area enhanced rather than minimized the mechanical differences between regions within this species (Table III).

Laticauda colubrina had the greatest minimum skin thickness of any of the studied taxa (Table II). However, even after converting load/width to stress, *L. colubrina* still had the greatest maximum stiffness (255 to 585 MN/m²), stress at beginning of failure (38.7 to 60.8 N/mm²) and maximum stress (44.9 to 83.0 N/mm²). Because the thickness of the skin of *L. colubrina* is insufficient to account for all differences in loading, *L. colubrina* probably has substantially different dermal collagen fibres compared to any of the other snakes of this study.

Of all the samples, the skin of *Hydrophis melanosoma*, *Enhydrina schistosa* and *Acrochordus granulatus* generally had the smallest loads and stresses at 0.10 and 0.15 strain (Tables II and III). As Table III indicates, the skin of *E. schistosa* skin had the three smallest values of mean maximum stiffness (15.4 to 24.3 MN/m²).

TABLE III

Mean results from uniaxial loading of snake skin after adjusting for minimum cross-sectional area of sample. V, VL and D = ventral, ventrolateral and dorsal regions, respectively. Means (n = sample size) were calculated using all samples for each dorsal-ventral region within each species. All stresses are in MN/m². Values in parentheses after stresses at 0.10 and 0.15 strain are the percentage of the stress at beginning of failure. Stiffness is in MN/m² and maximum stiffness occurred at the strain during beginning of failure. See text for more complete explanation

Sample	n	Stress (% begin failure) at strain of		Begin fail stress	Max. stiffness	Max. stress
		0.10	0.15			
NfV	4	0.39 (8.5)	0.94 (20.6)	4.57	41.4	5.00
NfVL	5	0.54 (4.8)	1.77 (18.5)	9.58	79.5	10.01
NfD	2	4.08 (14.2)	10.05 (34.9)	28.81	194.2	28.91
ApV	3	2.56 (46.9)	5.24 (96.0)	5.46	82.7	8.84
ApVL	5	1.41 (18.0)	5.61 (71.5)	7.85	54.7	9.17
ApD	3	2.13 (19.5)	3.53 (32.3)	10.93	60.6	13.03
LcV	1	1.67 (3.6)	5.60 (12.0)	46.73	255.0	55.85
LcVL	2	0.42 (1.1)	1.26 (3.3)	38.73	321.6	44.90
LcD	1	6.30 (10.4)	22.20 (36.5)	60.80	584.5	82.95
HmV	3	0.40 (1.5)	1.12 (4.3)	26.03	152.0	28.05
HmVL	4	0.17 (0.9)	0.38 (2.0)	18.90	113.2	17.48
HmD	3	0.45 (1.8)	1.46 (5.7)	25.64	204.3	27.91
EsV	2	0.12 (2.4)	0.25 (5.1)	4.91	24.3	7.91
EsVL	4	0.13 (4.4)	0.28 (8.9)	3.14	15.4	15.77
EsD	3	0.17 (3.1)	0.43 (7.9)	5.45	21.9	18.44
Ag V	1	0.24 (2.2)	0.68 (6.4)	10.70	50.4	12.68
Ag VL	2	0.24 (2.6)	0.54 (5.9)	9.08	43.0	9.54
Ag D	1	0.27 (4.4)	0.67 (10.8)	6.20	25.3	6.53

The greatest difference between characterizing mechanical behaviour of skin in units of stress rather than load/width occurred for *Ahaetulla prasina* which had extremely thin skin. The ventrolateral skin of *A. prasina* had a load/width, at 0.10 and 0.15 strain, slightly less than those of *Laticauda colubrina* (Table II); however, the stresses of these samples from *A. prasina* were about three times greater than those of *L. colubrina* (Table III). The load/width at the beginning of failure was about the same for the dorsal skin of *A. prasina* and the ventral skin of *Nerodia fasciata* (Table II), but this stress of skin from *A. prasina* was about twice that of *N. fasciata* (Table III). Between the different regions within *A. prasina*, the differences in stress and stiffness were less distinct than the differences based on load/width. Hence, variation in skin thickness seems to account for much of the variation in the loading between the different regions within *A. prasina*. Similarly, the relative thinness of *A. prasina* skin partially accounts for some small loads/width compared to those of other species.

Effect of scale size

To determine if the size of the scales affected the loading behaviour of the skin, I counted the number of scales in a 7 × 70 mm strip of skin for each sample region of each species that was tested (Table IV). No clear correlations are apparent when the sizes of scales are compared with loads or

TABLE IV
Approximate number of scales in longitudinal strips of skin
7 × 70 mm

Species	Sample		
	Ventral	Ventrolateral	Dorsal
<i>Nerodia f. pictiventris</i>	12	36	36
<i>Ahaetulla prasina</i>	14	42	56
<i>Laticauda colubrina</i>	14	42	42
<i>Enhydrina schistosa</i>	120	120	120
<i>Hydrophis melanosoma</i>	96	120	120
<i>Acrochordus granulatus</i>	1764	1274	764

stiffnesses at given strains. For example, within both *Nerodia fasciata* and *Ahaetulla prasina*, the mid-ventral skin samples had the largest scales. However, the mid-ventral skin of *N. fasciata* was the anatomical region of least stiffness, whereas within *A. prasina* the ventral skin was generally stiffer than the ventrolateral and mid-dorsal skin. As a group, the taxa with the smallest scales (*Hydrophis melanosoma*, *Enhydrina schistosa* and *Acrochordus granulatus*) generally had skin which had small slopes of the loading curves. However, when the different sample regions are compared within each of these taxa, increased scale size does not consistently predict increased loads or stiffness.

Discussion

Comparison with skin of other vertebrates

The mechanical properties of snake skin are intermediate to those of mammalian skin and eel and shark skin. Mammalian skin usually is very compliant at low strains. For example, when Veronda & Westman (1970) subjected cat skin to longitudinal uniaxial tensile loading, stress remained less than about 0.1 MN/m² for strains less than 0.45. Vogel & Hilgner (1979) recorded stresses less than 0.1 MN/m² at 0.10 strain and a stress of about 3 MN/m² at 0.40 strain during the longitudinal uniaxial loading of rat skin. In this study, stress of snake skin at 0.10 strain is generally greater than 0.1 MN/m² and ranged as high as 6.30 MN/m² for the dorsal skin of *Laticauda colubrina* (Table IV). When Wainwright *et al.* (1978) prestressed shark skin in the circumferential direction at 0.3 and 2.8 MN/m², longitudinal stresses were 0.25 and 1.6 MN/m², respectively, at 0.10 strain. Hebrank (1980) found that eel skin loaded in the direction of the dermal collagen fibres (about 45° to longitudinal axis) had the highest early loads (1.5 MN/m² at 0.05 strain), and uniaxial loading in the longitudinal direction gave the lowest early loads (< 0.1 MN/m² at 0.10 strain). Uniaxial, longitudinal loading of the skin of the Norfolk spot and skipjack tuna produced stresses less than 0.3 MN/m² at 0.10 strain (Hebrank & Hebrank, 1986).

The maximum stiffness (in MN/m²) derived from the stress and strain of snake skin in Table III is similar to the mean terminal elastic modulus (E) of teleost skin (Hebrank, 1980; Hebrank & Hebrank, 1986). E for longitudinally stressed snake skin, in the stiffest region of the loading curves, varies from about 15 to 585 MN/m². Maximum stiffness of the samples of snake skin occurred at strains ranging from 0.12 to 0.60 (Table II). Hebrank (1980) recorded a mean terminal E of

3.54 MN/m² for longitudinally stressed eel skin, and this occurred at the highest strain used by Hebrank which was about 0.50. Values of terminal E of the Norfolk spot and skipjack tuna were 2.41 and 6.92 MN/m², respectively, and they were determined at strains between 0.15 and 0.20 (Hebrank & Hebrank, 1986). Terminal E can also be estimated from the stress-strain curves available for mammalian skin. Terminal E of cat skin subjected to static longitudinal loading is about 58 MN/m² and occurs at approximately 1.0 strain (Veronda & Westman, 1970). Because increased strain rates increase the stiffness of skin during testing (Lanir & Fung, 1974), detailed comparisons of these E values are not possible. However, it is interesting to note that the range of values of terminal E of snake skin nearly spans the reported range of values of such widely divergent taxa as fish and mammals. Furthermore, restraint of the sides of skin orthogonal to sides undergoing loading significantly increases the stiffness of the skin (Lanir & Fung, 1974; Wainwright *et al.*, 1978; Hebrank, 1980). Thus, the stiffness of the skin in intact snakes may be even more variable than indicated by these *in vitro* tests.

Mode of failure

The loading curves of snake skin were usually smooth lines; however, slight discontinuities in these lines were common. These discontinuities were most noticeable for the ventral and ventrolateral samples of *Nerodia fasciata* skin (Fig. 1), but they were also evident in some tests of the skin of *Ahaetulla prasina* (Fig. 2) and of *Laticauda colubrina* (Fig. 3). Usually there was just one such discontinuity within a test and this generally occurred near 0.15 strain. Vogel & Hilgner (1979) observed a similar phenomenon for uniaxial loading of mammalian skin and they termed this the 'step phenomenon'. Vogel & Hilgner usually observed several of these 'steps' within a single test and the 'steps' were generally confined to the lower strain (<0.50) regions of curves. These steps may be considered either as transient loss of stress or as a gain in strain and are caused by partial failure of the sample. During the tests of snake skin, the stratum corneum was often observed breaking and peeling away from the deeper layers of the skin before they failed. This failure of the stratum corneum probably corresponds to the step observed near 0.15 strain. Thus, although the collagen fibres most likely dominate the mechanical behaviour of snake skin, the stratum corneum, which probably has a different elastic modulus than collagen, may contribute significantly to the low strain properties of snake skin.

Anatomical and functional correlations

The loading curves of the ventrolateral and ventral skin were usually most similar within species of snakes with well developed costocutaneous muscles. For example, the ventrolateral and ventral samples of *Nerodia fasciata* skin were very similar both in the early loads and maximum stiffness compared to the much stiffer skin from the dorsal region (Fig. 1). The ventrolateral and ventral samples of skin from *Acrochordus granulatus* also attained very similar maximum stiffness compared to the dorsal skin (Fig. 6). In *Laticauda colubrina*, the early loading was more similar between the ventral and ventrolateral samples than between the ventrolateral and dorsal samples (Fig. 3). Because of the antagonistic functions of the costocutaneous inferior and superior muscles, one might expect that the skin forming the insertions for these two muscles should have more similar mechanical properties than skin lacking insertions of costocutaneous and cutaneous muscles.

Lissmann (1950) analysed films of the rectilinear locomotion of a *Boa constrictor* and suggested that the cutaneous musculature contracts to produce the maximal shortening of the ventral skin, whereas the costocutaneous muscles move the skin relative to the skeleton. The costocutaneous inferior muscles probably propel the skeleton forward relative to the skin while it is maximally shortened and in static with the substratum. The more dorsally situated costocutaneous superior muscles then stretch the skin while moving it forward relative to the skeleton and substratum in preparation for the next propulsive phase. Hence Lissmann's proposed mechanism assumes no elastic recoil of the skin. The very compliant nature of the ventral and ventrolateral skin of *N. fasciata* may support Lissmann's suggestions of no elastic recoil and that activity of the cutaneous muscles prevents extension of the skin while it is transmitting propulsive forces. However, as Lissmann was careful to point out, the precise role of the cutaneous muscles can be changed by altering the timing of costocutaneous muscle activity. Future work combining electromyography with mechanical testing of snake skin should clarify the interesting relations of muscular and passive mechanisms of skin movement during rectilinear locomotion of snakes.

Studies of the cross helical arrangement of collagen fibres of fish skin have emphasized that skin becomes stiffer as uniaxial loads are applied more nearly parallel to the direction of the collagen fibres (Hebrank, 1980; Hebrank & Hebrank, 1986). When loaded longitudinally, the ventrolateral region of snake skin was usually more compliant than other regions within a single species (Table II). This might be expected since the lateral portions of the snake skin must accommodate the greatest changes in length caused by lateral flexions which are the primary movements of most snake vertebral columns. However, the costocutaneous superior muscles of most terrestrial snakes are oriented obliquely to the longitudinal axis and insert in the ventrolateral region (Buffa, 1905; Gasc, 1974; Voris & Jayne, 1976). Thus it seems likely that the skin can be relatively stiff in the direction of the forces applied by these muscles while simultaneously offering minimal resistance to lateral flexion.

One reason for studying *Laticauda colubrina* was that it has well developed costocutaneous musculature, which is an atypical condition for a hydrophiid. Furthermore, the fibres of the costocutaneous superior muscle are oriented more longitudinally than those of terrestrial species. The nature of the terrestrial locomotion of this species is not known, but it is clear that movement of the skin relative to the skeleton would not contribute to aquatic propulsion. This suggests that the costocutaneous superior muscles of this species might serve some different function such as facilitating lateral flexion. In order for these muscles to function in this manner, the skin would have to be sufficiently stiff to transmit forces of bending. At 0.10 strain, the loads of the ventrolateral skin of *L. colubrina* were much higher than those of the other species with well developed costocutaneous muscles (*N. fasciata* and *A. granulatus*). Hence, the function of the costocutaneous muscles and skin may include transmitting bending forces during aquatic locomotion.

The simple superficial morphology of the skin, such as scale size, is a poor predictor of the loading and stiffness of skin (Tables II, III and IV). Thus, the apparently reasonable suggestion that increased numbers of scale rows facilitate distension during swallowing (Pough & Groves, 1983) appears overly simplistic. Yet, the ability to swallow large prey may be interrelated to some of the mechanical properties observed in this study. *Enhydrina schistosa* consumes catfish which generally have a larger relative diameter than the eels consumed by *H. melanosoma* and *L. colubrina* (Voris & Voris, 1983). Perhaps the high compliance of the skin of *E. schistosa* in the longitudinal direction is correlated with a collagen fibre structure that accommodates such bulky prey.

The localized thickenings of snake scales may contribute to anisotropic (directionally dependent) behaviour of snake skin. Virtually all skin samples failed in the relatively thin regions between scales; therefore, the scales are the strongest portion of the skin. This may present a mechanism for controlling local deformations of skin. For example, the ventral scales of most terrestrial snakes are wide enough to extend from the left to the right ribs of a single vertebra. These ventral scales will resist distension due to loads in the hoop direction. With some auxiliary muscle activity, a mechanism is potentially available for supporting the weight of terrestrial snakes which tends to spread the tips of the ribs apart. Such local resistance to loads in the hoop direction need not interfere with rectilinear locomotion because the compliant skin between adjacent ventral scales could still permit the necessary longitudinal distension. Although several factors have probably contributed to a secondary reduction of ventral scale width in advanced snakes, it is interesting to note that this is most common in fully aquatic snakes whose weight is supported by the water.

An additional factor contributing to the regional differences in skin stiffness may be the extent of the mid-dorsal and mid-ventral septa. For example, in *Nerodia fasciata*, the mid-dorsal septum of connective tissue firmly attaches the skin to the neural spines of the underlying vertebrae. Hence, there is a slight thickening of connective tissue in the mid-dorsal skin of *N. fasciata*, and this region may have dominated the behaviour of the sample during loading. In contrast to *N. fasciata*, the mid-dorsal skin of *Acrochordus granulatus* is only very weakly attached to the vertebrae and this was the region of least stiffness with *A. granulatus*. *Acrochordus granulatus*, *Enhydrina schistosa* and, to some extent, *Hydrophis melanosoma* are laterally flattened with a pronounced mid-ventral keel. Gross examination of the mid-ventral keel of these snakes reveals a slight proliferation of connective tissue that contributes to the keel and this is likely to cause increased loading during extension. A more longitudinal orientation of fibres within these midline septa also may be increasing the stiffness of these regions. Future study of the nature of the dermal collagen fibres and the thickness of the skin between scales (i.e. the hinge region) should prove useful for predicting the stiffness of snake skin.

The skin of *Ahaetulla prasina* was interesting in many respects. Despite the thinness of this skin, loads at low strain were relatively large (Table II). Large loads were particularly evident for the ventral skin of *A. prasina*. The problem of supporting the weight of the viscera may be most extreme for highly arboreal species such as *A. prasina* which often has most of its ventral surface unsupported as it is suspended across very small branches. This role may explain why *A. prasina* was the only species lacking a mid-ventral keel that had ventral skin stiffer than the dorsal skin. Alternatively, the stiff ventral skin and reduced costocutaneous musculature may reflect specializations resulting from the abandonment of rectilinear locomotion.

As seen in Table II, for snakes of similar size, forces resisting distension of the skin may be increased either by increasing skin thickness (*L. colubrina*) or by altering the composition of the skin (*A. prasina*). As indicated in Table III, ten-fold differences in stress were also present at a given strain. Therefore, the skin of different regions and species probably encounters radically different regimes of stress during normal activity. Furthermore, stress at 0.10 and 0.15 strain expressed as the percentage of stress at the beginning of failure varies widely among species (Table III). One might expect that *in vivo* distension of skin would occur over a similar safety margin with respect to failure. For the dorsal skin of five of the six species, the stress at 0.10 strain was relatively closer to stress at failure than skin from other regions. *In vivo* distension of the dorsal skin is undoubtedly less than that of other regions; therefore, the *in vivo* stresses relative to failure would be more similar than those relative stresses in Table III that were calculated for a constant strain. Yet, it is

difficult to imagine that the *in vivo* skin strains of *A. prasina* are so different from other species that its skin functions at stresses which are a similar fraction of those at the beginning of failure. It would indeed be intriguing if the skin of some specialized species such as *A. prasina* normally functioned closer to failure than that of other species.

This study indicates substantial differences in the mechanical behaviour of snake skin. Despite some superficial similarities in the appearance of snakes, snakes occupy a great diversity of habitats. The skin of snakes probably serves several functions associated with this variety of habitats, and this may include acting as a physiological barrier or a transmitter of locomotor forces. For example, the primarily aquatic *Laticauda colubrina* provides a marked contrast to the almost exclusively arboreal *Ahaetulla prasina*. The skin of *L. colubrina* was much thicker and stiffer than that of the very thin and light-bodied *A. prasina*. Perhaps this difference reflects the protective function of skin or perhaps it indicates a different function in locomotion. Future integrated studies of muscle function and dermal morphology and mechanical behaviour should clarify some of the implications of this marked variability in the mechanical properties of snake skin.

Summary

The mechanical properties of snake skin varied significantly among samples from different dorsal-ventral locations and among the different species that were studied. The loads per width of sample indicate that resistance to a given distension may vary substantially, even among snakes of similar size. *Nerodia fasciata* was the most anatomically generalized species studied, and nearly identical loading curves were observed for skin samples from the regions of insertion of the well-developed costocutaneous superior and inferior muscles. The range in stiffness observed in snake skin is large compared to reported values for other vertebrate groups, and this probably indicates considerable diversity in the structure and function of dermal collagen fibres.

This work was completed as part of a PhD dissertation submitted to the Department of Zoology at Michigan State University, East Lansing, Michigan, USA. Financial support was provided by National Science Foundation Dissertation Improvement Grant No. BSR-8401874 and grants from the Michigan State University and national chapters of the Sigma Xi Society, as well as from NIH grant NS16270 to J. Edwards. R. Hubbard provided the facilities for conducting mechanical testing and M. Sacks, T. Segula and D. Petryga provided technical assistance. J. Edwards and R. Hubbard provided useful criticism of an earlier draft of this manuscript. Discussions with P. Wainwright also were helpful.

REFERENCES

- Alexander, A. A. & Gans, C. (1966). The pattern of dermal-vertebral correlation in snakes and amphisbaenians. *Zool. Meded., Leiden* **41** (11): 171-190.
- Buffa, P. (1905). Ricerche sulla muscolatura dei serpenti e considerazioni sulla locomozione di questi animali. *Atti Acad. Ven. Trent* (N.S.) **1**: 145-237.
- Finlay, B. (1970). Dynamic testing of human skin *in vivo*. *J. Biomechanics* **3**: 322-327.
- Gans, C. (1974). *Biomechanics: an approach to vertebrate biology*. Ann Arbor: University of Michigan Press.
- Gans, C. (1984). Slide pushing—A transitional locomotor method of elongate squamates. *Symp. zool. Soc. Lond.* No. 52: 13-26.
- Gans, C. & Baic, D. (1977). Regional specialization of reptilian scale surfaces; relation of texture and biologic role. *Science, Wash.* **195** (No. 4284): 1348-1350.

- Gasc, J.-P. (1974). L'interprétation fonctionnelle de l'appareil musculosquelettique de l'axe vertébral chez serpents (Reptilia). *Mém. Mus. natn. Hist. nat. Paris (Zool.)* **83**: 1-182.
- Gray, J. & Lissmann, H. W. (1950). The kinetics of locomotion of the grass snake. *J. exp. Biol.* **26**: 354-367.
- Hebrank, M. R. (1980). Mechanical properties and locomotor functions of eel skin. *Biol. Bull. mar. biol. Lab. Woods Hole* **158**: 58-68.
- Hebrank, M. R. & Hebrank, J. H. (1986). The mechanics of fish skin: Lack of an 'external tendon' role in two teleosts. *Biol. Bull. mar. biol. Lab. Woods Hole* **171**: 236-247.
- Jayne, B. C. (1985). *Mechanisms of snake locomotion: An electromyographic study*. PhD thesis, Michigan State University, East Lansing.
- Jayne, B. C. (1986). Kinematics of terrestrial snake locomotion. *Copeia* **1986**: 915-927.
- Lanir, Y. (1979). A structural theory for the homogeneous biaxial stress-strain relationships in flat collagenous tissues. *J. Biomechanics* **12**: 423-436.
- Lanir, Y. & Fung, Y. C. (1974). Two dimensional mechanical properties of rabbit skin—II. Experimental results. *J. Biomechanics* **7**: 171-182.
- 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.
- Lillywhite, H. B. & Maderson, P. F. A. (1982). Skin structure and permeability. In *Biology of the Reptilia* **12**: 397-442. Gans, C. & Pough, F. H. (Eds). New York: Academic Press.
- Lissmann, H. W. (1950). Rectilinear locomotion in a snake (*Boa occidentalis*). *J. exp. Biol.* **26**: 368-379.
- Motta, P. J. (1977). Anatomy and functional morphology of dermal collagen fibres in sharks. *Copeia* **1977**: 454-463.
- Pockrandt, D. (1936). Beitrage zur Histologie der Schlangenhaut. *Zool. Jb. Anat.* **62**: 275-322.
- Pough, F. H. & Groves, J. D. (1983). Specializations of the body form and food habits of snake. *Am. Zool.* **23**: 443-454.
- Smith, M. A. (1943). *The fauna of British India. Reptilia and Amphibia* **3**. London: Taylor & Francis Ltd.
- Veronda, P. R. & Westman, R. A. (1970). Mechanical characterization of skin—finite deformations. *J. Biomechanics* **3**: 111-124.
- Vogel, H. G. & Hilgner, W. (1979). The step phenomenon as observed in animal skin. *J. Biomechanics* **12**: 75-81.
- Voris, H. K. (1975). Dermal scale-vertebrae relationships in sea snakes (Hydrophiidae). *Copeia* **1975**: 746-757.
- Voris, H. K. & Jayne, B. C. (1976). The costocutaneous muscles in some sea snakes (Reptilia, Serpentes). *J. Herpet.* **10**: 175-180.
- Voris, H. K. & Voris, H. H. (1983). Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioural and ecological relationships. *Am. Zool.* **23**: 411-425.
- Wainwright, S. A., Vosburgh, F. & Hebrank, J. H. (1978). Shark skin: Function in locomotion. *Science, Wash.* **202** (17): 747-749.