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, boids, 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 vipersid 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 vertebræ in the vipersid 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 vertebræ 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 boid. 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 vipherina* (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.
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*

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<th>Habitat, constriction</th>
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<td>Thelotornis k. kirlandi (USNM 167090)</td>
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<td>ELAPIDAE</td>
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<td>Agkistrodon piscivorus (USNM 212252)</td>
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<td>4</td>
<td>14</td>
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</tr>
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</table>

Table 2 continued on next page.
TABLE 2. Variation in segments of the spinalis for midbody dissections of 107 specimens from 94 species\(^1\) (continued)

<table>
<thead>
<tr>
<th>Species (museum number)</th>
<th>Number of vertebrae</th>
<th>Body (=BV)</th>
<th>Post. tendon</th>
<th>Muscle tissue</th>
<th>Ant. tendon</th>
<th>Spinalis length (%BV)</th>
<th>Habitat, constrictor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bothrops atrox (FMNH 2617)</td>
<td>194</td>
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<td>3</td>
<td>7</td>
<td>19</td>
<td>29(14.9)</td>
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</tr>
<tr>
<td>Bothrops bilineatus (FMNH 197875)</td>
<td>198</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>16</td>
<td>24(12.1)</td>
<td>ab</td>
</tr>
<tr>
<td>Crotaulus adamanus (USNM 212253)</td>
<td>172</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>14</td>
<td>21(12.2)</td>
<td>tr</td>
</tr>
<tr>
<td>Crotaulus cerastes (USNM 212254)</td>
<td>175</td>
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<td>3</td>
<td>4</td>
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<td>2</td>
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<tr>
<td>Lachesis muta (FMNH 59181)</td>
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<td>2</td>
<td>5</td>
<td>15</td>
<td>22(9.9)</td>
<td>tr</td>
</tr>
<tr>
<td>Trimeresurus flavoviridis (FMNH 48787)</td>
<td>224</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>27</td>
<td>35(15.6)</td>
<td>ab</td>
</tr>
</tbody>
</table>

\(^1\)Species are arranged alphabetically within families and subfamilies. (\(\dag\)) 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.

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 boid families (Acrochordidae, Loxocemidae, Xenopeltidae, Anilidae, Boiidae, and Tropidophidae) 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 Rohl, 69). The segments of the spinalis in Boiidae 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 spinals for families**

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of vertebrae</th>
<th>Body vertebral Origin</th>
<th>Post. tendon</th>
<th>Muscle tissue</th>
<th>Ant. tendon</th>
<th>Spinalis length</th>
<th>Spinalis length</th>
<th>Body vertebral</th>
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<td>13</td>
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<td>4-8</td>
<td>2.7</td>
<td>7-11</td>
<td>16-16</td>
<td>8.2-4.4</td>
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<td>0.67</td>
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<td>1.40</td>
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<td>b</td>
<td>c</td>
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<td>range 117-272</td>
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<td>2-7</td>
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<td>b</td>
<td>a</td>
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</tbody>
</table>

1 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 spinals 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 spinals. 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 spinals (r = 0.187, P < 0.05). Even within genera there was no correlation. Eight congeneric species pairs (*Python, Midon, Bungurus, Dendroaspis, Laticauda, Hydrophis, Bitis, and Crotalus*) with varying numbers of vertebrae were examined. In four of the genera (*Bungurus, Dendroaspis, Laticauda, and Hydrophis*) the species with more body vertebrae had shorter segmental lengths of the spinals, 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 differences between habitat types occurred in segmental lengths of the spinals 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 spinals 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 spinals (x̄ = 15) which resulted in a small relative length of the spinals (x̄ = 7.9%). Among colubroids, burrowers also averaged slightly more vertebrae of origin (x̄ = 2.5) than arboreal (x̄ = 1.8) and terrestrial species (x̄ = 1.9).

Aquatic and arboreal colubroid species showed nearly opposite trends in segmental length (x̄ = 13 vs 33) and numbers of body vertebrae (x̄ = 162 vs 212). Aquatic colubroids were tied with burrowers for the greatest average number of vertebrae of origin (x̄ = 2.5). Arboreal colubroids had the greatest average
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 spinales 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 Athelis 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 spinales (41), which gave it the greatest relative length of the spinales (28.7%) of any species examined. Interestingly, Thelotornis and Imantodes also had a marked reduction 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 spinales 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 spinales ($\bar{x} = 9.0\%$ vs 13.1\%). Most terrestrial constrictors had a relative length of the spinales 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)

<table>
<thead>
<tr>
<th>Colubroid habitat type</th>
<th>Number of vertebrae</th>
<th>Spinalis origin</th>
<th>Muscle tissue</th>
<th>Ant. tendon origin</th>
<th>Spinalis tendon length</th>
<th>(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burrowing (n = 13)</td>
<td>× 196</td>
<td>2.5</td>
<td>1.6</td>
<td>3.8</td>
<td>9.5</td>
<td>15</td>
</tr>
<tr>
<td>range 146-268</td>
<td>SD 38.9</td>
<td>0.52</td>
<td>0.51</td>
<td>1.17</td>
<td>2.22</td>
<td>3.1</td>
</tr>
<tr>
<td>Aquatic (n = 14)</td>
<td>× 162</td>
<td>b,c</td>
<td>a</td>
<td>n</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td>range 117-234</td>
<td>SD 31.7</td>
<td>0.52</td>
<td>0.77</td>
<td>1.03</td>
<td>1.70</td>
<td>2.8</td>
</tr>
<tr>
<td>Arboreal (n = 13)</td>
<td>× 212</td>
<td>1.8</td>
<td>2.3</td>
<td>4.8</td>
<td>25.7</td>
<td>33</td>
</tr>
<tr>
<td>range 156-268</td>
<td>SD 31.4</td>
<td>0.44</td>
<td>0.63</td>
<td>1.09</td>
<td>6.81</td>
<td>6.5</td>
</tr>
<tr>
<td>Terrestrial nonconstrictor (n = 27)</td>
<td>× 170</td>
<td>1.9</td>
<td>2.3</td>
<td>4.5</td>
<td>14.5</td>
<td>21</td>
</tr>
<tr>
<td>range 118-242</td>
<td>SD 37.4</td>
<td>0.49</td>
<td>0.76</td>
<td>1.12</td>
<td>3.38</td>
<td>3.6</td>
</tr>
<tr>
<td>Terrestrial constrictor (n = 9)</td>
<td>× 225</td>
<td>2.0</td>
<td>2.3</td>
<td>4.0</td>
<td>14.2</td>
<td>21</td>
</tr>
<tr>
<td>range 175-272</td>
<td>SD 35.9</td>
<td>0.50</td>
<td>0.50</td>
<td>1.00</td>
<td>3.19</td>
<td>3.94</td>
</tr>
</tbody>
</table>

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 vipers 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 5.4% 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 postzygophyses of the same vertebra. The medial tendons of the M. longissimus dorsi distinctly extended to the neural spine in all booids.

In all vipers 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, Imanodes, Masticophis, Nerodia, Opheodrys, Oxylulus, Pituophis, Regina, Spilotes, and Stiliosoma. Cerberus, Chionactis, Erpeton, Heterodon, Pseudaspis, Sphalerophis, 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, ’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 Pitoinops melanolueus (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. semispinalis-spinalis may help in solving a phylogenetic problem. Smith (’26) placed Laticauda in its own subfamily within the Hydrophidae. 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 Hydrophidae. 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 variences in segmental length were also the most homogeneous for habits and habitat. All of the Boidae are constrictors and all of the Hydrophidae 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 close connections among the axial muscles have continued to discourage more extensive studies.

The proportionate elongation of the tendinous elements of segments of the M. semispinalis-spinalis correlates well with relative increases in the lengths of tendons of the M. longissimus dorsi and the M. ilio-costalis (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., Ophedrys) were considered terrestrial. Crotaulus 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 colubrid 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 opisthognathids.

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 colubrid) 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 colubrid 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 colubrid 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 colubrid constrictors (19.0%) averaged slightly less than nonconstrictors (21.4%) in proportional muscle tissue length. Among colubroid families, the relatively heavy-bodied vipers had the greatest average absolute length of contractile tissue (5.7 vertebræ) per segment of the spinalis as well as a rather large proportional length of contractile tissue per muscle segment (27.1%). Since vipers 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 different 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, provided 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. *Stilodora* 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 morphologies 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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LITERATURE CITED


