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The Costocutaneous Muscles in Some Sea Snakes (Reptilia, Serpentes)

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ABSTRACT—Data on the size, origin and insertion of the superior and inferior costocutaneous muscles are presented in 11 terrestrial, two amphibious and 11 completely aquatic species of snakes. The aquatic species differ in these muscles from the terrestrial species. Either or both the superior and inferior muscles may be inserted more dorsally. Of the species with more dorsal insertions for the inferior costocutaneous, most showed an origin proximal to the cartilaginous tip of the rib. Some of the fully aquatic forms showed a reduction in the size of the inferior costocutaneous.

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INTRODUCTION

The costocutaneous muscle system of snakes was first surveyed by Buffa in 1904. He described both the size and position of the costocutaneous muscles in relation to the ribs (origin) and scalation (insertions). His sample consisted of 23 species representing 7 families. Two species, *Laticauda colubrina* and *Pelamis platurus*, represented the Hydrophiidae. In general, the data he collected indicate *Laticauda colubrina* to be rather similar to the advanced terrestrial snakes he examined, and *Pelamis platurus* to be quite distinct from all other forms which he considered. Although our data have been collected somewhat differently, our results for these species correspond closely with his findings. Lissmann (1950), in his work on rectilinear locomotion in *Boa occidentalis*, has demonstrated the role of the costocutaneous muscles in rectilinear locomotion.

The purpose of this paper is to describe a part of the costocutaneous muscular system in several species of sea snakes and to relate these findings to certain other aspects of sea snake morphology and their marine existence.

MATERIAL AND METHODS

Dissections of the costocutaneous muscle system (Buffa, 1904 Mm. costocutanei superiori and Mm. costocutanei inferiori; Mosauer, 1935 Mm. costocutanei superiores and Mm. costocutanei inferiores) were first performed on several species of terrestrial snakes in order to become familiar with the basic arrangement and the range of variation in these muscles (Table 1). Nineteen specimens of sea snakes representing 12 species and 8 genera, were then dissected (Table 1).

Large adults were dissected in order to minimize the variable of age and to facilitate dissection (Table 1). Although the sample sizes are small, the available data indicate that neither sex nor geography contribute any noticeable variation in the muscles studied (e.g. *Hydrophis klossi* and *Pelamis platurus*).

For both the superior and inferior costocutaneous muscles, the most anterior incision of the dissection was made starting at a point 75% of the total ventral scale count from the neck,

TABLE 1. Data on the costocutaneous muscles of 31 specimens representing 20 genera of snakes.

Species	Museum[3] number	Sex	S-V Length (cm.)	Scale rows at incision	Insertion location In scale rows from ventral scale[4] Sup. C-Cutaneous		Inf. C-Cutaneous		Muscle Mass[1]		Origin[2] of inf. C-Cut.
					Dorsal	Ventral	Dorsal	Ventral	S.C.C.	I.C.C.	
Constrictor c. imperator	43732	♀	135	52	8(.31)	3(.12)	3(.12)	0	3	3	1
Dromicus chamissonis	31610	♂	64	15	3(.40)	0	0	0	3	3	1
Elaphe o. obsoleta	8945	♂	124	25	5(.40)	1(.08)	0	0	3	3	1
Natrix s. sipedon	37983	♀	61.5	21	3(.29)	1(.10)	0	0	3	3	1
Pituophis melanoleucus mugitus	6143	♀	131	24	4(.33)	2(.17)	1(.08)	0	3	3	1
Spalerosophis d. diadema	83200	♂	136	22	3(.27)	2(.18)	0	0	3–	3–	1
Thamnophis radix radix	22612	♀	56	17	1(.12)	0	0	0	3	3	1
Zaocys dhumnades oshimai	120831	♂	142.5	14	1(.14)	0	0	0	3	3	1
Acrochordus granulatus	93592	♂	56.5	90	37(.82)	29(.64)	27(.60)	20(.44)	3	3	1
Crotalus v. viridis	1892	♂	77	23	4(.35)	0	0	0	3	3	1
Naja naja	165085	♀	108	16	3(.38)	0	0	0	3	3	1+
Pseudechis porphyriacus	11120	♂	124	17	1(.12)	0	0	0	3	3	1+
Laticauda colubrina (no data)	–	♂	82	23	6(.52)	4(.35)	1(.09)	0	3	3	1+
Laticauda colubrina (Formosa)	13818	♀	97	22	6(.54)	4(.36)	2(.18)	0	3	3	1
Laticauda colubrina (Solomon Ids.)	13817	♂	72	21	5(.48)	4(.38)	0	0	3	3	1

TABLE 1. Cont'd.

Laticauda semifasciata	120649	♂	75	21	6(.57)	4(.38)	2(.19)	0	3	3	1
Aipysurus eydouxi	93509	♂	65.5	15	3(.40)	3(.40)	1(.13)	0	3	3	1
Thalassophina viperina	93508	♀	101.5	44	10(.45)	9(.41)	5(.23)	0	2	1	2
Pelamis platurus (Panama)	154858	♂	53	44	11(.50)	8(.36)	6(.27)	0	2–	1	1
Pelamis platurus (Panama)	154861	♂	46	47	11(.47)	8(.34)	6(.26)	0	2	1	1
Pelamis platurus (Panama)	154879	♀	46	52	11(.42)	8(.31)	6(.23)	0	2–	1	1
Enhydrina schistosa	79989	♂	78	54	13(.48)	10(.37)	5(.19)	0	3	3–	2
Kerilia jerdoni	133059	♀	65.5	23	6(.52)	4(.35)	0	0	2+	1	1
Lapemis hardwickii (N. Borneo)	133065	♀	51	30	9(.60)	0	3(.20)	1	3	1	1
Lapemis hardwickii (N. Borneo)	141146	♀	56	32			3(.19)	0	3	1+	2
Hydrophis brookii	164973	♂	64	39	11(.56)	8(.41)	4(.21)	0	3	2	2
Hydrophis cyanocinctus	141141	♀	135	41	10(.49)	8(.39)	3(.15)	0	3	3	2
Hydrophis fasciatus	142455	♀	104.5	54	13(.48)	8(.30)	6(.22)	0	3–	1+	2
Hydrophis klossi (N. Borneo)	141151	♀	98.5	34	10(.59)	7(.41)	3(.18)	0	3–	3–	2
Hydrophis klossi (N. Borneo)	141155	♀	95	34	9(.53)	7(.41)	3(.18)	0	3	3–	2
Hydrophis klossi (Malaya)	165003	♂	83.5	33	9(.55)	7(.42)	2(.12)	0	3	3	2

[1] 1 = Highly reduced, nearly transparent; 2 = Intermediate; 3 = Thick, well developed, opaque.
[2] 1 = Origin lies on the cartilaginous tip of the rib; 2 = Origin is proximal to the cartilaginous tip.
[3] All specimens are from the Field Museum of Natural History except *A. granulatus* (IMR 93592) and *A. eydouxi* (IMR 93509) which are from the Institute of Medical Research (Malaysia).
[4] Figures in parentheses equal $\frac{\text{number of scale rows at insertion}}{\text{1/2 number of total scale rows at point of dissection}}$

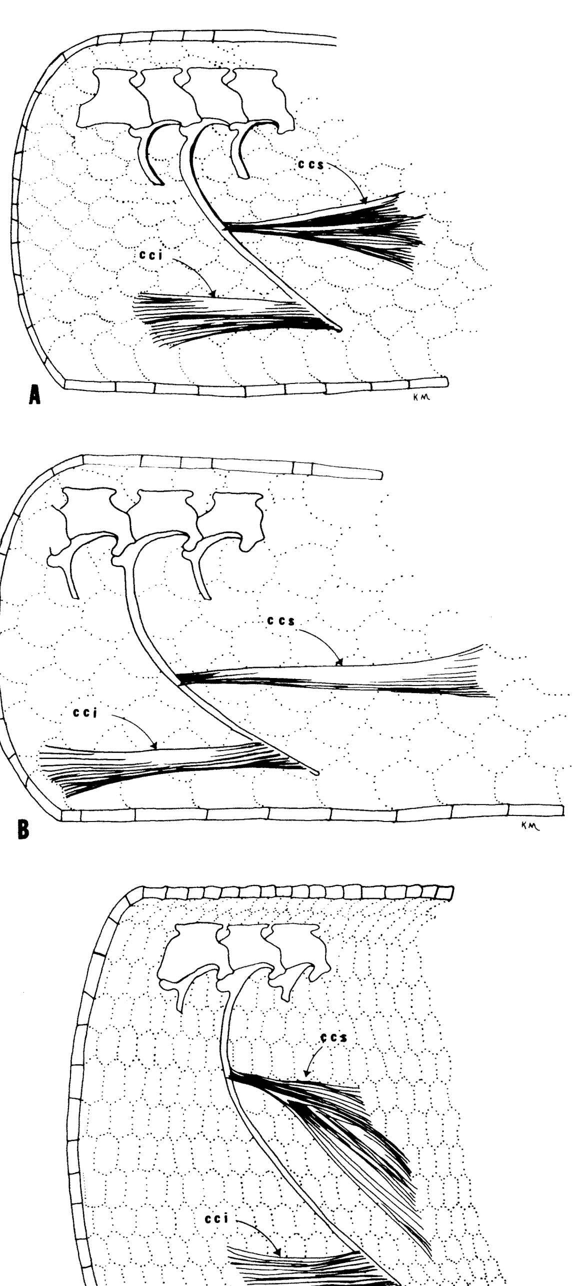

FIGURE 1. Lateral, cut-away views schematically showing the superior costocutaneous (ccs) and inferior costocutaneous (cci) muscles in: A. *Laticauda colubrina* (drawn from FMNH 13818); B. *Aipysurus eydouxi* (drawn from IMR 93509); C. *Lapemis hardwickii* (drawn from FMNH 133065).

continuing posteriorly over about ten vertebrae. For the superior costocutaneous muscle, the initial incision was made along the mid-dorsal line. Two more skin-deep incisions were then made perpendicular to and at the ends of the first incision, extending approximately two-thirds of the way down the side of the snake. The skin was peeled back while cutting through fascia and the tendons of the iliocostalis group. The superior costocutaneous muscles were visible ventral to the iliocostalis group and could be studied after removing some connective tissue. The initial incision to expose the inferior costocutaneous muscles was made along the mid-ventral line and deep enough to cut through cutaneous muscles present on the ventrals. Two skin-deep incisions were then made perpendicular to and at the ends of the original mid-ventral incision and extended dorsally to allow enough peeling of the skin to expose the inferior costocutaneous muscles.

The insertions of the costocutaneous muscles were determined by sliding a dull probe between the costocutaneous muscle and the skin until significant resistance was encountered. Thin pins were then inserted through the skin at both the most dorsal and most ventral portion of the insertions of the muscle being studied. The positions of the pins on the external surface of the skin were determined by counting the number of scale rows from the ventral scale to the protrusion of the pin. The most dorsal and most ventral points of insertion were recorded for both the superior and inferior costocutaneous muscles, as well as the total number of scale rows at the point of dissection (see Table 1). The position of the origin of the inferior costocutaneous muscle was also noted.

A subjective judgment was made on the relative bulk of the costocutaneous muscles (Table 1), but the state of preservation of the snakes affected the appearance of the muscles enough to jeopardize these estimates. Most notably, *Spalerosophis d. diadema* and *Thalassophina viperina* were difficult to assess in this regard.

RESULTS AND DISCUSSION

Data on the superior and inferior costocutaneous muscles for the 31 specimens examined are given in Table 1. The most dorsal aspect of the superior costocutaneous insertion ranges from the first (in *Pseudechis porphyriacus*) to the eighth (in *Constrictor c. imperator*) scale row among the terrestrial forms examined. In the sea snakes the range is from the third row in *Aipysurus eydouxi* to the thirteenth in *Enhydrina schistosa* and *Hydrophis fasciatus*. It is not surprising that the most dorsal insertions of the superior costocutaneous muscles, in terms of scale rows, occur in completely aquatic forms in which the ventral scales are highly reduced and the total number of scale rows is high. The marine *Acrochordus granulatus* has the most dorsal insertions of all forms examined and its scales are by far the smallest with 90 scale rows at the incision (Table 1). Among the sea snakes the percentage of the total number of rows to the dorsal aspects of this insertion ranges from 40 to 60%. In terrestrial species the range is from 12 to 40%. It should be noted that because the size (width) of scales around the body does vary in some species the percent values give only an approximate measure of the insertion position relative to the body cylinder.

The most ventral insertion of the superior costocutaneous muscles show a similar pattern of variation. In the terrestrial species the most ventral insertion ranges from the ventral scale to the fourth scale row. Among the sea snakes the range is from the ventral scale to the tenth row with all but one value at three or above (Table 1). It should be noted that the structure of the insertion itself varies. In some cases, the insertion is fan-like, spread over a relatively large area, making it difficult (particularly in *Lapemis hardwickii*) to determine the exact points of insertion (see Fig. 1C). *Aipysurus eydouxi* represented the other extreme with a very definite insertion entirely on one scale (Fig. 1B). It is the only fully aquatic species examined having a broad ventral with a deep central keel. *Laticauda colubrina* seemed somewhat intermediate in having three nearly separate bundles with distinct insertions (Fig. 1A).

The most ventral aspect of the insertion of the inferior costocutaneous muscles is either on the ventral scute or on the first scale row in all specimens examined with only one exception, *Acrochordus granulatus*. However, the position of the dorsal aspect of this insertion is variable and is generally most dorsal in the fully aquatic sea snakes, *Thalassophina viperina* and following in Table 1. In addition, it is in most of these latter species that the origin of this muscle is slightly proximal to its usual position on the cartilaginous tip of the rib. The superior costocutaneous muscles were generally similar in bulk among the species examined. However, several of the fully aquatic sea snakes showed a marked reduction in the size of the inferior costocutaneous (Table 1).

The modifications observed in the superior and inferior costocutaneous muscles of sea snakes are not unexpected. A 1:1:1 relationship of vertebrae, ribs and ventral scutes is apparently universal in advanced terrestrial snakes (Alexander and Gans, 1966:182; Voris, 1975). The occurrence of one superior and one inferior costocutaneous muscle per rib and ventral scute is also the case in all advanced terrestrial snakes examined so far (Buffa, 1904; Lissmann, 1950; Mosauer, 1935; Gasc, 1974; Table 1). The function of these muscles in conjunction with the ventral scutes is well documented in rectilinear locomotion (Gans, 1962; Lissmann, 1950). In *Laticauda*, the amphibious sea snakes, the ventral scales are wide, a 1:1:1:1 correspondence exists between vertebrae, ribs, costocutaneous muscles and ventral scutes, and terrestrial locomotion is efficient (Voris, 1975). The costocutaneous musculature in the *Laticauda* examined here is similar in most respects to the terrestrial forms examined. The fully aquatic *Aipysurus eydouxi* has a 1:1:1:1 correspondence of vertebrae, ribs, costocutaneous muscles and ventrals. The ventrals are wide but with a deep median keel and terrestrial locomotion is awkward. The deep central keel on the ventrals is apparently an adaptation to facilitate lateral flattening of the body which in turn increases the lateral force surface involved in aquatic locomotion (Hertel, 1963:177). The remaining sea snakes examined in this study are completely aquatic and show a reduction in ventral scale size and although a 1:1:1 relationship is retained between vertebrae, ribs, and costocutaneous muscles, the ventral scutes outnumber these elements (Voris, 1975). Scale rows also generally increase from anterior to posterior. These modifications in the scalation and the accompanying changes in the insertion positions of the costocutaneous muscles are strongly correlated with the completely marine existence. These forms, and *Acrochordus granulatus* do not (Voris, per. ob.) and presumably cannot perform rectilinear locomotion but the more lateral insertions of the muscles likely play a role in the primary type of locomotion utilized, namely lateral undulation. Although the muscles may not be directly involved in the undulation, one role may be to help maintain the laterally flattened body shape which improves the efficiency of lateral undulation in the aquatic medium (Hertel, 1963).

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