

Comparative Morphology of the Semispinalis-Spinalis Muscle of Snakes and Correlations With Locomotion and Constriction

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ABSTRACT Segments of the spinalis portion of the *M. semispinalis-spinalis* (SSP) were examined in 107 snakes representing 94 species, 85 genera, and 11 families. Allowing for slight variation within individuals and species, the following generalizations can be made. (1) Three major types of segments of the SSP were found in *Typhlops*, booids, and colubroids. (2) Within each type, differences in the segmental length of the spinalis result primarily from different lengths of the anterior tendons. (3) Specializations in habitat and locomotor modes usually account for variations in the segmental lengths of the spinalis. (4) Constrictors seem to have undergone selection for increased flexibility which is gained by having relatively more vertebrae and, in some cases, shorter muscle segments.

Mosauer ('35) surveyed axial musculature in the trunk of snakes and, after examining 51 species, formulated a tripartite classification of myological types based on family lines. In the boid type the *M. semispinalis-spinalis* arises from a single head via the tendinous arch of the *M. multifidus*, whereas in both the viperid and colubrid types, this muscle arises from two distinct heads: a dorsomedial spinalis portion and a ventrolateral semispinalis portion. The semispinalis portion arises directly from the vertebrae in the viperid type, whereas it arises from the medial tendon of the *M. longissimus dorsi* in the colubrid type. For all snakes that Mosauer examined, segments of the *M. semispinalis-spinalis* tapered anteriorly to form a relatively long and thin tendon which inserted onto the lateral face of the neural spine of a vertebra. Auffenberg ('58, '61, '62, '66) confirmed Mosauer's general observations but stressed the oversimplified nature of Mosauer's classification by describing intermediate myological arrangements. Gasc ('67, '74) described axial musculature in the trunk of limbless lizards and snakes; his detailed figures and text contain numerous refinements of earlier descriptions. Ruben ('77) briefly dealt with correlations between locomotor and predatory modes and the axial musculature in *Lichanura* and *Masticophis*. Although Pregill ('77) concentrated on the musculature of the neck in *Coluber*, he also included some observations on the musculature of the trunk. Despite all these studies, the segmental lengths of the

axial muscles are only known for some two-dozen species of snakes.

The purpose of this study was to examine variation in configuration and in segmental length of the spinalis portion of the axial muscles in order to determine whether this variation is correlated with phylogeny, presence or absence of constriction, or other specializations in habitat or locomotor mode. The spinalis portion was chosen for study because (1) it is one of the most massive axial muscles, (2) it is the only superficial epaxial muscle that always extends between vertebrae without forming confusing connections with adjacent muscles (Mosauer, '35; Gasc, '74; Fig. 1), and (3) its segmental length correlates well with that of two other major epaxial muscles, the *M. longissimus dorsi* and the *M. iliocostalis* (Mosauer, '35; Gasc, '74).

MATERIALS AND METHODS

Segments of the spinalis were dissected in 107 snakes representing 11 families, 85 genera, and 94 species. Specimens preserved in alcohol were borrowed from collections at the University of South Florida, Tampa (USF), Field Museum of Natural History (FMNH), Smithsonian Institution, National Museum of Natural History (USNM), and the Florida State Museum, University of Florida (UF). With the exceptions of *Heterodon* and *Boiga*,

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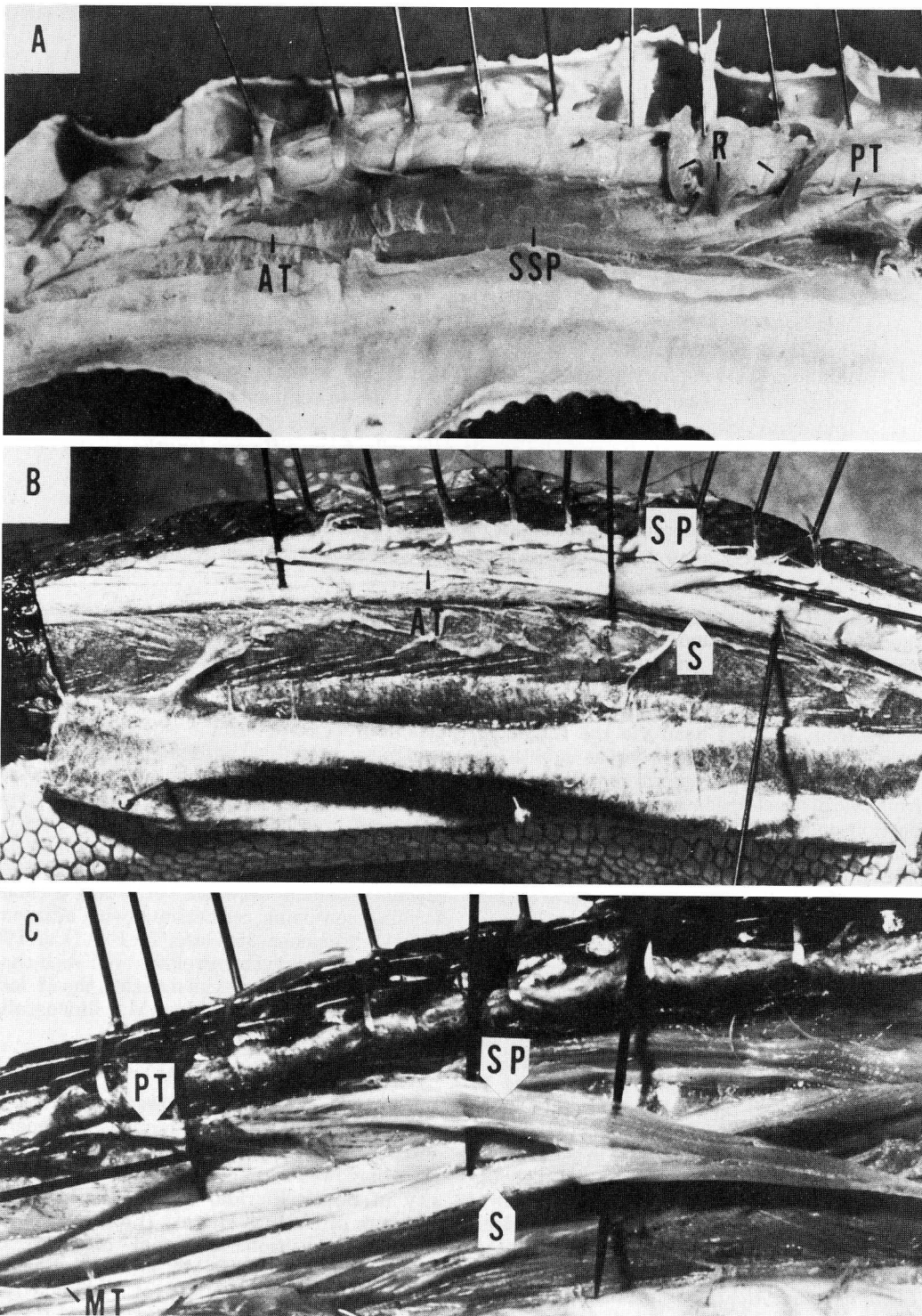


Fig. 1. A. Left lateral view of a complete SSP segment in *Acrochordus javanicus*, a representative booid. Note that muscle fibers arising from the more anterior vertebrae of origin are attached in successively more dorsal positions on the posterior tendons of the tendinous arches. B. Left lateral

view of a complete SSP segment in *Thalassophina viperina* (colubroid). C. Right lateral close-up view of a SSP segment in *Nerodia f. pictiventris* (colubroid). In all photographs, anterior tendons of more posterior SSP segments were pinned laterally to mark vertebrae.

Abbreviations

AT, Anterior tendon of SSP
 MT, Medial tendon of *M. longissimus dorsi*
 PT, Posterior tendon of SSP
 R, Muscle tissue remnants from a removed posteriorly adjacent SSP segment
 S, Semispinalis head of the SSP
 SP, Spinalis head of the SSP
 SSP, *M. semispinalis-spinalis*

species were classified as constrictors or non-constrictors according to Greene ('77). For this study constrictors were defined as snakes which regularly use a stereotyped pattern of coil application in order to subdue and usually kill their prey. Thus, the rather unpredictable coil application of *Heterodon* and *Boiga* caused them to be classified as nonconstrictors. By reviewing general accounts (e.g., Wright and Wright, '57), species were also categorized as burrowing, arboreal, aquatic, or terrestrial.

For most snakes, numbers of body vertebrae could be determined by counting ventral scales (Alexander and Gans, '66). In species with reduced ventrals, counts of body vertebrae were estimated by examining skeletons (*Acrochordus* and *Erpeton*), x-rays (*Typhlops*), or literature (Voris, '75, for most *Hydrophiinae*). The relative position of a muscle was calculated by dividing the number of vertebrae from the head to the anterior tendon's insertion by the total number of body vertebrae. When possible, the relative position of muscles used for comparison approximated 50% (101 of 107 dissections were between 45% and 55%).

A low-power dissecting scope was used to examine small specimens. Segments of the spinalis were exposed first by making a skin-deep middorsal incision and reflecting the skin laterally. The fascia sheaths surrounding the muscle tissue and anterior tendons of the *M. semispinalis-spinalis* then were severed, which

facilitated separating the anterior tendons of adjacent muscle segments. The anterior tendons of segments superficial and posterior to the segment of interest were then cut near the muscle tissue and reflected; this permitted direct counting of vertebrae for measurements of muscles. Finally, the muscle tissue of a few posterior and adjacent segments was removed. For each dissected segment of the spinalis, the number of vertebrae involved in the origin, and the numbers of body segments spanned by the posterior tendon, muscle tissue, anterior tendon, and the entire segment (including the body segments of origin and insertion) were recorded. Notes on the semispinalis were also taken.

RESULTS

One specimen each of *Boa constrictor*, *Nerodia fasciata pictiventris*, and *Crotalus adamanteus* was dissected at relative positions of 25%, 50%, and 75% of the body length to determine the amount of variation within individuals (Table 1). The exact configuration of the spinalis varied slightly; however, the segmental length of the spinalis was constant in both *N. f. pictiventris* and *C. adamanteus*. In *Boa constrictor* the midbody spinalis spanned one more vertebra than its serial homologues at relative positions of 25% and 75%; however, the amount of muscle fiber contributed from the extra vertebra was relatively small and may not be functionally significant. Overall, segments of the spinalis appeared to be relatively uniform within individuals.

Five specimens each of *Coluber constrictor priapus*, *Nerodia f. pictiventris*, and *Pituophis melanoleucus* were dissected to determine intraspecific variation (Table 2). Within species, lengths of the posterior tendons were constant and the number of vertebrae of origin varied in only two cases (one *Coluber* and one *Pituophis*

TABLE 1. Variation in the segments of the spinalis for relative muscle positions of 25%, 50%, and 75% in *Boa constrictor*, *Nerodia f. pictiventris*, and *Crotalus adamanteus* (— indicates very few muscle fibers were contributed from one of the vertebrae of origin)

Species (museum number)	Relative position (%)	Number of vertebrae					Spinalis length body vertebrae (%)
		Origin	Posterior tendon	Muscle tissue	Anterior tendon	Spinalis length	
<i>Boa constrictor</i> (USNM 212225)	28.1	5	2	5	8	15	6.4
	56.2	5	2	7	7	16	6.8
	74.9	6	2	6	7	15	6.4
<i>Nerodia f. pictiventris</i> (USNM 212243)	24.8	2—	2	3	15	20	16.0
	48.8	2	2	5	13	20	16.0
	72.0	2—	3	4	13	20	16.0
<i>Crotalus adamanteus</i> (USNM 212253)	24.4	3—	2	6	13	21	12.2
	48.8	2	3	4	14	21	12.2
	76.2	2	3	3	15	21	12.2

TABLE 2. Variation in segments of the spinalis for midbody dissections of 107 specimens from 94 species¹

Species (museum number)	Number of vertebrae					Spinalis length (%BV)	Habitat, constriction
	Body (=BV)	Origin	Post. tendon	Muscle tissue	Ant. tendon		
TYPHLOPIDAE							
<i>Typhlops schlegelii brevis</i> (FMNH 62348)	179	4	0	5	5	10(5.6)	br
ACROCHORDIDAE							
<i>Acrochordus javanicus</i> (USF)	204	5	2	5	4	11(5.4)	aq*
LOXOCEMIDAE							
<i>Loxocemus bicolor</i> (USF)	215	5	1	8	6	15(7.0)	br*
ANILIIDAE							
<i>Cylindrophis rufus</i> (USF)	190	6	1	8	5	14(7.4)	br*
XENOPELTIDAE							
<i>Xenopeltis unicolor</i> (FMNH 169411)	183	4	2	4	5	11(6.0)	br*
TROPIDOPHIIDAE							
<i>Tropidophis h. haetianus</i> (USF)	177	5	1	5	4	10(5.6)	tr*
BOIDAE							
<i>Acrantophis dumerili</i> (FMNH 73107)	226	5	1	6	7	14(6.2)	tr*
<i>Boa constrictor</i> (USNM 212225)	235	5	2	7	7	16(6.8)	tr*
<i>Candoia carinata</i> (FMNH 41361)	194	6	1	6	4	11(5.7)	tr*
<i>Corallus caninus</i> (FMNH 27018)	203	5	1	5	6	12(5.9)	ab*
<i>Epicrates cenchria</i> (FMNH 26769)	256	5	1	6	5	12(4.7)	tr*
<i>Eryx colubrinus</i> (USNM 212226)	185	3*	2	7	6	15(8.1)	br*
<i>Eunectes murinus</i> (FMNH 45696)	254	6	1	7	5	13(5.1)	tr*
<i>Lichanura roseofusca</i> (UF 45320)	230	5	2	6	5	13(5.6)	tr*
<i>Morelia spilotes variegatus</i> (UF 45225)	284	6—	3	6	5	14(3.8)	tr*
<i>Python curtus</i> (UF 42781)	171	5	2	7	2	11(6.4)	tr*
<i>Python reticulatus</i> (UF 42864)	316	6	2	8	4	14(4.4)	tr*
<i>Sanzinia madagascariensis</i> (FMNH 73973)	201	5	1	4	6	11(5.5)	tr*
COLUBRIDAE							
<i>Ahaetulla prasina</i> (USNM 212227)	219	1	2	4	30	36(16.4)	ab
<i>Alsophis cantheridgerus</i> (UF 44827)	175	2	2	4	13	19(10.9)	tr*
<i>Aparallactus lunulatus</i> (FMNH 62228)	165	3	2	4	11	17(10.3)	br
<i>Arizona elegans</i> (USNM 48696)	207	2—	3	3	14	20(9.7)	tr*
<i>Atractaspis microlepidata</i> (FMNH 58400)	231	3	1	7	14	22(9.5)	br
<i>Atractus manizalensis</i> (FMNH 54869)	150	2	2	4	9	15(10.0)	br
<i>Boaedon fuliginosus</i> (USNM 49024)	231	2	2	5	11	18(7.8)	tr*
<i>Boiga dendrophila</i> (USNM 49784)	235	2	2	5	30	37(15.7)	ab
<i>Calamaria lumbricoidea</i> (FMNH 147650)	195	2	1	4	6	11(5.6)	br
<i>Cemophora coccinea</i> (USNM 212228)	177	2	2	5	11	18(10.2)	br*
<i>Cerberus rynchops</i> (FMNH 199680)	148	3—	2	5	7	14(9.5)	aq
<i>Chilorhinophis carpenteri liwalensis</i> (FMNH 81032)	247	2	1	3	7	11(4.4)	br
<i>Chionactis occipitalis</i> (USNM 212229)	149	2	2	3	9	14(9.4)	br

Table 2 continued on next page.

TABLE 2. Variation in segments of the spinalis for midbody dissections of 107 specimens from 94 species¹ (continued)

Species (museum number)	Number of vertebrae					Spinalis length (%BV)	Habitat, constriction
	Body (=BV)	Origin	Post. tendon	Muscle tissue	Ant. tendon		
<i>Chrysopelea ornata</i> (USNM 72058)	227	2	3	4	19	26(11.5)	ab*
<i>Coluber constrictor priapus</i> (USNM 212230)	182	2	2	5	17	24(13.2)	tr
(USNM 212231)	180	2	2	3	20	25(13.9)	
(USNM 212233)	180	3	2	4	20	26(14.4)	
(USNM 212232)	177	2	2	5	19	26(14.7)	
(USNM 212234)	178	2	2	4	19	25(14.0)	
<i>Dipsas variegatus</i> (UF 44301)	199	2	3	5	23	31(15.6)	ab
<i>Dispholidus typus</i> (FMNH 134256)	182	2	2	4	27	33(18.1)	ab
<i>Drymarchon corais couperi</i> (USNM 212235)	187	2	2	2	17	21(11.2)	tr
<i>Elaphe obsoleta quadrivittata</i> (USNM 212236)	242	2	2	3	13	18(7.4)	tr*
<i>Erpeton tentaculatum</i> (USNM 212237)	117	3—	2	4	7	13(11.1)	aq
<i>Geophis nasalis</i> (FMNH 20356)	118	2—	2	6	18	26(22.0)	tr
<i>Heterodon platyrhinos</i> (USNM 212238)	122	2	3	4	17	24(19.7)	tr
<i>Hydrops triangularis</i> (UF 10602)	179	2—	2	2	7	11(6.1)	aq
<i>Imantodes cenchoa</i> (UF 30606)	255	2	2	6	37	45(17.6)	ab
<i>Lampropeltis getulus floridana</i> (USNM 212239)	221	2	2	3	11	16(7.2)	tr*
<i>Masticophis f. flagellum</i> (USNM 212240)	212	1*	2	4	18	24(11.3)	tr
<i>Miodon acanthias</i> (FMNH 19836)	196	3	2	3	10	15(7.7)	br
<i>Miodon gabonensis christyi</i> (FMNH 12825)	217	2	2	3	12	17(7.8)	br
<i>Nerodia f. pictiventris</i> (USNM 212244)	127	2	2	5	12	19(14.7)	tr
(USNM 212241)	126	2	2	6	13	21(16.7)	
(USNM 212242)	128	2	2	5	14	21(16.4)	
(USNM 212243)	125	2	2	5	13	20(16.0)	
(USNM 212245)	122	2	2	4	15	21(17.2)	
<i>Opheodrys aestivus</i> (USNM 212246)	166	2	1	6	15	22(13.3)	tr
<i>Oxybelis fulgidus</i> (UF 45227)	209	1	2	6	26	34(16.3)	ab
<i>Pareas malaccanus</i> (USNM 70864)	164	2	3	6	11	20(12.2)	tr
<i>Pituophis m. melanoleucus</i> (USNM 101310)	217	2	2	4	12	18(8.3)	tr*
<i>P. m. deserticola</i> (USNM 212248)	244	2	2	4	14	20(8.2)	
<i>P. m. lodingi</i> (USNM 212249)	213	2	2	4	12	18(8.5)	
<i>P. m. mugitus</i> (USNM 212247)	226	2	2	3	12	17(7.5)	
<i>P. m. sayi</i> (USNM 157292)	224	3—	2	5	14	21(9.4)	
<i>Pseudaspis cana</i> (FMNH 77625)	186	2	2	3	10	15(8.1)	br*
<i>Regina alleni</i> (USNM 212250)	124	2	2	4	10	16(12.9)	aq
<i>Sonora semiannulata</i> (USNM 126480)	146	3	1	3	7	11(7.5)	br
<i>Spalerosophis diadema cliffordi</i> (USNM 130358)	224	2	3	4	19	26(11.6)	tr*
<i>Spilotes p. pullatus</i> (USNM 193747)	229	2	3	4	14	21(9.2)	tr*
<i>Stilosoma extenuatum</i> (USNM 212251)	268	3	1	4	8	13(4.9)	br*

Table 2 continued on next page.

TABLE 2. Variation in segments of the spinalis for midbody dissections of 107 specimens from 94 species¹ (continued)

Species (museum number)	Number of vertebrae					Spinalis length (%BV)	Habitat, constriction
	Body (=BV)	Origin	Post. tendon	Muscle tissue	Ant. tendon		
<i>Thelotornis k. kirtlandi</i> (USNM 167090)	173	2	2	4	35	41(23.7)	ab
<i>Trimorphodon b. biscutatus</i> (USNM 110403)	272	2	2	6	20	28(10.5)	tr*
ELAPIDAE							
<i>Acanthophis antarticus</i> (FMNH 20769)	118	2	3	3	13	19(16.1)	tr
<i>Boulengerina annulata</i> (USNM 142589)	215	1	1	6	16	23(10.7)	tr
<i>Bungarus fasciatus</i> (FMNH 128262)	228	1	3	4	15	22(9.6)	tr
<i>Bungarus multicinctus</i> (FMNH 140150)	212	2—	3	5	16	24(11.3)	tr
<i>Demansia textilis</i> (FMNH 75131)	209	1	2	4	12	18(8.6)	tr
<i>Dendroaspis polylepis</i> (FMNH 77631)	268	2	3	4	22	29(10.8)	ab
<i>Dendroaspis viridis</i> (FMNH 191438)	214	1	2	3	28	33(15.4)	ab
<i>Micrurus microfrontalis</i> (FMNH 195889)	218	3	2	3	10	15(6.9)	br
<i>Naja n. naja</i> (USNM 212255)	190	2	2	4	21	27(14.2)	tr
<i>Oxyuranus scutellatus</i> (FMNH 97690)	242	1	3	3	18	24(9.9)	tr
<i>Pseudechis porphyriacus</i> (FMNH 166906)	182	2	3	4	14	21(11.5)	tr
HYDROPHIIDAE,							
Laticaudinae							
<i>Laticauda colubrina</i> (FMNH 202799)	234	3	2	5	9	16(6.8)	aq
<i>Laticauda semifasciata</i> (FMNH 202823)	198	3	4	5	11	20(10.1)	aq
Hydrophiinae							
<i>Acalyptophis peronii</i> (FMNH 201922)	172'	2*	1	5	6	12(7.0)	aq
<i>Aipysurus eydouxii</i> (FMNH 201470)	141	2	2	4	6	12(8.5)	aq
<i>Enhydrina schistosa</i> (FMNH 198710)	158'	2	1	3	7	11(7.0)	aq
<i>Hydrophis caeruleus</i> (FMNH 202067)	196'	3—	2	4	5	11(5.6)	aq
<i>Hydrophis ornatus</i> (FMNH 202913)	159'	3	2	4	6	12(7.5)	aq
<i>Lapemis hardwickii</i> (FMNH 198468)	136'	3—	1	4	6	11(8.3)	aq
<i>Pelamis platurus</i> (FMNH 154858)	147'	2	2	3	6	11(7.2)	aq
<i>Thalassophina viperina</i> (FMNH 202182)	156'	2	1	2	7	10(6.4)	aq
VIPERIDAE, Viperinae							
<i>Atheris squamigera</i> (FMNH 154890)	156	2	1	7	14	22(14.1)	ab
<i>Bitis gabonica</i> (FMNH 62181)	130	3	3	5	13	21(16.2)	tr
<i>Bitis nasicornis</i> (USF)	119	2	2	6	11	19(16.0)	tr
<i>Causus rhombeatus</i> (FMNH 134251)	142	2	1	5	17	23(16.2)	tr
<i>Cerastes cerastes</i> (FMNH 164715)	141	2	2	5	8	15(10.6)	tr
<i>Eristicophis macmahoni</i> (FMNH 142681)	143	2—	1	4	7	12(8.4)	tr
<i>Vipera russelli</i> (FMNH 127242)	159	3	3	4	12	19(11.9)	tr
Crotalinae							
<i>Agkistrodon piscivorus</i> (USNM 212252)	142	2	4	4	14	22(15.5)	tr

Table 2 continued on next page.

TABLE 2. Variation in segments of the spinalis for midbody dissections of 107 specimens from 94 species¹ (continued)

Species (museum number)	Number of vertebrae					Spinalis length (%BV)	Habitat, constriction
	Body (=BV)	Origin	Post. tendon	Muscle tissue	Ant. tendon		
<i>Bothrops atrox</i> (FMNH 2617)	194	2—	3	7	19	29(14.9)	tr
<i>Bothrops bilineatus</i> (FMNH 197875)	198	2	3	5	16	24(12.1)	ab
<i>Crotalus adamanteus</i> (USNM 212253)	172	2	3	4	14	21(12.2)	tr
(USNM 212254)	175	2	3	4	14	21(12.0)	
<i>Crotalus cerastes</i> (FMNH 26163)	144	2	2	4	10	16(11.1)	tr
<i>Lachesis muta</i> (FMNH 59181)	223	2	2	5	15	22(9.9)	tr
<i>Trimeresurus flavoviridis</i> (FMNH 48787)	224	2	3	5	27	35(15.6)	ab

¹Species are arranged alphabetically within families and subfamilies. (†) indicates data were taken from Voris ('75). (*) indicates some difficulty in dissection caused by partial intermingling of muscle fibers between segments. br, burrowing; aq, aquatic; ab, arboreal; tr, terrestrial; +, constrictor.

m. sayi). The lengths of muscle tissue and anterior tendons varied slightly with a resulting variation of three to four vertebrae in the total segmental length of the spinalis of a species. Yet the standard deviations of segmental length of the spinalis in *C. constrictor priapus*, *N. f. pictiventris*, and *P. melanoleucus* were only 0.84, 0.89, and 1.64 vertebrae, respectively. The rather small respective standard deviations in relative segmental length of the spinalis were 0.57%, 0.94%, and 0.68%. Furthermore, no significant ($P < 0.05$) correlations were found between the segmental lengths of the spinalis muscles and the numbers of body vertebrae in either *C. constrictor priapus* ($r = -0.67$), *N. f. pictiventris* ($r = -0.27$), or *P. melanoleucus* ($r = 0.44$).

Tremendous interspecific variation was apparent (Table 2). Notably, total segmental length of the spinalis ranged from ten to 45 vertebrae, relative length varied from 4.4% to 23.7%, and numbers of body vertebrae varied from 117 to 316. Segments of the M. semispinalis-spinalis also exhibited variation that was not recorded in Table 2. The M. semispinalis-spinalis of *Typhlops* differed from all other snakes in that the muscle fibers arose directly from the vertebra rather than from an intervening tendon. In *Typhlops* this muscle was not divided into separate spinalis and semispinalis portions. In all snakes belonging to booid families (Acrochordidae, Loxocemidae, Xenopeltidae, Aniliidae, Boidae, and Tropidophiidae) the M. semispinalis-spinalis was not divided and arose via the tendinous arches of the Mm. multifidus (Fig. 1A). Distinct spinalis and semispinalis portions (Fig. 1B,C) were observed in all snakes from colubroid families

(Colubridae, Elapidae, Viperidae, and Hydrophiidae). In nearly all species, a single tendon served both the spinalis portion and the M. multifidus (Fig. 1A,B,C); however, in both species of *Bungarus*, the posterior tendon of the spinalis exhibited a slight separation from the anterior region of the tendon of the M. multifidus. In *Pareas malaccanus*, the spinalis tapered posteriorly to a thin tendon (about 1½ vertebrae long) which then connected to the tendon of the M. multifidus.

Measurements of the spinalis were grouped for each family (Table 3) and compared using two-tailed Mann-Whitney *U*-tests (Sokal and Rohlf, '69). The segments of the spinalis in Boidae differed significantly ($P < 0.05$) from all colubroid families by having more vertebrae of origin ($\bar{x} = 5.2$ for boids, 1.6–2.5 for others), greater segmental length of muscle tissue ($\bar{x} = 6.3$ vs 3.9–5.7), and a much shorter anterior tendon ($\bar{x} = 5.2$ vs 6.9–16.8). The relatively homogeneous Hydrophiidae, when compared to the remaining colubroid families, had shorter anterior tendons ($\bar{x} = 6.9$ vs 14.1–16.8), shorter segmental length of the spinalis ($\bar{x} = 13$ vs 21–23), and smaller relative length of the spinalis ($\bar{x} = 7.4\%$ vs 11.4–12.8%). Elapidae had the greatest number of species (5) in which the origin of the segment of the spinalis was confined to one vertebra. The segmental length of muscle tissue in the Viperidae ($\bar{x} = 5.7$) was longer than in the other three colubroid families ($\bar{x} = 3.9$ –4.2). Despite phylogeny (at the family level) accounting for some trends, large ranges of variation in segmental length of the spinalis were present in Colubridae (11–45), Elapidae (15–33), and Viperidae (12–35). By using the variance in the segmental length of

TABLE 3. Mean segmental measurements of the spinalis for families¹

Family	Number of vertebrae					Spinalis length	
	Body vertebrae	Origin	Post. tendon	Muscle tissue	Ant. tendon	Spinalis length	body vertebrae (%)
Boidae (n = 12)	\bar{X} 230 range 171-316 SD 42.6 d	5.2 3-6 0.83	1.6 1-3 0.67 a	6.3 4-8 1.06	5.2 2-7 1.40	13 11-16 1.7 a	5.8 3.4-8.1 1.02
Colubridae (n = 41)	\bar{X} 193 range 117-272 SD 42.0 b,c	2.1 1-3 0.49 a,b	2.0 1-3 0.57 a,b	4.2 2-7 1.17 a	15.3 6-37 7.84 a	22 11-45 8.5 b	11.5 4.4-23.7 4.54 a
Elapidae (n = 11)	\bar{X} 209 range 118-268 SD 38.0 c,d	1.6 1-3 0.67 a	2.5 1-3 0.69 b	3.9 3-6 0.94 a	16.8 10-28 5.17 a	23 15-33 5.1 b	11.4 6.9-15.4 2.83 a
Hydrophiidae (n = 10)	\bar{X} 170 range 136-234 SD 30.8 a,b	2.5 2-3 0.53 b	1.8 1-4 0.92 a,b	3.9 2-5 0.99 a	6.9 6-11 1.79 a	13 10-20 3.1 a	7.4 5.6-10.1 1.26
Viperidae (n = 14)	\bar{X} 163 range 130-224 SD 33.7 a	2.1 2-3 0.36 a,b	2.4 1-4 0.93 b	5.7 4-7 1.04	14.1 8-27 4.98 a	21 12-35 5.7 b	12.8 7.4-13.5 2.04 a

¹ \bar{X} = mean. SD = standard deviation. n = number of species. Groups within a column marked by the same letter are not significantly different ($P < 0.05$) using a two-tailed Mann-Whitney U -test.

the spinalis of *P. melanoleucus* (2.69) as the best estimate of intraspecific variance, F -tests were used to compare intrafamilial to intraspecific variance in the segmental length of the spinalis. Thus, variation within Colubridae ($F = 28.86$), Elapidae ($F = 9.67$), and Viperidae ($F = 12.10$) was significantly greater than intraspecific variance ($P < 0.05$), whereas within Boidae ($F = 1.07$) and Hydrophiidae ($F = 3.57$) variation in the segmental length was no greater than that found within a species.

When all species were considered, no apparent correlation existed between the number of body vertebrae and segmental length of the spinalis ($r = 0.187$, $P < 0.05$). Even within genera there was no correlation. Eight congeneric species pairs (*Python*, *Miodon*, *Bungarus*, *Dendroaspis*, *Laticauda*, *Hydrophis*, *Bitis*, and *Crotalus*) with varying numbers of vertebrae were examined. In four of the genera (*Bungarus*, *Dendroaspis*, *Laticauda*, and *Hydrophis*) the species with more body vertebrae had shorter segmental lengths of the spinalis, while the converse was true for the other four genera.

Finally, species were grouped by habitat type and presence or absence of constriction (Fig. 2). Statistical comparisons among habitat types (Table 4) were confined to colubroids because of their numerous previously mentioned differences from booids. The primary differ-

ences between habitat types occurred in segmental lengths of the spinalis and numbers of body vertebrae, but as Figure 2 shows, these two quantities did not always significantly correlate ($P < 0.05$) with each other. In contrast to grouping data by family, when types of habitats of colubroids were the grouping criteria, the variance in the segmental length of the spinalis was usually not significant (burrowers: $F = 3.57$; aquatic: $F = 2.91$; terrestrial nonconstrictors: $F = 4.80$; and terrestrial constrictors: $F = 5.77$; $P > 0.05$) compared to intraspecific variance (estimated from *P. melanoleucus*). The arboreal colubroids were the only exception to this trend ($F = 15.71$, $P < 0.01$).

Burrowers (Fig. 2) had a wide range in the number of body vertebrae (146-268) and colubroid burrowers possessed relatively short segments of the spinalis ($\bar{x} = 15$) which resulted in a small relative length of the spinalis ($\bar{x} = 7.9\%$). Among colubroids, burrowers also averaged slightly more vertebrae of origin ($\bar{x} = 2.5$) than arboreal ($\bar{x} = 1.8$) and terrestrial species ($\bar{x} = 1.9$).

Aquatic and arboreal colubroid species showed nearly opposite trends in segmental length ($\bar{x} = 13$ vs 33) and numbers of body vertebrae ($\bar{x} = 162$ vs 212). Aquatic colubroids were tied with burrowers for the greatest average number of vertebrae of origin ($\bar{x} = 2.5$). Arboreal colubroids had the greatest average

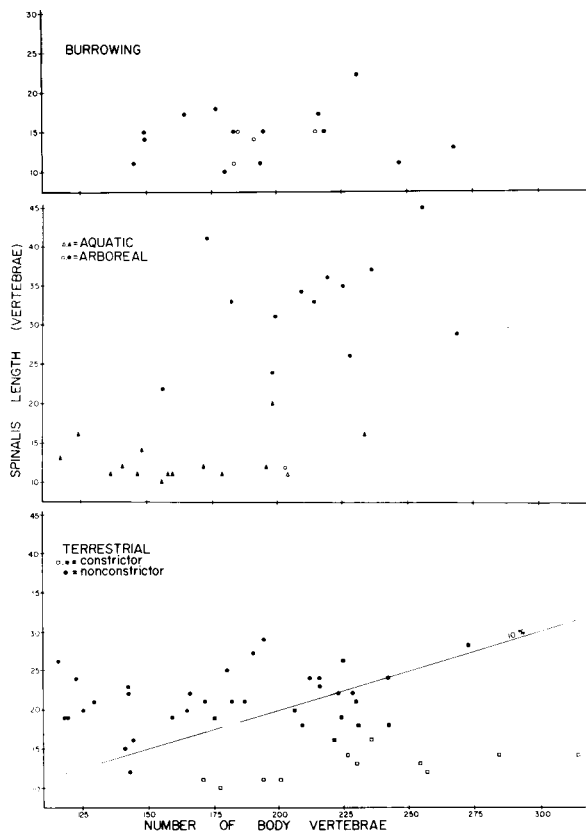


Fig. 2. Segmental length of the spinalis versus number of body vertebrae for all burrowing, aquatic, arboreal, and terrestrial species. Solid symbols represent colubroids and hollow symbols are booids. Note that terrestrial constrictors usually had a segmental length less than 10% of the number of body vertebrae (indicated by the line). For colu-

broid habitat types the following correlation coefficients of segmental length versus number of body vertebrae were obtained: burrowing $r = 0.59$ ($P < 0.05$), aquatic $r = 0.0006$ ($P > 0.05$), arboreal $r = -0.35$ ($P > 0.05$), terrestrial nonconstrictors $r = 0.85$ ($P < 0.01$), and terrestrial constrictors $r = 0.48$ ($P > 0.05$).

segmental length of muscle tissue ($\bar{x} = 4.8$); however, the cross-sectional area subjectively appeared to be the smallest in arboreal species. The relative length of the spinalis of arboreal colubroids ($\bar{x} = 15.6\%$) was more than twice as large as in aquatic colubroids ($\bar{x} = 7.4\%$). Of arboreal species, *Corallus* (a booid) had the shortest segmental length (12), whereas within the arboreal colubroids *Atheris* had the shortest (22) and *Imantodes* had the longest (45). Although *Thelotornis* (a colubrid) had only 173 body vertebrae, it had the second longest segments of the spinalis (41), which gave it the greatest relative length of the spinalis (23.7%) of any species examined. Interestingly, *Thelotornis* and *Imantodes* also had a marked reduc-

tion in mass of the costocutaneous muscles.

Terrestrial species were subdivided into constrictors and nonconstrictors (Fig. 2). Colubroid constrictors had the same average segmental length of the spinalis as nonconstrictors ($\bar{x} = 21$), but the constrictors also had more body vertebrae ($\bar{x} = 225$ vs 170) and, consequently, a smaller relative length of the spinalis ($\bar{x} = 9.0\%$ vs 13.1%). Most terrestrial constrictors had a relative length of the spinalis less than 10%, whereas nonconstrictors were usually greater than 10% (Fig. 2). The constrictors *Alsophis* (10.9%), *Spalerosophis* (11.6%), and *Trimorphodon* (10.5%) were exceptions to this trend. The nonconstrictors *Bungarus fasciatus* (9.6%), *Demansia* (8.6%), and

TABLE 4. Mean segmental measurements of the spinalis for colubroid habitat types (symbols as in Table 3)

Colubroid habitat type	Number of vertebrae					Spinalis length	
	Body vertebrae	Origin	Post. tendon	Muscle tissue	Ant. tendon	Spinalis length	body vertebrae (%)
Burrowing (n = 13)	\bar{X} 196	2.5	1.6	3.8	9.5	15	7.9
	range 146-268	2-3	1-2	3-7	7-14	11-22	4.4-10.3
	SD 38.9	0.52	0.51	1.17	2.22	3.1	2.00
	- b	b,c	a	a	a	a	a
Aquatic (n = 14)	\bar{X} 162	2.5	1.9	3.9	7.1	13	7.4
	range 117-234	2-3	1-4	2-5	6-11	10-20	5.6-10.1
	SD 31.7	0.52	0.77	1.03	1.70	2.8	1.23
	- a	c	a,b	a,b	a	a	a
Arboreal (n = 13)	\bar{X} 212	1.8	2.3	4.8	25.7	33	15.6
	range 156-268	1-2	1-3	3-7	14-37	22-45	10.8-23.7
	SD 31.4	0.44	0.63	1.09	6.81	6.5	3.31
	- b	a	b	b	a	b	a
Terrestrial nonconstrictor (n = 27)	\bar{X} 170	1.9	2.3	4.5	14.5	21	13.1
	range 118-242	1-3	1-4	2-7	11-21	12-29	8.4-22.0
	SD 37.4	0.49	0.76	1.12	3.38	3.6	3.29
	- a	a	b	a,b	a	b	b
Terrestrial constrictor (n = 9)	\bar{X} 225	2.0	2.3	4.0	14.2	21	9.0
	range 175-272	2	2-3	3-6	11-20	16-28	6.0-11.6
	SD 25.9	0	0.50	1.00	3.19	3.94	1.80
	b	a,b	b	a,b	a	b	a

Oxyuranus (9.9%) were also exceptions; however, their small relative lengths of the spinalis are mainly the result of high numbers of body vertebrae. The desert viperids *Crotalus cerastes*, *Cerastes*, and *Eristicophis* had the three shortest segmental lengths for terrestrial nonconstrictors (16, 15, and 12) and *Eristicophis* also had a relative length of 8.4% for the spinalis muscle.

The complex connections between the semispinalis and the medial tendon of the M. longissimus dorsi prohibited a tabular summary of the semispinalis utilizing Mosauer's categories. In all booid species, the semispinalis was not differentiated from the spinalis, which arose from tendinous arches extending from a neural spine to the postzygopophysis of the same vertebra. The medial tendons of the M. longissimus dorsi distinctly extended to the neural spine in all booids.

In all viperids the semispinalis arose from vertebrae, and in most species the medial tendon of the M. longissimus dorsi attached to the neural spine. However, both species of *Bitis* showed no trace of the medial tendon extending to the neural spine. *Eristicophis* had a medial tendon of the longissimus that both extended to the neural spine and also contributed to an intermuscular septum between the M. semispinalis-spinalis and the M. longissimus dorsi.

The medial tendon of the M. longissimus dorsi remained a distinct, ribbonlike structure

that clearly connected to the semispinalis (Fig. 1C) in the following snakes: *Ahaetulla*, *Coluber*, *Dispholidus*, *Drymarchon*, *Elaphe*, *Imantodes*, *Masticophis*, *Nerodia*, *Opheodrys*, *Oxybelis*, *Pituophis*, *Regina*, *Spilotes*, and *Stilosoma*. *Cerberus*, *Chionactis*, *Erpeton*, *Heterodon*, *Pseudaspis*, *Spalerosophis*, *Bungarus*, *Dendroaspis*, and *Aipysurus* all had a relatively robust portion of the medial tendon extending to the neural spines, but the connections of the remaining part of the medial tendon were indistinct.

In some particularly clear dissections such as those of *Coluber* and *Nerodia*, segments of the semispinalis were observed arising from two vertebral units. In the booid snakes, the number of vertebral units contributing to the ventral aspect of a segment of the M. semispinalis-spinalis was never clearly distinguished; however, more than one vertebrae appeared to be involved.

DISCUSSION

After allowing for intraspecific variation, the segmental lengths of the spinalis muscles described herein generally agree well with values given by previous authors for the same or closely related species (Mosauer, '35; Auffenberg, '58, '61, '66; Gasc, '67, '74; Pregill, '77; Ruben, '77). However, the nature of this muscle's origin has been described differently by two groups of studies. Some authors (Auffenberg, '61, for *Xenopeltis unicolor*; Gasc, '67, '74,

for various colubroids and booids; Kramer, '77, for *Vipera aspis*) reported the origin of the spinalis as involving more than one vertebra. A second group (Mosauer, '35, for various booids and colubroids; Auffenberg, '58, '61, '66, for several booids; Pregill, '77, for *Coluber constrictor*; Ruben, '77, for *Masticophis flagellum* and *Lichanura roseofusca*) found only one vertebra of origin. In this study, the vast majority of species (87 of 94), including all booids, had multiple vertebrae of origin. In addition, all species of colubroids which the second group of authors had described and which I also examined were found to have multiple vertebrae of origin in this study. These disputes may be the result of different dissection procedures, since the muscle origins are extremely fragile and overlap extensively. Furthermore, if muscle fibers contributing to the segment from the most posterior vertebrae were destroyed, this would result in shorter reported segmental lengths. Segmental lengths of the colubroids *Masticophis flagellum* (Mosauer, '35; Ruben, '77) and *Coluber constrictor* (Pregill, '77) and the booid *Lichanura roseofusca* (Ruben, '77) were reported as 20, 18-20, and nine, respectively, whereas I found longer segmental lengths for each of these three species (24, 20-24, and 13).

Two additional considerations may further explain different reported values for the length of the spinalis of a species. Unless figures are presented it may be difficult from the text to determine whether some previous authors included the vertebrae of origin and insertion in segmental lengths. Thus, terminology could readily account for discrepancies of up to two vertebrae. Secondly, in this study the wide ranging *Pituophis melanoleucus* (with several subspecies) had the greatest variance in segmental length. Consequently, some differences in segmental lengths found in this study versus others (e.g., Ruben, '77; Pregill, '77) may be due to subspecific variation.

In one case the morphology of the M. semi-spinalis-spinalis may help in solving a phylogenetic problem. Smith ('26) placed *Laticauda* in its own subfamily within the Hydrophiidae. McDowell ('72) placed all sea snakes in the Elapidae. Heatwole ('78) suggested familial status for *Laticauda*, and Voris ('77) recognized *Laticauda* as one of three distinct lineages of Hydrophiidae. The relatively long segments of *Laticauda* (16-20) further support recognizing it as distinct from all other sea snakes (10-12).

Generally, the segmental length of the spinalis appears to be minimally useful for gaining

greater phylogenetic insight at the familial level. The two families with the smallest variances in segmental length were also the most homogeneous for habits and habitat. All of the Boidae are constrictors and all of the Hydrophiidae are aquatic. Perhaps the most phylogenetic information can be obtained by comparative studies of the shape and interrelationships of the axial muscles (e.g., Auffenberg, '61; Gasc, '74), whereas lengths of muscle segments may correlate best with function. For example, the colubroids (advanced snakes) usually had two or fewer vertebrae of origin compared to an average of about five for the boidlike snakes and four for *Typhlops*. Elapids, which are presumably among the more advanced colubroids, had the most species (five) with muscle segments arising from a single vertebra. Perhaps a trend for increased muscular segmentation has accompanied a trend toward increased correspondence between vertebrae, ventrals, and dorsal scale rows (barring some secondary loss). Certainly little can be implied about phylogeny by examining one muscle, but the extremely complex connections among the axial muscles have continued to discourage more extensive studies.

The proportionate elongation of the tendinous elements of segments of the M. semi-spinalis-spinalis correlates well with relative increases in the lengths of tendons of the M. longissimus dorsi and the M. iliocostalis (Mosauer, '35; Gasc, '74; personal observation). These three muscles comprise some two-thirds of the major axial muscle mass (Ruben, '77). Based on the directions of the muscle fibers and the locations of the origins and insertions, Gasc ('74) deduced that these muscles provide the majority of the forces necessary for lateral flexion of the vertebral column; therefore, they should be most important for locomotion and constriction.

One obvious difficulty with attempting to analyze results by habits and habitats was that few snakes live exclusively in one manner. Snakes that are only semiaquatic (e.g., *Nerodia*), occasional burrowers (e.g., *Heterodon*), or semiarboreal (e.g., *Opheodrys*) were considered terrestrial. *Crotalus cerastes*, *Cerastes*, and *Eristicophis* were considered terrestrial nonconstrictors, but they had the three shortest segmental lengths of their group. All three species are proficient sidewinders and commonly *Eristicophis* rapidly buries itself with a peculiar sideways motion (Bellairs, '70). Therefore, sidewinders may be somewhat different in their musculature than more typical

terrestrial species. Presumably, other species show a compromise between opposing selective pressures. For example, *Chrysopelea* had the shortest segmental length of any arboreal colubroid but it is also reported to constrict (Greene, '77). Distinguishing constrictors from nonconstrictors is complicated especially because of the existence of rear-fanged "constrictors" (e.g., *Trimorphodon*). It is uncertain whether constriction of venom is killing the prey in many opisthoglyphs.

Ruben ('77) suggested that the relatively long proportional length of contractile tissue in the muscle segments of *Lichanura* (a booid) increases its power of constriction, whereas the smaller proportion of muscle tissue in the segments of *Masticophis* (a colubroid) may not enable it to exert the tension necessary for constriction. Although this was certainly a logical suggestion, generalizations based on a comparison of a booid and a colubroid are complicated by differences in phylogeny and body shape. Boidae had a greater average proportional length of contractile tissue per segment of the spinalis (48.5%) than any colubroid family (16.9%–30.0%). However, constricting terrestrial colubroids examined in this study had an average proportional length of contractile tissue (19.0%) which was less than half that of boids. Even within the colubroids, high proportional length of contractile tissue does not appear to have much predictive value for constriction, since terrestrial colubroid constrictors (19.0%) averaged slightly less than nonconstrictors (21.4%) in proportional muscle tissue length. Among colubroid families, the relatively heavy-bodied viperids had the greatest average absolute length of contractile tissue (5.7 vertebrae) per segment of the spinalis as well as a rather large proportional length of contractile tissue per muscle segment (27.1%). Since viperids do not constrict but frequently do resemble the stout body-form common in the booids, proportionately more contractile tissue per muscle segment may be necessary just for the terrestrial locomotion of heavy-bodied snakes.

Ruben ('77) also suggested that shorter muscle segments could enhance strength of constriction because greater numbers of complete muscle segments could fit into a given length of body. However, the consequences of numbers of complete muscle segments are not simple because of the overlapping arrangements of muscle segments. For example, one may consider two snakes that both have equal lengths and numbers of body vertebrae but dif-

ferent segmental lengths of axial muscles (15 vs 30). Any one vertebra in the first snake would then be crossed only by 15 muscle segments, whereas 30 muscle segments would cross each vertebra in the other snake. If individual muscle segments generated equal tensions and these forces were distributed evenly across all the vertebrae spanned by each segment, then theoretically the snake with longer muscle segments could generate just as much force across a single vertebra as the other snake could, providing all 30 segments could contract simultaneously.

Alternatively, one may assume the action of axial muscle is confined mainly to the body segments to which muscles are directly attached. In this case snakes which have several vertebrae of origin would move more body segments when a single muscle segment contracts, although the extent of the total flexion is, admittedly, not obvious. Another consequence of having several vertebrae of "origin" is that more muscle segments (up to six in some booids) could exert force directly on a single vertebra. Thus, for future understanding of the generation of forces by the axial muscles of snakes one will have to determine the movement caused by single muscle segments as well as the number of muscle segments actually used at any one time.

In addition to considering the forces that must be generated during constriction, some passive properties of the snake's musculoskeletal system, such as flexibility, may be extremely important. All constrictors (booids and colubroids) had relatively high numbers of body vertebrae. This may result from selection for increased flexibility in constrictors. Flexibility could also be enhanced by having shorter muscle segments because of the relationship between muscle tissue length and tension. When muscle tissue is stretched beyond its resting length, tension is generated passively (Aidley, '78). During lateral flexion, the muscle segments on the convex side of the body are stretched. Because tendons stretch relatively little, primarily contractile tissue must accommodate the increase in length. Among most species of snakes differences in the length of the muscle segments are just the result of different lengths of tendon (Table 2). Therefore, for lateral flexions with equal radii of curvature, longer muscle segments on the convex side will be stretched more than shorter muscle segments would. Because these longer segments would passively generate more tension, lateral flexion would be resisted and over-

all flexibility would be less. For two muscle segments of equal length but different proportions of contractile tissue, the segment with more contractile tissue would passively generate less tension and hence increase flexibility.

Low relative segmental length of the spinalis may thus be a good indicator of flexibility. *Stilosoma* had a very small relative length of the spinalis (4.9%) and Wright and Wright ('57) mentioned its remarkable powers of constriction. Some hydrophiids are flexible enough to tie themselves in a knot to assist shedding their skins (Voris, personal communication). Certain burrowers and aquatic snakes therefore could be "preadapted" for constriction. Interestingly, one commonly offered speculation on the evolution of snakes is that they arose from a highly fossorial stock of lizards (Bellairs, '70). Booids are considered to be among the more primitive snakes, and comparative behavioral observations of constricting in these snakes suggest a rather early origin of constriction behavior (Greene and Burghardt, '78).

In addition to possible effects on the efficiency of constriction, the morphology of the spinalis and other axial muscles may affect the efficiency of locomotion of snakes. Specializations in habitat are presumed to be closely correlated with specializations in modes of locomotion. In the confined space of burrows, snakes are most likely heavily reliant on rectilinear and concertina locomotion. Presumably snakes in water can only generate propulsive thrust by propagating traveling waves; therefore, one would expect fully aquatic snakes to be highly specialized for lateral undulatory locomotion. The three modes of locomotion most likely to be used by arboreal snakes are rectilinear, concertina, and lateral undulation. Rectilinear locomotion requires the use of the costocutaneous muscles (Lissman, '50) and certain slender arboreal snakes (e.g., *Thelotornis* and *Imantodes*) show a marked reduction in these muscles similar to that found in some of the highly specialized Hydrophiidae (Voris and Jayne, '76). Many slender-bodied arboreal snakes are quite active and move quickly; therefore, the relatively slow concertina mode of locomotion would appear to be used minimally by these snakes. Thus, aquatic snakes and a select group of active, slender-bodied arboreal snakes are both likely to be highly specialized for lateral undulatory locomotion.

A seeming paradox exists as both aquatic and some arboreal snakes are specialized for the same type of locomotion but the morpholo-

gies of their axial muscles are radically different. Two main considerations may explain the tendinous elongation of arboreal forms versus the rather short tendons of aquatic forms. First, in contrast to aquatic snakes, arboreal snakes have large proportions of their bodies unsupported by the substrate as they move among branches. The longer muscle segments should increase the lever arm through which the muscle acts, thereby conveying a mechanical advantage. This mechanical advantage may enhance the efficiency of lateral undulation as well as the ability to support the weight of the snake. Because the elongation is accomplished by increasing the lengths of relatively lightweight tendon, minimal weight is added to the snake. Weight reduction without a loss in locomotor efficiency should be especially important to arboreal snakes as they move about supported only by a few small twigs. Similarly, Ruben ('77) suggested that such weight loss may convey an advantage to the slender, fast-moving terrestrial snakes such as *Masticophis*.

Second, the different lengths of muscle segments may indicate that different optimal passive properties of the locomotor system may be required for efficient lateral undulations in water versus those waves being propagated against a few points of lateral contact. Recent authors (Grillner and Kashin, '76; Blight, '77) have emphasized that during swimming by lateral undulations, it is the combination of the muscle contraction and the passive properties of the system that will determine the waveform. Grillner and Kashin ('76) studied the lateral undulatory swimming of the eel and they found a significant phase lag between the wave of muscle contraction and the mechanical wave traveling down the body. The discussed above effect of different lengths of muscle segments on the passively generated tensions on the convex side of the body may prove crucial in understanding the apparently dichotomous requirements for the morphology of aquatic versus arboreal (and terrestrial) lateral undulators. Perhaps different phase lags are present in these two groups and each is more efficient in its respective habitat. In addition, if the force of muscle contraction is combined with the passive tension of the convex side of waves in arboreal snakes, more propulsive thrust may be generated from a relatively small amount of contractile tissue. Hence arboreal snakes may possess yet another mechanical advantage that enables them to preserve locomotor efficiency while conserving weight.

Without a thorough knowledge of such properties as "stiffness," one is unlikely to predict adequately the mechanism of wave propagation (Blight, '77). Thus, future studies combining electromyography with quantification of passive properties of the system should prove to be most enlightening.

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