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Vascularization of skeletal muscles in some *Caudata*

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Introduction

Studies on the vascularization of skeletal muscles in amphibians, though comparatively scarce, have demonstrated that in this class of animals the number of capillaries per 1 mm^2 muscle cross-sectional area is several times smaller than in homoiothermal animals. It has also been found that muscle vascularization in *Salientia* is better than in *Caudata*. Great differences have been found in the degree of vascularization of the particular skeletal muscles as well as in the thickness of the fibres and their number per unit cross area [SCHIEFFERDECKER, 1911; ZEPP, 1923; LINHARD, 1926; VOSS, 1932; STEUDEL, 1938; DAVISON, 1955; CZOPEK, 1963; SHOSHENKO, 1963; CZOPEK and CZOPEK, 1967].

The vascularization of skeletal muscles in amphibians shows a definite correlation with the intensity of vascularization of the skin, the lungs and the mouth. In species with abundant respiratory capillaries per 1 g of body mass (e.g., *Bufo calamita* Laur., *Hyla arborea* L.) the number of muscle capillaries is two or even three times more than in those whose respiratory surfaces are not so well supplied (e.g., *Salamandra salamandra* L.) [CZOPEK, 1963].

In the course of the last few years, close investigations of the vascularization of respiratory surfaces have been carried out in over 40 amphibian species, the results being collected by CZOPEK [1965]. On the other hand, the vascularization of skeletal muscles has been examined and compared with that of the respiratory surfaces in only 5 species of *Salientia* and 3 of *Caudata* [CZOPEK, 1963; CZOPEK and CZOPEK, 1967]. It seems necessary therefore, to continue the study of the vascularization of skeletal muscles in more of those *Caudata* in which the vascularization of respiratory surfaces has already been studied.

Material and methods

The material was collected and injected by H. SZARSKI in the U.S.A. in 1959. All the individuals were injected with Prussian blue through the truncus arteriosus. Out of the 11 specimens used in this work, 6 were studied in more detail. Here is a list of the species and of the weights of the 6 specimens:

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1. *Dicamptodon ensatus* (Eschscholz): 1 specimen, 76.00 g;
2. *Taricha granulosa* (Skilton): 2 specimens, 13.33, 13.63 g;
3. *Gyrinophilus porphyriticus* Green: 1 specimen, 14.98 g;
4. *Eurycea longicauda* Green: 2 specimens, 1.43, 3.85 g.

The first of these species belongs to the family *Ambystomidae*, the second to the *Salamandridae*, and the last two are representatives of the *Plethodontidae*. *D. ensatus* was caught in Saratoga Springs, Santa Cruz, California, the specimens of *T. granulosa* were found at Hoberg's, in the region Clear Lake, California. *G. porphyriticus* was purchased; it was caught near Murphy, North Carolina. The specimens of *E. longicauda* were injected in Geinesville, Florida, and supplied by Mr. CHARLES W. MYERS. Their catching place is unknown. The species under study will be discussed in the above systematic order. The fact that only one or two specimens of each species were studied may raise objections. The species being comparatively rare, however, it was very difficult to obtain more specimens. Besides, the studies mentioned in the Introduction have revealed that in individuals of one species having similar body sizes, the lengths of muscle capillaries per 1 g of body mass are very much the same [CZOPEK, 1963; CZOPEK and CZOPEK, 1967].

The injected animals were fixed in 10% formalin, and, after washing in water, kept in 70% ethyl alcohol. The studies were carried out on the muscles of the arm, forearm, thigh, lower leg and tail, the particular muscles not being separated on account of their small size and the difficulty in isolating each of them. Besides these, m. submaxillaris, m. rectus abdominalis and m. longissimus dorsi were also examined.

Vascularization of muscles and size of muscle fibres

D. ensatus

The poorest vascularization is found in the tail muscles, with an average of 101.8 capillaries/1 mm^2 muscle cross-section area. The vascularization is somewhat better in m. rectus abdominis (119.0 capillaries/mm^2) and in m. longissimus dorsi (127.4 capillaries/mm^2), and next in the muscles of the limbs (154.0 to 186.2 capillaries/mm^2). The most intense vascularization is found in m. submaxillaris (233.9 capillaries/mm^2). The diameters of muscle capillaries vary only very little: from 16.0 to 17.0 μ. The numbers of muscle fibres per mm^2 of muscle cross-section area follow the same order, the latter being 30 to 50% greater than the former (table I). The diameters of the muscle fibres are 3 to 4 times those of the capillaries, and range from 42.5 μ in m. submaxillaris to 64.5 μ in the caudal muscles.

The most favourable ratio of capillary to muscle fibre surface area was found in m. submaxillaris (1:3.63), the least favourable in the caudal muscle (1:5.64). In the remaining muscles the ratio ranges from 1:4.23 in the arm muscles to 1:5.00 in the lower leg muscles.

Table I. Dicamptodon ensatus Eschscholtz, ♀, 76.0 g

Muscle	Number of capillaries/ 1 mm² of cross-section area	Number of muscle fibres/ 1 mm² of cross-section area	Number of capillaries/ 100 fibres	Mean diameter of capillaries (μ)	Mean diameter of muscle fibres (μ)	Surface area of capillaries of 1 mm³ of muscle (mm²)	Surface area of muscle fibres of 1 mm³ of muscle (mm²)	Ratio of surface of capillaries to surface of muscle fibres
Mm. arm	186.2	230.0	80.9	16.5	56.5	9.64	40.80	1:4.23
Mm. forearm	172.7	221.3	78.0	16.0	59.7	8.68	41.49	1:4.78
Mm. thigh	173.8	241.0	72.1	16.7	51.5	9.11	38.99	1:4.28
Mm. lower leg	154.0	225.5	68.3	16.2	55.3	7.83	39.17	1:5.00
M. submaxillaris	233.9	320.1	73.1	16.0	42.5	11.75	42.73	1:3.63
M. rectus abdominis	119.0	152.3	78.1	16.7	64.3	6.24	30.76	1:4.93
M. longissimus dorsi	127.4	159.4	79.8	17.0	63.2	6.80	31.64	1:4.65
M. tail	101.8	149.5	68.1	16.8	64.5	5.37	30.29	1:5.64
Weighted mean	154.8	183.8	74.4	16.7	57.8	7.16	34.13	1:4.87

T.granulosa

The vascularization of muscles in this species is better than in the former. The poorest vascularization is also found in the tail muscles (116.7 to 119.5 capillaries/mm^2), and the most intense in m.submaxillaris (280.0 to 285.4 capillaries/mm^2). Unlike in *D.ensatus*, however, the vascularization of m.rectus abdominis is over one half higher than that of m.longissimus dorsi, and ranges from 175.7 to 180.3 capillaries/mm^2. In the muscles of the limbs the number of capillaries varies from 208.2 to 222.4/mm^2. The number of muscle fibres/mm^2 muscle cross-section area is over 60% greater than in *D.ensatus* and ranges from 245.2 (m.caudalis) to 552.0 (m.submaxillaris). The diameters of the capillaries do not exceed 13.0 μ, while those of the muscle fibres range from 35.0 μ in m.submaxillaris to 50.8 μ in the tail muscles.

The ratio of capillary to muscle fibre surface area is much less favourable than in the former species, ranging from 1:5.06 to 1:8.80 (table II).

G.porphyriticus

The lowest degree of vascularization is found in the tail muscles (98.9 capillaries/mm^2), next in the m.rectus abdominis (102.3 capillaries/mm^2) and in m.longissimus dorsi (104.5 capillaries/mm^2). The muscles of the limbs are vascularized nearly twice as intensely. Unlike in the two previous species, m.submaxillaris is vascularized somewhat less intensely than the muscles of the limbs (table III). The number of muscle fibres per mm^2 cross-section area, however, is the highest in this muscle (387.5 fibres). In the remaining muscles, the number of fibres varies from 203.8/mm^2 (tail muscles) to 273.2/mm^2 (muscles of the arm). The diameters of the capillaries never exceed 15.0 μ, while those of the muscle fibres vary from 36.3 μ (m.submaxillaris) to 54.4 μ (tail muscles).

The most favourable ratio of capillary to muscle fibre surface area is found in the muscles of the limbs (1:4.14 in the lower leg to 1:4.64 in the arm). In the remaining muscles this ratio deteriorates considerably, ranging from 1:5.41 (m.submaxillaris) to 1:7.55 (m.caudalis).

E.longicauda

Also in this species the vascularization of the tail muscle is the lowest, with 93.5 to 97.7 capillaries/1 mm^2 cross-section area.

Table II. Taricha granulosa Skilton

Muscle	Specimen[1]	Number of capillaries/ 1 mm^2 of cross-section area	Number of muscle fibres/ 1 mm^2 of cross-section area	Number of capillaries/ 100 fibres	Mean diameter of capillaries (μ)	Mean diameter of muscle fibres (μ)	Surface area of capillaries of 1 mm^3 of muscle (mm^2)	Surface area of muscle fibres of 1 mm^3 of muscle (mm^2)	Ratio of surface of capillaries to surface of muscle fibres
Mm. arm	A	219.7	352.2	62.4	12.6	40.6	8.69	44.91	1: 5.17
	B	222.4	350.7	63.4	12.1	40.4	8.45	44.51	1: 5.27
Mm. forearm	A	210.1	346.1	60.7	11.7	41.4	7.72	45.01	1: 5.83
	B	208.2	338.1	61.5	11.7	41.2	7.65	43.76	1: 5.72
Mm. thigh	A	221.0	350.3	63.1	12.7	41.3	8.81	45.44	1: 5.16
	B	220.9	342.5	64.5	12.3	40.1	8.53	43.14	1: 5.06
Mm. lower leg	A	209.9	334.2	62.8	11.9	43.2	7.84	45.35	1: 5.78
	B	212.9	330.4	64.4	11.5	42.0	7.68	43.59	1: 5.68
M. submaxillaris	A	285.4	529.8	53.9	11.8	35.5	10.57	59.08	1: 5.59
	B	280.0	552.0	50.7	12.0	35.0	10.55	60.69	1: 5.75
M. rectus abdominis	A	180.3	332.6	54.2	12.9	42.2	7.30	44.09	1: 6.04
	B	175.7	324.7	54.1	12.5	43.3	6.89	44.16	1: 6.41
M. longissimus dorsi	A	121.0	328.3	36.9	13.0	43.2	4.94	33.27	1: 6.73
	B	122.8	305.5	40.2	12.9	45.6	4.97	43.76	1: 8.80
M. tail	A	116.7	245.2	47.6	12.2	49.6	4.47	38.20	1: 8.54
	B	119.5	250.2	47.7	12.5	50.8	4.69	39.92	1: 8.51
Weighted mean	A	170.1	317.4	51.5	12.5	43.9	6.51	44.77	1: 6.58
	B	170.4	309.4	52.3	12.4	44.6	6.42	42.85	1: 7.08

[1] A = specimen weighing 13.33 g, ♀; B = specimen weighing 13.63 g, ♂.

Table III. Gyrinophilus porphyriticus Green, ♀, 14.98 g

Muscle	Number of capillaries/ 1 mm² of cross-section area	Number of muscle fibres/ 1 mm² of cross-section area	Number of capillaries/ 100 fibres	Mean diameter of capillaries (μ)	Mean diameter of muscle fibres (μ)	Surface area of capillaries of 1 mm³ of muscle (mm²)	Surface area of muscle fibres of 1 mm³ of muscle (mm²)	Ratio of surface of capillaries to surface of muscle fibres
Mm. arm	190.8	273.2	69.8	14.4	46.6	8.62	39.99	1:4.64
Mm. forearm	191.3	266.4	71.8	14.9	47.5	8.95	39.75	1:4.44
Mm. thigh	192.3	253.2	75.9	14.2	48.6	8.57	38.65	1:4.51
Mm. lower leg	199.6	269.5	74.0	14.7	45.2	9.21	38.26	1:4.15
M. submaxillaris	185.7	387.5	47.9	14.0	36.3	8.16	44.18	1:5.41
M. rectus abdominis	102.3	214.6	47.7	14.8	51.7	4.75	34.85	1:7.34
M. longissimus dorsi	104.5	219.5	47.6	15.0	52.6	4.92	36.27	1:7.37
M. tail	98.9	203.8	48.5	14.9	54.5	4.62	34.89	1:7.55
Weighted mean	134.9	231.9	57.0	14.7	50.8	6.20	36.75	1:6.36

Table IV. Eurycea longicauda Green

Muscle	Specimen[1]	Number of capillaries/ 1 mm² of cross-section area	Number of muscle fibres/ 1 mm² of cross-section area	Number of capillaries/ 100 fibres	Mean diameter of capillaries (μ)	Mean diameter of muscle fibres (μ)	Surface area of capillaries of 1 mm³ of muscle (mm²)	Surface area of muscle fibres of 1 mm³ of muscle (mm²)	Ratio of surface of capillaries to surface of muscle fibres
Mm. arm	A	246.8	466.1	52.9	10.6	35.0	8.21	51.24	1: 6.24
	B	240.8	461.7	52.1	10.6	37.1	8.01	53.81	1: 6.72
Mm. forearm	A	200.6	430.5	46.6	10.1	35.2	6.36	47.60	1: 7.48
	B	202.1	438.3	46.1	10.3	36.3	6.53	49.97	1: 7.65
Mm. thigh	A	243.9	470.8	51.8	10.8	38.3	8.27	56.64	1: 6.85
	B	237.5	479.7	49.5	11.0	36.1	8.20	54.40	1: 6.63
Mm. lower leg	A	246.3	465.5	52.9	10.2	39.1	7.89	57.17	1: 7.25
	B	235.0	460.4	51.0	10.5	36.9	7.75	53.36	1: 6.89
M. submaxillaris	A	228.0	501.0	45.5	10.6	36.5	7.59	57.44	1: 7.57
	B	252.2	506.0	49.8	10.5	35.1	8.31	55.79	1: 6.71
M. rectus abdominis	A	138.2	286.6	48.2	10.1	45.4	4.38	40.87	1: 9.33
	B	142.5	293.3	48.6	10.7	45.2	4.78	41.64	1: 8.71
M. longissimus dorsi	A	162.2	338.0	47.9	10.2	43.7	5.19	46.40	1: 8.94
	B	173.4	347.8	49.8	10.2	44.7	5.55	48.83	1: 8.80
M. tail	A	97.7	268.4	36.4	10.5	46.0	3.22	38.78	1: 12.05
	B	93.5	266.4	35.0	11.5	47.8	3.37	40.00	1: 11.87
Weighted mean	A	171.1	358.6	47.7	10.6	42.2	5.56	46.61	1: 9.04
	B	172.2	362.6	47.5	10.7	42.5	5.73	47.21	1: 8.84

[1] A = specimen weighing 1.43 g, ♂; B = specimen weighing 3.85 g, ♂.

M. rectus abdominis is vascularized nearly 50% better (138.2 to 142.5 capillaries/mm^2), while m. longissimus dorsi is even better (162.2 to 173.4 capillaries/mm^2). The vascularization of the remaining muscles is nearly 3 times that of the tail muscles. As in *G. porphyriticus*, the vascularization of m. submaxillaris is less intense than that of the muscles of the limbs. The relevant data appear in table IV.

The number of muscle fibres per mm^2 cross-section area averages twice as much as that of capillaries, varying from 266.4 (m. caudalis) to 506.0 (m. submaxillaris). The capillaries in *E. longicauda* are particularly thin: their diameters vary from 10.1 to 11.5 μ. The diameters of muscle fibres vary from 35.1 μ in the arm muscles to 47.8 μ in the tail muscles. Due to the extreme thinness of the capillaries, the ratio of their surface area to that of the muscle fibres is particularly unfavourable: from 1:6.24 (arm muscles) to 1:12.05 (tail muscle).

Discussion

As shown by the data in tables I–IV, there are marked differences between species in the vascularization of the particular skeletal muscles, the thickness of their fibres and the ratio of capillary to muscle fibre surface areas. The poorest vascularization is found invariably in the tail muscles (93.5 to 119.5 capillaries/mm^2 cross-section area), and next in the muscles of the trunk. The vascularization of the muscles of the limbs is more than twice that of the tail muscles. Still better vascularization is found in m. submaxillaris. This is the case with *D. ensatus* and *T. granulosus*, while in *G. porphyriticus* and *E. longicauda* this muscle is vascularized less intensely than the limb muscles (185.7 and 252.2 capillaries/mm^2, respectively). It should be noted that a similarly poor vascularization of m. submaxillaris has been found in *Demognathus quadramaculatus* Holbrook, which is also a member of the family *Plethodontidae* [Czopek and Czopek, 1967]. In *Salientia* (which the exception of *Xenopus laevis* Daud.) m. submaxillaris has a far better vascularization than the muscles of the limbs. The number of capillaries per 1 mm^2 cross-section area of this muscle varies from 336.0 in *Bombina bombina* to 807.6 in *Bufo calamita*. The vascularization of other skeletal muscles is also much more intense in *Salientia* than in *Caudata* [Steudel, 1938; G. Czopek, 1963].

The total length of muscle capillaries per 1 g of body mass is not much different from that in other *Caudata* so far investigated, namely, from 43.20 m in *G. porphyriticus* to 55.00 m in *E. longicauda*. The differences are much greater with regard to the surface area and volume of muscle capillaries per 1 g of body mass. These are from 18.32 cm^2/g (*E. longicauda*) to 26.02 cm^2/g (*D. ensatus*), and from 4.85 mm^3/g to 10.85 mm^3/g, respectively.

The great differences in surface area and volume of muscle capillaries between the species studied are due to the differences in the diameters of these capillaries. The thinnest capillaries are found in *E. longicauda* (10.6 μ), the thickest in *D. ensatus* (16.7 μ).

The numbers of muscle fibres in the particular skeletal muscles follows more or less the same order as those of muscle capillaries (tables I–IV). The number of muscle fibres per unit cross-section area, however, by far exceeds that of capillaries (from 30% in *D. ensatus* to over 100% in *E. longicauda*). The largest number of fibres is always found in m. submaxillaris (from 320.1 fibres/mm^2 in *D. ensatus* up to over 500 fibres/mm^2 in *E. longicauda* and *T. granulosa*). There are also definite differences in the thickness of the fibres. The thickest muscle fibres are found in *D. ensatus:* their diameters vary from 42.5 μ (m. submaxillaris) to 64.5 μ (m. caudalis). The thinnest fibres have been found in the muscles of *E. longicauda:* 35.1 μ in m. submaxillaris to 47.8 μ in m. caudalis. The diameters of muscle fibres in m. submaxillaris in *Caudata* and *Salientia* are much alike and vary between 30 and 42 μ.

As mentioned before, in the muscles of *Caudata* there are much fewer capillaries per 1 mm^2 cross-section area than in those of *Salientia*, the differences being particularly great in the degree of vascularization of m. submaxillaris. The poor vascularization of this muscle in lungless salamanders seems strange and apparently difficult to account for, since all species belonging to this group are characterized by very quick movements of the mouth floor, especially in high temperatures [Herter, 1941]. Whitford and Hutchison [1965] revealed that at a temperature of 15 °C, 15 to 24% of the oxygen requirement of these animals is covered by respiration through the mouth. It could be surmised, therefore, that the vascularization of m. submaxillaris in *Plethodontidae* would be intenser than in *Salientia* [Czopek, 1963]. It should be kept in mind, however, that for an adequate supply of the muscle, and, consequently, for its efficiency, the number of capillaries per mm^2 cross-section area of the muscle is less essential than the ratio of muscle capillary to muscle fibre surface area. This ratio ranges from 1:3.63 in *D.ensatus* to 1:7.57 in *E.longicauda* (tables I–IV). For *B.calamita* it does not exceed 1:5.87, though the number of muscle capillaries per unit cross-section area is several times greater than in the species studied [CZOPEK, 1963]. In the remaining muscles the ratio in question is most favourable in *D.ensatus*, varying from 1:4.23 (arm muscles) to 1:5.64 (tail muscle), and the least favourable in *E.longicauda:* 1:6.24 (arm muscles) to 1:12.05 (tail muscle).

Thus, despite the lower degree of vascularization of the muscles in *Caudata* they may have no worse a blood supply than in *Salientia*. The favourable ratio of capillary to fibre surface area in *Caudata* is due to the considerable thickness of the capillaries, whose diameters average 50% more than in *Salientia*. Also the erythrocytes are much larger in *Caudata* than in *Salientia* [HERTER, 1941; FOXON, 1964].

The efficiency of muscles also depends to a large extent on their being well supplied with oxygen, and thus on the ratio of the length of respiratory capillaries to that of muscle capillaries. Although muscle contraction takes place under anaerobic conditions, oxygen is indispensable during the resting period, when re-synthesis of some substances proceeds, in particular that of lactic acid, formed during contraction, to glycogen.

The species studied show considerable differences in the lengths of respiratory capillaries per 1 g of body mass. The smallest amount of capillaries was found in *D.ensatus* (5.38 m/g), the largest in the young specimen of *E.longicauda* (14.82 m/g). The lengths of respiratory capillaries in the remaining species are much alike and amount to about 10 m/g [CZOPEK, 1961, 1962].

The least favourable ratio of length of respiratory to muscle capillaries is found in *D.ensatus* (1:9.2), the most favourable in the young specimen of *E.longicauda* (1:3.7). The ratio deteriorates with the animal's growth, and in the adult specimen of *E.longicauda* it is only 1:5.3. The deterioration is due solely to the decrease in length of respiratory capillaries per 1 g of body mass as the animal grows in size, for the lengths of muscle capillaries in the 1.43 g specimen and in the 3.85 g one are the same, namely, 55.00 m/g (tables V and VI). From the above data it may be concluded that despite the particularly favourable ratio of muscle capillary to muscle fibre surface area in *D.ensatus*, this species will have much less chance of its muscles being well supplied with oxygen than the

Table V

Species Body weight and sex of specimens examined		Number of capillaries/ 1 mm² of cross-section area [1]	Number of muscle fibres/ 1 mm² of cross-section area [1]	Length of capillaries in m/1 g of muscle	Surface area of capillaries in cm²/1 g of muscle	Volume of capillaries in mm³/1 g of muscle	Length of capillaries in m/1 g of body mass	Surface area of capillaries in cm²/1 g of body mass	Volume of capillaries in mm³/1 g of body mass
D. ensatus	76.00 g ♀	154.8	183.8	116.5	61.11	25.49	49.60	26.02	10.85
T. granulosa	13.33 g ♀	170.1	317.4	128.1	50.29	15.71	54.50	21.39	6.66
T. granulosa	13.63 g ♂	170.4	309.4	128.0	49.85	15.43	54.50	21.22	6.57
G. porphyriticus	14.98 g ♀	134.9	231.9	101.5	46.89	17.21	43.20	19.95	7.33
E. longicauda	1.43 g ♂	171.1	358.6	129.0	42.95	11.37	55.00	18.32	4.85
E. longicauda	3.85 g ♂	172.2	362.6	129.1	43.39	11.59	55.00	18.48	4.94

[1] Weighted means.

Table VI

Species	Body weight and sex of specimens examined	Length of capillaries of all respiratory organs in m/1 g of body mass	Ratio of length of respiratory capillaries to length of muscle capillaries	Ratio of surface area of respiratory capillaries to surface area of muscle capillaries
D. ensatus	76.00 g ♀	5.38[1]	1:9.2	1:6.0
T. granulosa	13.33 g ♀	9.89[1]	1:5.5	1:3.6
T. granulosa	13.63 g ♂	9.92[1]	1:5.5	1:3.6
G. porphyriticus	14.98 g ♀	–	–	–
E. longicauda	1.43 g ♂	14.82[2]	1:3.7	1:2.8
E. longicauda	3.85 g ♂	10.30[2]	1:5.3	1:3.8

[1] After J. CZOPEK [1962].
[2] After J. CZOPEK [1961].

remaining species. The differences between species both in the ratio of capillary to fibre surface area and in the ratio of respiratory capillary to muscle capillary length may largely decide on the degree of motor efficiency of the species in question. Other important factors which will certainly bear on motor efficiency are the number of erythrocytes per 1 mm^3 of blood, the amount of hemoglobin and its varying capacity of binding and giving up oxygen and the degree of innervation of the muscles.

Summary

The vascularization of some skeletal muscles has been investigated and the surface area of the muscle fibres has been estimated in *D. ensatus*, *T. granulosa*, *G. porphyriticus* and *E. longicauda*. The lengths of muscle capillaries per 1 g of body mass are fairly similar in all the species in question, varying from 43.20 m (*G. porphyriticus*) to 55.00 m (*E. longicauda*). The ratio of capillary to muscle fibre surface area is from 30 to 100 % higher in the muscles of the limbs than in the tail muscle. The most favourable ratio of the length of respiratory capillaries to that of muscle capillaries was found in a young specimen of *E. longicauda* (1:3.7), and the least favourable in *D. ensatus* (1:9.2). In the remaining species this ratio was 1:5.5.

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