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# A comparison of the vibratory muscle, tail epaxial muscle, and body epaxial muscle respiratory activities in *Sistrurus miliarius*, *Coluber constrictor*, and *Natrix fasciata*

Craig Todd Kerins

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A COMPARISON OF THE VIBRATORY MUSCLE, TAIL  
EPAXIAL MUSCLE, AND BODY EPAXIAL MUSCLE  
RESPIRATORY ACTIVITIES IN SISTRURUS MILIARIUS,  
COLUBER CONSTRICTOR, AND NATRIX FASCIATA

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL  
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DEGREE OF MASTER OF ARTS

BY

CRAIG TODD KERINS  
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TABLE OF CONTENTS

Abstract. . . . .	1
Acknowledgements. . . . .	2
Introduction. . . . .	3
Methods and Materials . . . . .	5
Results . . . . .	8
Discussion. . . . .	10
Summary . . . . .	13
Literature Cited. . . . .	14
Tables. . . . .	16
Figures . . . . .	20
Vita. . . . .	26

## ABSTRACT

This study compares tail muscle respiratory activity to body epaxial muscle respiratory activity in three snake species to determine if snake species tail musculature is specialized for vibration. Sistrurus miliarius (the eastern pigmy rattlesnake) was compared to Coluber constrictor (the black racer), a tail vibrating snake, and to Natrix fasciata (the southern banded watersnake), a non-tail vibrator. Significant differences (at the five percent level of confidence) were found in three indices of respiratory activity ( $QO_2$ , succinic dehydrogenase and cytochrome oxidase activities) between the vibratory muscle and the body epaxial muscle in S. miliarius. No such differences were found in C. constrictor and N. fasciata. It was concluded that the vibratory muscle of S. miliarius is specialized for vibrating.

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## INTRODUCTION

The rattlesnake can be distinguished from other types of snakes by its rattling apparatus. Klauber (1956) describes the rattle as an apparatus consisting of varying numbers of three lobed keratin segments. The segments are arranged in a string by the loose interlocking of the segment lobes. The rattle is attached to the snake by the style, the modified terminal vertebra of the rattlesnake. The style is distally branched, forming a rigid core for the proximal rattle segments. A sound, unique to the rattlesnake, is produced when the segments are vibrated at great frequencies by the snake's posterior tail musculature (Klauber, 1956).

Rattlesnakes have historically received much attention, but most work has centered around the snakes' rattle: its function, its formation, and its operation. Until recently, little attention has been given to the vibratory muscles which motivate the rattling apparatus. According to Zimmermann and Pope (1948), six muscles, three on each side of the vertebral column, comprise the vibratory musculature. The vibratory muscles insert into the base of the style, the pivotal point of vibration. These muscles are capable of vibrating the rattlesnake tail at very high rates. From a study of seventeen species of rattlesnakes, Klauber (1956) reported rattling frequencies averaged 48 cycles per second, the frequencies seldom varying above a maximum of 60 cycles per second or below a minimum of 40 cycles per second. Schaefer,<sup>Department of Biology, Kent State</sup> (personal communication) has observed Crotalus horridus (the timber rattlesnake) to rattle for two hours when constantly disturbed.

Forbes (1967) used isolated tissue  $QO_2$ 's, succinic dehydrogenase activity, and cytochrome oxidase activity to compare the tail respiratory activities of a number of snakes. The vibratory muscle respiration of C. horridus was compared to two non-rattling snakes: Agkistrodon contortrix (the copperhead snake) a non-rattling tail vibrator belonging to the rattlesnake family, Crotalidae; and Thamnophis sirtalis (the garter snake), a non-vibrating member of the family Colubridae. Forbes (1967) found that the rattlesnake vibratory muscle was very specialized in

respiratory activity when compared to its own body epaxial muscle. This specialization was also present, but not as great in A. contortrix. Thamnophis sirtalis showed no tail muscle respiratory specialization.

The present investigation seeks to expand Forbes' study by determining if muscle respiratory specialization exists in another rattlesnake, and to determine if a tail vibrator of another family, Colubridae, possesses any degree of tail muscle specialization. Sistrurus miliarius (the pigmy rattlesnake) was chosen to be compared with a tail vibrator, Coluber constrictor (the black racer), and with a non-tail vibrator, Natrix fasciata (the southern banded water snake), both members of the family Colubridae. Rate of oxygen consumption and the activities of two respiratory enzymes (succinic dehydrogenase and cytochrome oxidase) of isolated muscle were used as indices of respiratory activity.



## METHODS AND MATERIALS

Ten snakes, five males and five females, of S. miliarius, and four snakes, one male and three females, of C. constrictor, were obtained from Tarpon Zoo, Incorporated. These animals (Table I) were collected within a thirty mile radius of Tarpon Springs, Florida. Nine snakes, all females, of N. fasciata were obtained from Tote-Em-In Zoo, in Wilmington, North Carolina (Table I). All animals were obtained in June, 1968 and used within a three week period after receipt.

The snakes were killed by severing the head from the body, skinned, and the tissue removed as quickly as possible. The body epaxial muscle samples were obtained from an approximate midpoint between the snake's head and its vent. In N. fasciata and C. constrictor, tail epaxial muscle samples were taken from the most distal tail musculature. In S. miliarius, the three terminal pairs of muscle comprising the vibratory musculature were removed. Muscle tissue was placed on foil-covered ice to prevent its deterioration.

Muscle samples used for oxygen consumption measurements were divided into 100 mg samples, except rattlesnake vibratory muscle samples which were 50 mg or less because of the very limited amount of vibratory muscle available. Samples were carefully teased until the pieces of tissue were  $\frac{1}{2}$  mm or smaller in thickness.

Muscle samples for the enzyme assays were weighed, and ten per cent homogenates in distilled water were made according to the method of Schneider and Potter (1943). Samples were homogenized with a Potter-Elvehjem glass on glass homogenizer for ten minutes. Tissue samples were kept in ice during homogenization to retard cell deterioration. The homogenates were diluted to 0.67 per cent by the addition of 0.03 M phosphate buffer (pH 7.4). A sample of each type of muscle tissue was placed in an oven at 65°C overnight and weighed to constant dry weight.

The standard Warburg technique (Umbreit, et al., 1967) was used to determine the rate of oxygen consumption. Each tissue sample was placed in a Warburg flask containing:

0.3 ml - 0.5 M sodium succinate in Krebs bicarbonate

1.1 ml - glass distilled water

0.4 ml -  $10^{-4}$  M cytochrome c in Krebs bicarbonate

0.2 ml - 20% KOH (placed in a greased center well)

2 X 2 cm fluted filter paper wick (placed in center well)

A constant temperature (29°C) water bath and shaker were employed. Measurements were taken at thirty minute intervals for three hours. Oxygen consumption ( $QO_2$ ) was expressed in microliters of oxygen consumed per hour per milligram dry weight of tissue.

Succinic dehydrogenase and cytochrome oxidase activities were measured spectrophotometrically. In the succinic dehydrogenase assay (Cooperstein and Lazarow, 1950) the optical densities (O.D.) of a blank cuvette and an experimental cuvette were measured at a wave length of 550 mu. Optical densities were recorded at thirty second intervals for three minutes. The blank cuvette contained:

0.1 ml - muscle homogenate

1.5 ml - glass distilled water

0.8 ml - cytochrome c ( $1.5 \times 10^{-4}$  M Plus 0.17 M phosphate buffer of pH 7.4 in a 7:4.2 ratio of buffer to cytochrome c)

0.3 ml - KCN ( $5 \times 10^{-4}$  M)

The experimental cuvette contained:

0.1 ml - muscle homogenate

1.2 ml - glass distilled water

0.8 ml - cytochrome c

0.3 ml - KCN

0.3 ml - 0.33 M sodium succinate

Approximately 0.9 mg of sodium hydrosulfite was added to the cuvettes to completely reduce the cytochrome c, and the optical density recorded.

Cytochrome oxidase was measured according to the method of Cooperstein and Lazarow (1951). In this technique the optical densities of an experimental cuvette were measured at 550 mu. Optical densities were recorded at thirty second intervals for three minutes. The experimental cuvette contained:

- 3.0 ml - reduced cytochrome c (prepared by shaking 0.15 ml sodium hydrosulfite solution, 30 mg/ml H<sub>2</sub>O, in 30 ml of 1.5 X 10<sup>-4</sup> M cytochrome c under aspiration)

0.04 ml - muscle homogenate

Approximately 0.4 mg of potassium ferricyanide were added to the cuvettes to completely oxidize the cytochrome c. Both enzyme activities were expressed as change in O.D. units X 10<sup>-4</sup> per minute per milligram dry weight of tissue.

Data were treated with square root transformation, because the assumption of homogeneity of error variance was violated. A t-test for matched samples was used to compare mean differences between tail and body epaxial muscles of the various snake species. Differences among the species were tested by a single factor analysis of variance for unequal sample sizes and the Newman-Keuls test (Winer, 1962).

Differences were considered significant at the five per cent level of confidence.

## RESULTS

In S. miliarius, respiratory activity ( $QO_2$ , succinic dehydrogenase and cytochrome oxidase activities) of vibratory muscle was significantly higher than that of body epaxial muscle (Table II). The  $QO_2$  of vibratory muscle ( $\bar{X} = 10.88$ ) was about five times greater than that of body epaxial muscle ( $\bar{X} = 2.39$ ). Similar differences between vibratory and body epaxial muscles existed in respiratory enzyme activities. Succinic dehydrogenase activity of vibratory muscle ( $\bar{X} = 138.08$ ) was over twice that of body epaxial muscle ( $\bar{X} = 53.83$ ); while cytochrome oxidase activity of vibratory muscle ( $\bar{X} = 299.34$ ) was almost four times as great as body epaxial muscle ( $\bar{X} = 67.28$ ).

There were no significant differences in respiratory activity between tail epaxial and body epaxial muscle in either C. constrictor or in N. fasciata (Tables III and IV).

In comparing the different snakes, S. miliarius vibratory muscle was found to be significantly higher in  $QO_2$  (Figure I), succinic dehydrogenase (Figure II) and cytochrome oxidase (Figure III) activities than all other muscles studied. None of the muscles of C. constrictor and N. fasciata differed significantly in respiratory activity. A statistically significant difference was found, however, in succinic dehydrogenase activity between S. miliarius body epaxial muscle and C. constrictor tail epaxial muscle. Since C. constrictor tail and body epaxial muscle were very similar in this respect, no biological significance was attached to this difference.

A meaningful expression of a species' tail muscle specialization is the ratio of its tail muscle respiratory activity to its body epaxial muscle respiratory activity. This ratio was used to compare relative tail muscle specialization in S. miliarius, C. constrictor, and N. fasciata, to tail muscle specialization in Forbes' (1967) snakes: C. horridus, A. contortrix, and T. sirtalis. The mean ratios of tail  $QO_2$  to body epaxial  $QO_2$  (Figure IV) in C. horridus ( $\bar{X}_{\text{ratio}} = 11.33$ ),

S. miliarius ( $\bar{X}_{\text{ratio}} = 4.55$ ), and A. contortrix ( $\bar{X}_{\text{ratio}} = 3.11$ ) differed significantly from each other and from the other snakes studied. The ratio of the tail to body succinic dehydrogenase activity in S. miliarius ( $\bar{X}_{\text{ratio}} = 2.87$ ) differed significantly from the same ratio in all other snakes studied (Figure V), its activity being higher than all snakes except C. horridus ( $\bar{X}_{\text{ratio}} = 9.19$ ) and A. contortrix ( $\bar{X}_{\text{ratio}} = 9.56$ ). The ratio of tail to body epaxial muscle succinic dehydrogenase activity did not differ significantly between C. horridus and A. contortrix. The ratio of tail to body epaxial muscle cytochrome oxidase activity (Figure VI) was significantly higher in C. horridus ( $\bar{X}_{\text{ratio}} = 29.94$ ) than in S. miliarius ( $\bar{X}_{\text{ratio}} = 7.98$ ) or in A. contortrix ( $\bar{X}_{\text{ratio}} = 6.79$ ). The ratio of tail to body epaxial cytochrome oxidase activity did not vary significantly between S. miliarius and A. contortrix, both being significantly higher than the same ratio in C. constrictor, N. fasciata, and T. sirtalis. Coluber constrictor, N. fasciata, and T. sirtalis did not vary significantly from one another in this respect.

## DISCUSSION

This study, and previous work by Forbes (1967) indicate that at least three members of the family Crotalidae: S. miliarius, C. horridus, and A. contortrix have a significantly higher respiratory activity in tail muscle tissue than in body epaxial muscle tissue. Respiratory activity ( $QO_2$ , succinic dehydrogenase activity, and cytochrome oxidase activity) was generally higher in S. miliarius than in the other snakes, but the ratios of each species' vibratory muscle respiratory activity to its body epaxial muscle activity indicate that the vibratory muscle is more highly specialized in C. horridus than in either S. miliarius or A. contortrix. The three members of the family Colubridae studied: T. sirtalis (Forbes, 1967), N. fasciata, and C. constrictor showed no specialization in respiratory activity of tail musculature. The high tail muscle respiratory activity of the members of the family Crotalidae studied indicates a muscle specialization that is not present in the family Colubridae.

The rattlesnake vibratory muscle can easily be distinguished from tail and body epaxial muscle by its reddish color, probably due to high concentrations of myoglobin in the muscle cells. Romanul (1964) found red muscle tissue to have very high concentrations of myoglobin and Needham (1926) found this tissue to have very dense capillary networks. Since the vibratory muscle is red, it is likely that this muscle also has these two characteristics, enabling it to have high respiratory activities. Although myoglobin concentration in the vibratory muscle has not been studied, Martin, <sup>Department of Zoology and Entomology, Univ. of Tenn.</sup> (personal communication) has shown vibratory muscle to be one of the more highly vascularized tissues of C. horridus. Furthermore, Pastore (1967) has shown vibratory muscle in C. horridus to have abundant, large mitochondria with highly branched cristae. Such mitochondria were not found in body epaxial muscles.

Two types of fibers, red and white, are found in all muscle tissue, red muscle having a higher proportion of red fibers, and white muscle having a higher proportion of white fibers (Needham, 1926). In characterizing these two muscle types, Romanul (1965) stated that red muscles, such as the heart and diaphragm, have slow but continuous contractions, while white

skeletal muscle is capable of very rapid contractions over relatively short periods of time. Red muscles have higher concentrations and activities of succinic dehydrogenase and cytochrome oxidase than do white muscle fibers, indicating that red muscles have the greater quantities of myoglobin. The oxidative capacity of muscle has been shown to be directly proportional to both respiratory enzyme concentrations and myoglobin concentrations (Romanul, 1965).

Red muscles are well adapted to continued contractions because they do not depend upon stored energy as do white muscles. Red muscles are capable of the efficient aerobic oxidation of glucose from the blood for energy, and do not have to acquire energy from the relatively inefficient anaerobic breakdown of stored substrate. Large quantities of myoglobin enable the red muscle tissue to concentrate the oxygen required to accept resultant electrons of this aerobic process (Lawrie, 1953).

Although the rattlesnake's vibratory muscle is an anatomically specialized skeletal muscle (Zimmermann and Pope, 1948) it has many of the specializations of red muscle. Oxygen consumption ( $QO_2$ ) of the vibratory muscle is much greater than other white skeletal muscle studied in this project, and higher than similarly expressed  $QO_2$ 's of other vertebrate white skeletal muscle: rat 2.3-3.1; dog 1.2; frog 0.18-0.24 and pigeon 2.1 (Spector, 1956). The oxygen consumption of the S. miliaris vibratory muscle ( $\bar{X}_{QO_2} = 10.88$ ) does compare with, and usually exceeds the  $QO_2$ 's of red muscle tissue from other vertebrates: rat diaphragm<sup>9</sup> 6.3; rat heart 3.8-10.4; dog heart 6.3, and six day old chicken heart 14.9 (Spector, 1956). This extraordinary specialization of the rattlesnake vibratory muscle allows the rattles to vibrate for extended periods of time.

Paradoxically, red muscles studied to date have functioned in slow and continuous contractions. However, rattlesnake vibratory muscle is capable of extremely rapid contractions, which can be approached in other vertebrates only by the hummingbird's wings (Klauber, 1956). Dawson and Romanul (1964) suggest that the speed of red muscle must by no means be

constant, leading to the speculation (Forbes, 1967) that the vibratory muscle's ability of rapid contraction is also related to its innervation. Kluffer (et al., 1953) working with Rana pipens (the leopard frog), and Hess (1963), working with T. sirtalis striated muscle, suggest that motor end plates are characteristic of twitch muscle cells, rather than end plate and en grappe terminations which innervate many of the fibers of slow skeletal muscles. Hess (1965) found that twitch muscle cells possessed extensive sarcoplasmic reticulum arranged in triads which are responsible for quickly conducting nerve impulses from the motor end plate to the cells' fibrils. These triads are reduced or absent in slow muscle cells, where almost all muscle fibers must presumably be innervated by a nerve fiber. Although the rattlesnake nerve supply has not been studied, Pastore (1967) showed that the vibratory muscle does contain a very highly developed sarcoplasmic reticulum, characteristic of motor end plate innervation. This type of innervation would give a red muscle the capability of very rapid contraction.

The vibratory muscle of rattlesnakes thus appears to be very specialized for its unique function of rapid and sustained contraction. Pastore (1967) has shown the C. horridus vibratory muscle to be structurally specialized, and Forbes (1967) has shown the C. horridus vibratory muscle to be functionally specialized in terms of respiratory activity. The present study with S. miliarius indicates that this rattlesnake has tail muscle specialization similar to other members studied of its family. Very rapid tail vibration frequencies (probably due to innervation) and the  $QO_2$ 's, and respiratory enzyme assays of C. horridus, A. contortrix, and S. miliarius tail musculature are indicative of red muscles capable of enduring extended periods of continued contraction.



## SUMMARY

1. The  $QO_2$ , succinic dehydrogenase activity and cytochrome oxidase activity of vibratory muscle differed significantly from ~~that~~ <sup>those</sup> of body epaxial muscle in S. miliarius.
2. The  $QO_2$ 's, succinic dehydrogenase activities, and cytochrome oxidase activities of tail epaxial muscle and body epaxial muscle did not differ significantly in C. constrictor, or in N. fasciata.
3. The S. miliarius vibratory muscle was found to have higher respiratory activities than any of the muscles studied in C. constrictor, N. fasciata, or T. sirtalis (Forbes, 1967).
4. Using the ratio of vibratory muscle activity to body epaxial muscle activity as an expression of tail muscle specialization, C. horridus (Forbes, 1967) was more highly specialized for vibrating than was S. miliarius or A. contortrix (Forbes, 1967).

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TABLE I  
SEX, BODY WEIGHT, AND BODY LENGTH

<u>ANIMAL NO.</u>	<u>SEX</u>	<u>WEIGHT</u>	<u>SNOUT/VENT LENGTH</u>	<u>TAIL LENGTH</u>	<u>TOTAL LENGTH</u>
<u>S. miliaris</u>					
1.	female	79.0 grams	513 mm	78 mm	591 mm
2.	female	42.5	427	50	477
3.	male	66.4	465	80	545
4.	male	68.1	442	71	513
5.	female	46.4	538	65	603
6.	female	9.9	314	43	357
7.	male	26.6	397	40	437
8.	male	18.5	377	42	419
9.	female	34.9	420	52	472
10.	male	10.4	340	36	376
<u>C. constrictor</u>					
1.	male	29.7	600	237	837
2.	female	29.7	585	123	708
3.	female	43.4	762	274	1036
4.	female	147.8	902	296	1198
<u>N. fasciata</u>					
1.	female	224.4	693	61	754
2.	female	211.5	714	221	935
3.	female	162.2	696	168	864
4.	female	193.4	652	214	866
5.	female	417.4	812	36	848
6.	female	195.4	646	51	697
7.	female	174.4	720	218	938
8.	female	188.1	712	226	938
9.	female	116.0	552	217	769

TABLE 2

Oxygen Consumption, SDHase Activity, and Cyt. Ox. Activity in *S. miliaris*

ANIMAL NO.	QO <sub>2</sub> *		SDHase Activity**		Cyt. Ox. Activity***	
	VIBRATORY	BODY EPAXIAL	TAIL EPAXIAL	BODY EPAXIAL	TAIL EPAXIAL	BODY EPAXIAL
1	4.10	1.84	-	-	-	-
2	-	-	76.78	48.85	645.83	41.67
3	12.69	3.78	85.83	18.07	196.87	145.83
4	4.93	1.90	128.02	56.25	87.25	50.49
5	-	-	-	-	-	-
6	12.90	2.15	-	-	-	-
7	19.70	2.28	-	-	-	-
8	-	-	179.30	51.57	278.92	82.84
9	-	-	220.49	94.41	278.84	15.55
10	10.97	2.43	-	-	-	-
MEAN	10.88	2.39	138.08	53.83	299.34	67.28
SD	5.28	0.63	54.95	24.34	171.64	44.77
	t <sub>observed</sub> = 4.85 significant at 5% level of confidence		t <sub>observed</sub> = 5.70 significant at 5% level of confidence		t <sub>observed</sub> = 3.24 significant at 5% level of confidence	

\* QO<sub>2</sub> =  $\mu\text{O}_2/\text{hr}/\text{mg}$  dry wt\*\* SDHase (succinic dehydrogenase) activity = O.D. units  $\times 10^{-4}/\text{min}/\text{mg}$  dry wt\*\*\* Cyt. ox. (cytochrome oxidase) activity = O.D. units  $\times 10^{-4}/\text{min}/\text{mg}$  dry wt

TABLE 3

Oxygen Consumption, SDHase Activity, and Cyt. Ox. Activity in C. constrictor

ANIMAL NO.	QO <sub>2</sub> *		SDHase Activity**		Cyt. Ox. Activity**	
	TAIL EPAXIAL	BODY EPAXIAL	TAIL EPAXIAL	BODY EPAXIAL	TAIL EPAXIAL	BODY EPAXIAL
1	3.27	2.64	9.26	11.48	126.95	223.96
2	0.78	0.84	30.79	31.86	111.26	69.91
3	1.32	2.73	5.18	14.24	48.14	142.17
4	1.74	1.45	30.79	31.86	127.11	110.40
MEAN	1.78	1.92	19.00	22.36	103.36	136.61
SD	0.92	0.79	11.88	8.58	32.57	57.07
	t <sub>observed</sub> = 1.43 not significant		t <sub>observed</sub> = 1.61 not significant		t <sub>observed</sub> = 0.83 not significant	

\* QO<sub>2</sub> =  $\mu\text{lO}_2/\text{hr}/\text{mg}$  dry wt\*\* Enzyme Activity = O.D. units  $\times 10^{-4}/\text{min}/\text{mg}$  dry wt

TABLE 4

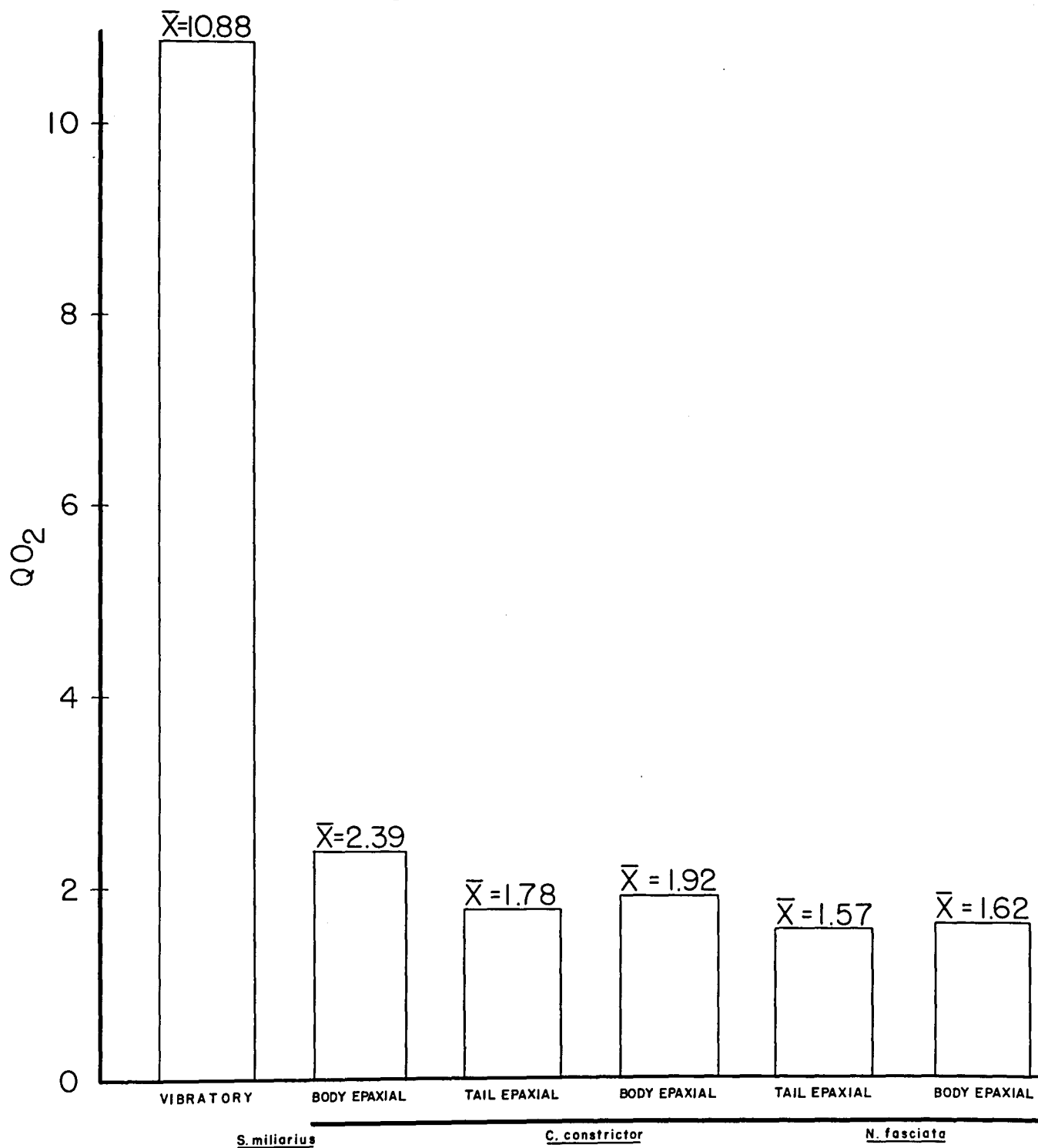
Oxygen Consumption, SDHase Activity, and Cyt. Ox. Activity of *N. fasciata*

ANIMAL NO.	QO <sub>2</sub> *		SDHase Activity**		Cyt. Ox. Activity**	
	TAIL EPAXIAL	BODY EPAXIAL	TAIL EPAXIAL	BODY EPAXIAL	TAIL EPAXIAL	BODY EPAXIAL
1	1.52	1.08	-	25.35	-	61.94
2	1.40	1.99	27.22	22.78	115.74	114.84
3	2.28	2.10	26.53	31.20	100.54	63.88
4	1.07	1.69	37.07	33.01	124.67	162.67
5	1.33	1.35	42.02	41.31	115.22	112.83
6	2.08	2.10	30.57	40.00	161.17	121.04
7	2.96	2.40	27.44	25.86	120.05	132.32
8	1.07	1.35	21.33	6.89	190.83	143.33
9	0.41	0.55	19.22	12.44	60.08	62.24
MEAN	1.57	1.62	28.92	26.54	123.53	108.34
SD	0.72	0.57	7.12	10.87	36.50	35.34
	t <sub>observed</sub> = 0.019 not significant		t <sub>observed</sub> = 1.17 not significant		t <sub>observed</sub> = 0.9 not significant	

\* QO<sub>2</sub> =  $\mu\text{lO}_2/\text{hr}/\text{mg}$  dry wt\*\* Enzyme Activity = O.D. units X 10<sup>-4</sup>/min/mg dry wt

FIGURE 1

Comparison of  $QO_2$ 's\* in S. miliaris, C. constrictor, and N. fasciata



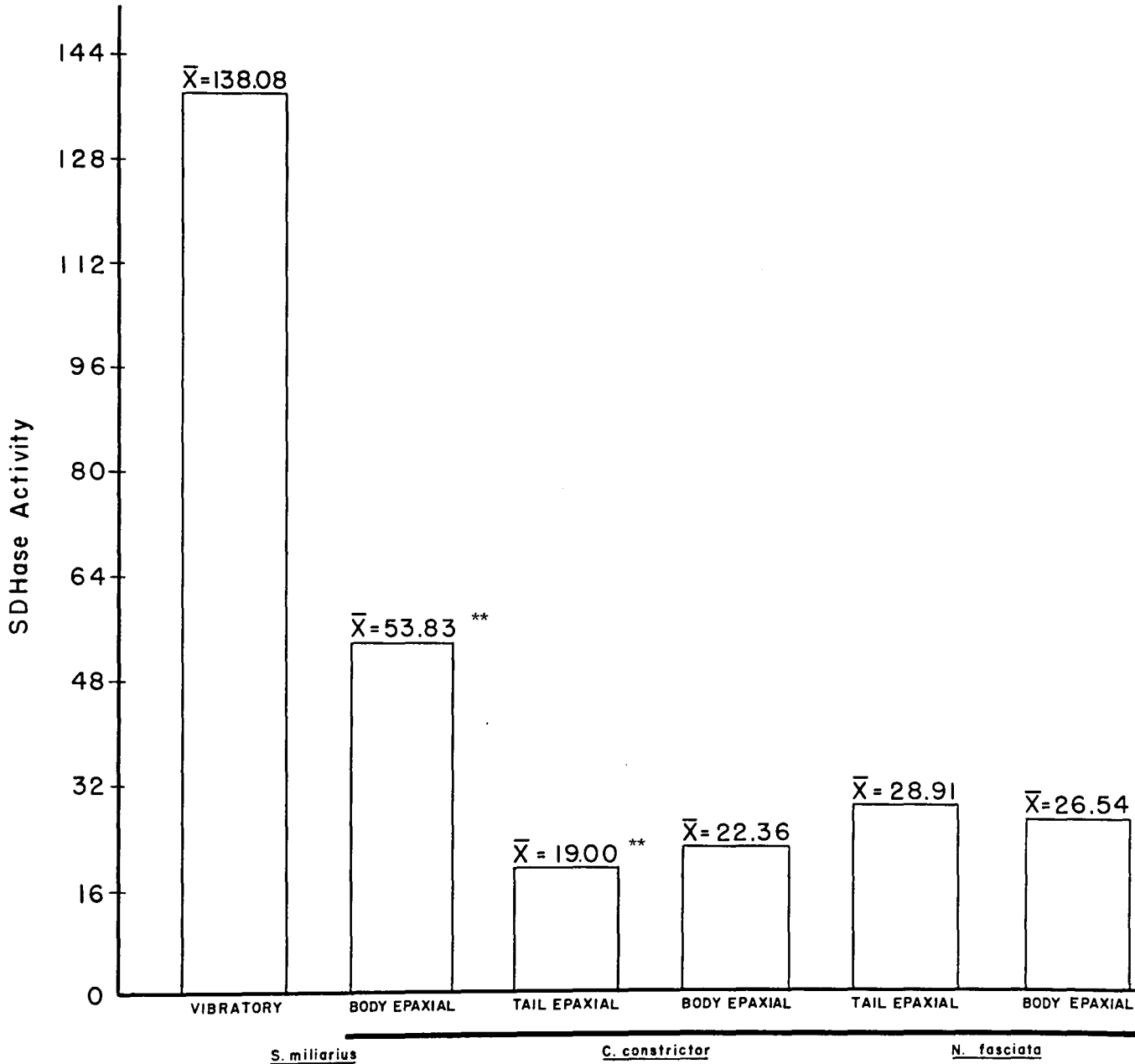
Those muscles joined by a common underline do not vary significantly. All others do.

\*  $QO_2$  =  $\mu l O_2 / hr / mg$  dry wt



FIGURE 2

Comparison of SDHase Activity\* in S. miliaris, C. constrictor, and S. miliaris



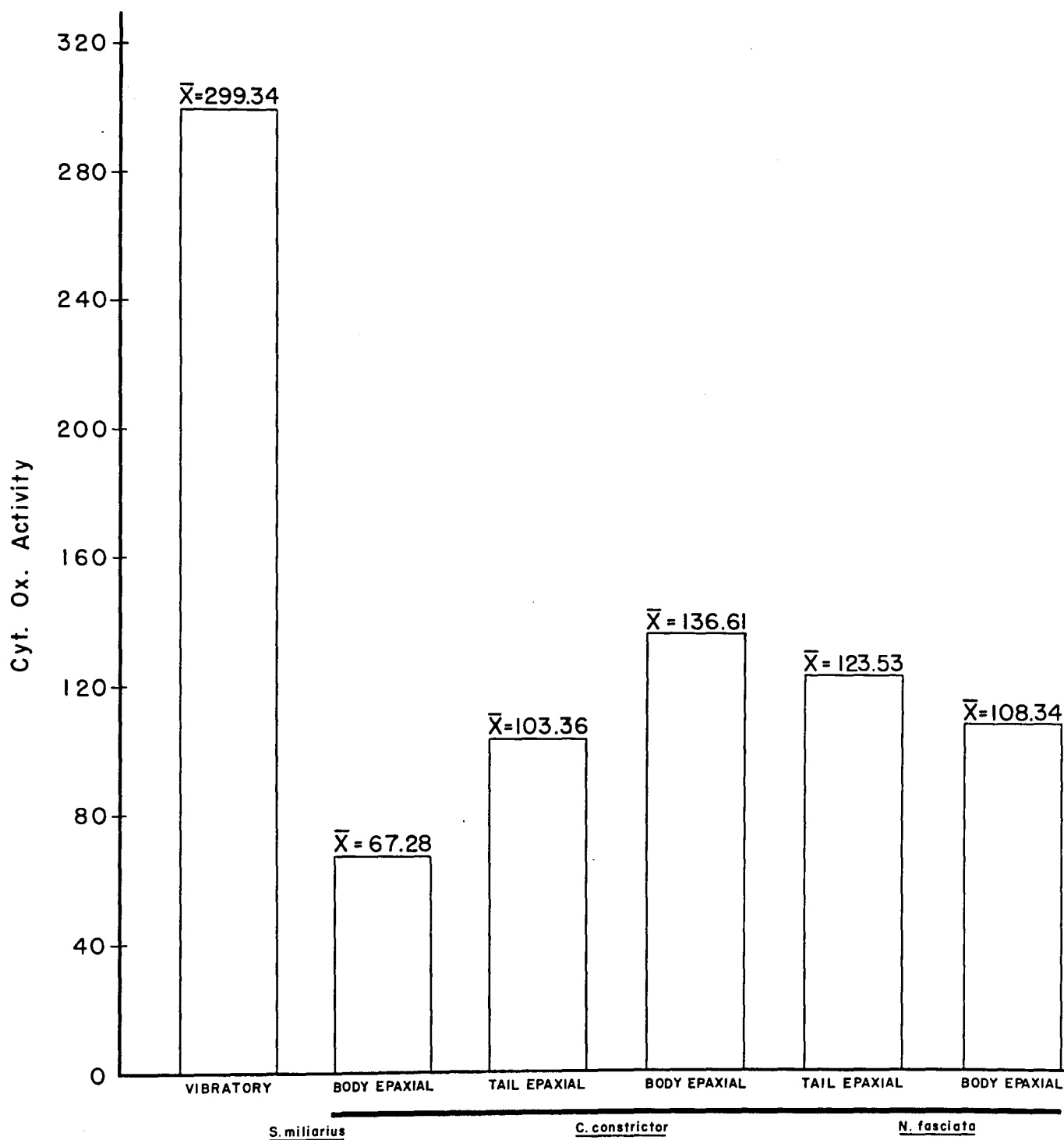
Those muscles joined by a single underline do not vary significantly. All other muscles do.

\* SDHase Activity = O.D. units  $\times 10^{-4}$ /min/mg dry wt

\*\* A significant difference was also found between S. miliaris body epaxial muscle and C. constrictor tail epaxial muscle.

FIGURE 3

Comparison of Cytochrome Oxidase Activity\* in S. miliaris, C. constrictor, and N. fasciata

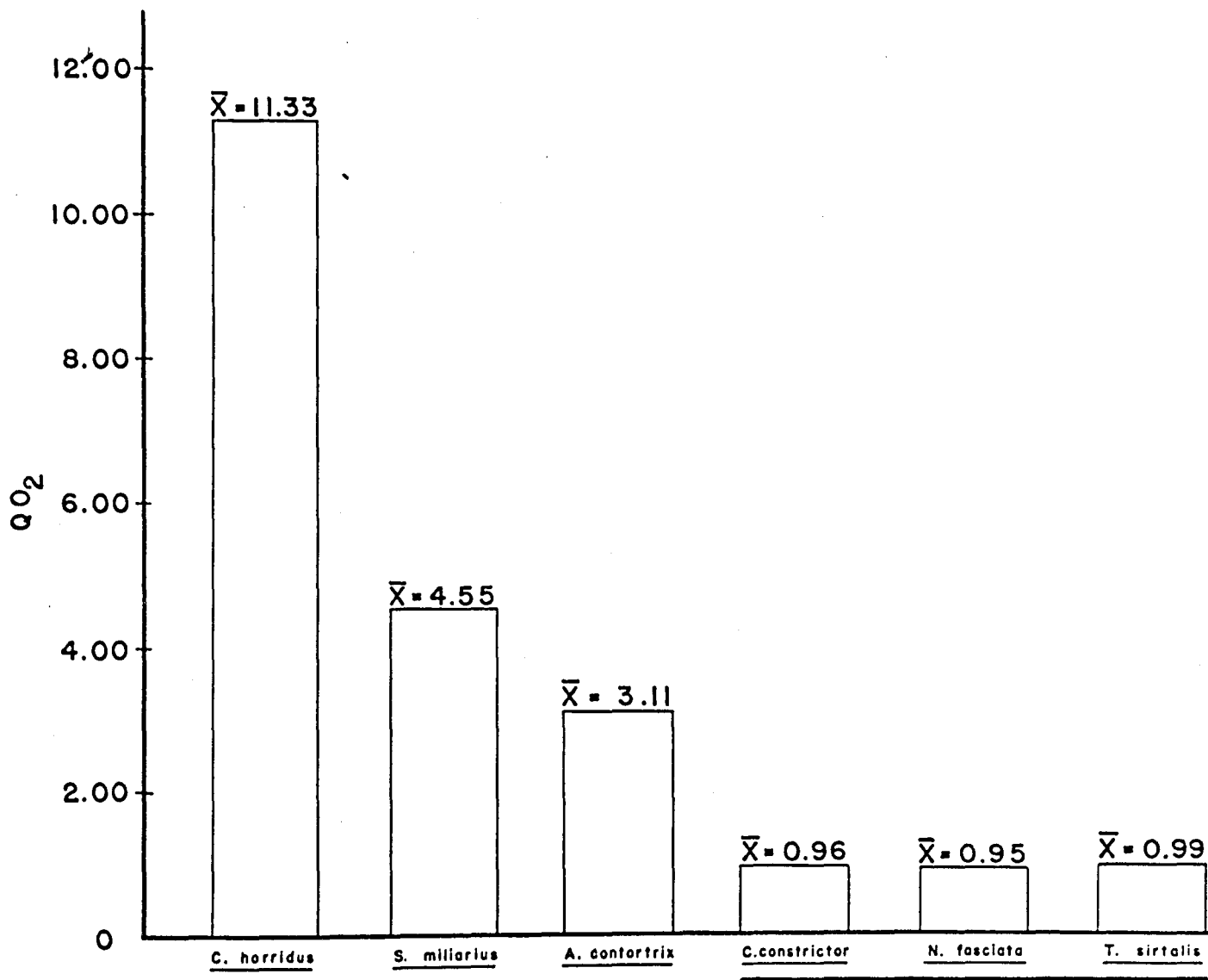


Those muscles joined by a common underline do not vary significantly. All other muscles do.

\* Cytochrome Oxidase Activity = O.D. units  $\times 10^{-4}$ /min/mg dry wt

FIGURE 4

Mean Ratios of Tail  $QO_2$ 's\* to Body Epaxial  $QO_2$ 's

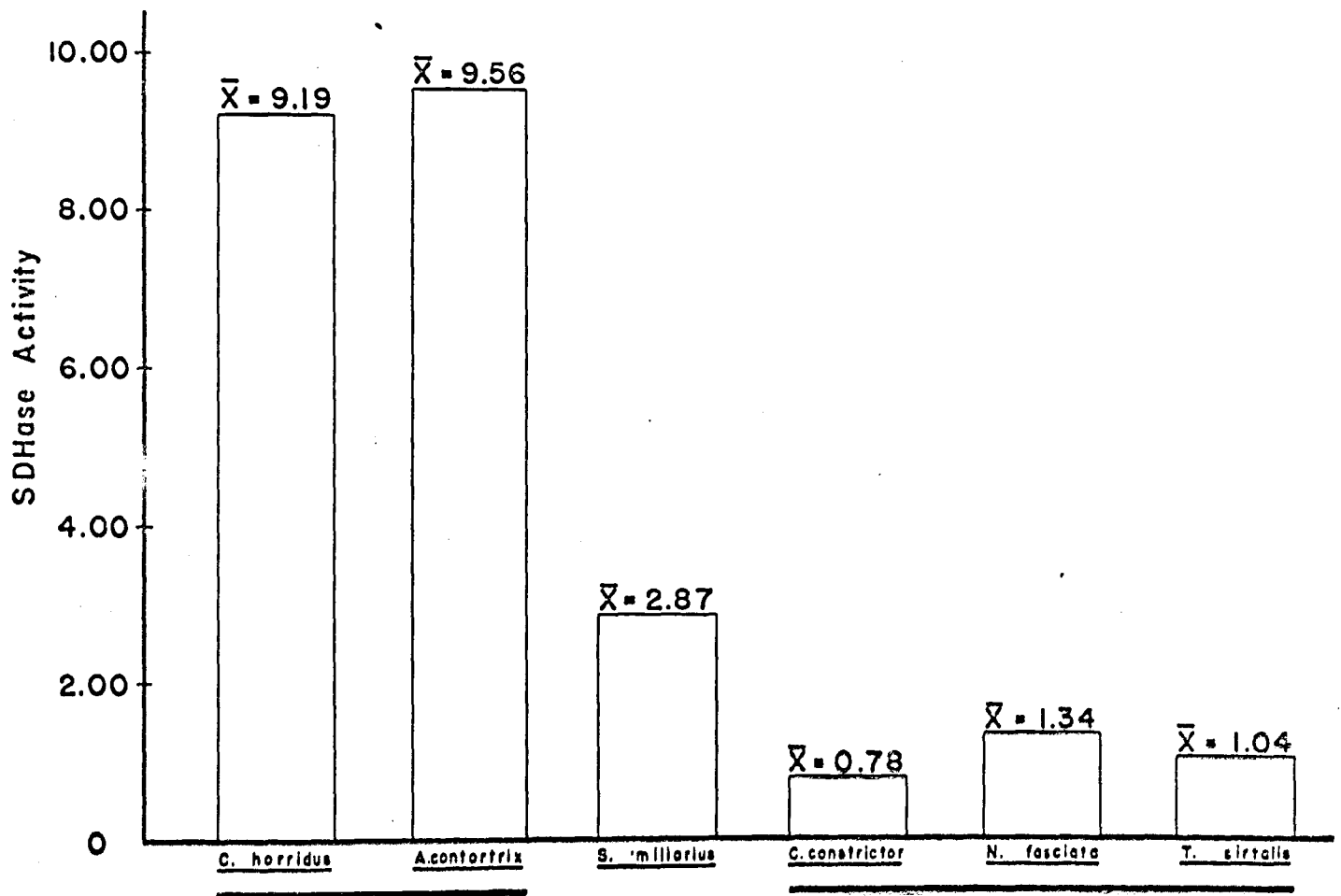


Those species joined by a common underline do not differ significantly. All other species do.

\*  $QO_2$  =  $\mu lO_2/hr/mg$  dry wt

FIGURE 5

Mean Ratios of Tail SDHase Activity\* to Body Epaxial SDHase Activity



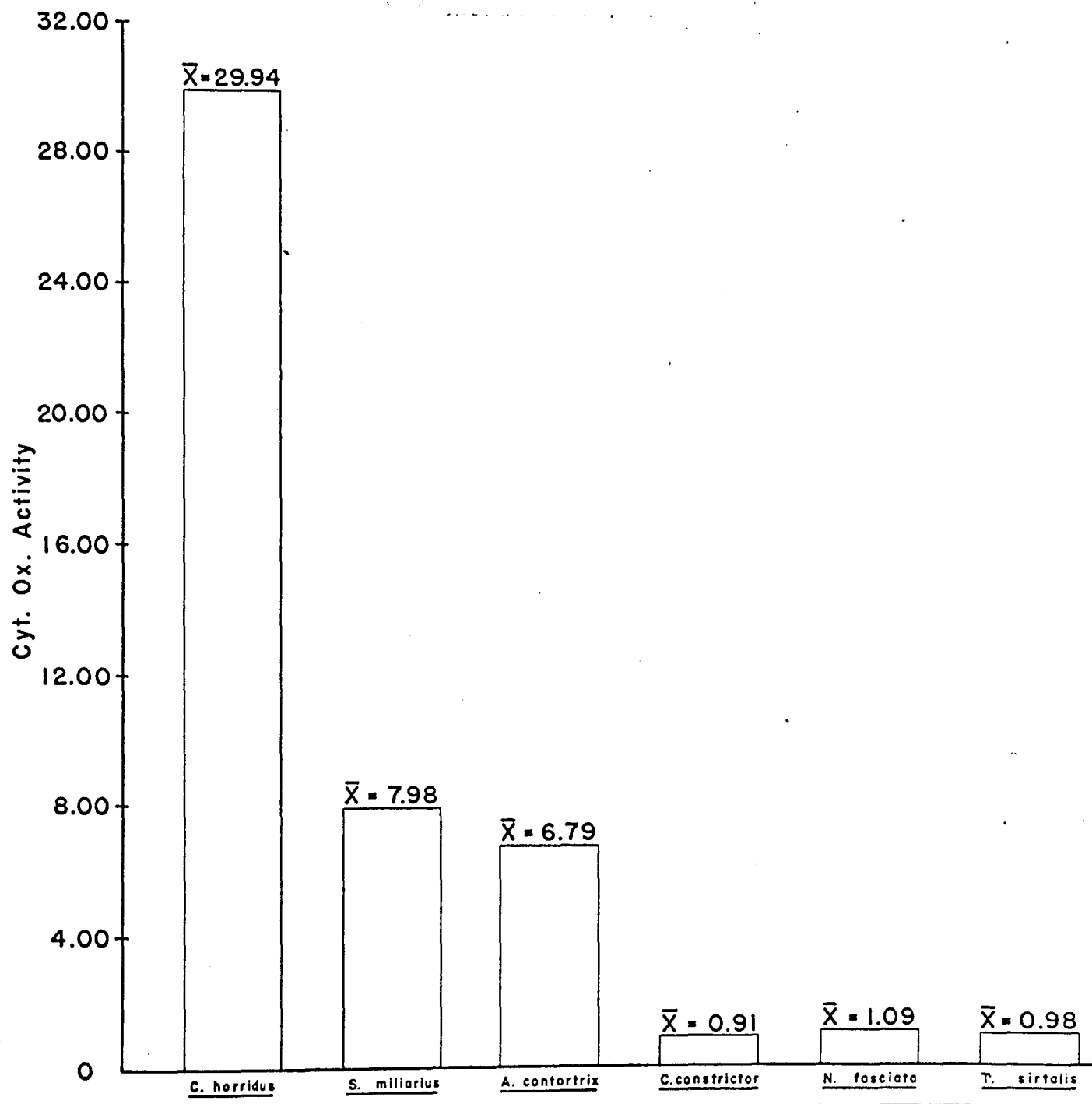
Those species joined by a common underline do not differ significantly. All other species do.

\* SDHase Activity = O.D. units  $\times 10^{-4}$ /min/mg dry wt

FIGURE 6

Mean Ratios of Tail Cyt. Ox. Activity\* to Body Epaxial

Cyt. Ox. Activity



Those species joined by a common line do not differ significantly from each other. All other species do.

\* Cyt. Ox. Act. = O.D. units  $\times 10^{-4}$  /min/mg dry wt

## VITA

Craig Todd Kerins was born September 23, 1945, in Pittsburgh, Pennsylvania. He received his primary education in the Baldwin Township Public School System and graduated from Shady Side Academy in 1963. After graduating from high school, he entered Dartmouth College in Hanover, New Hampshire, where he majored in English. He graduated from college in June, 1967 with an A.B. degree, and entered the University of Richmond as a special student in biology. He was accepted as a candidate for a Masters of Arts degree in February, 1968, after completing the equivalent of an undergraduate major in biology. While at the University of Richmond, he was elected to the Beta Beta Beta Honorary Biological Society. He received a Masters of Arts degree in biology from the University of Richmond in August, 1969. He will enter the Medical College of Virginia in September 1969 to work towards the degree of Doctor of Medicine.