STUDIA SOCIETATIS SCIENTIARUM TORUNENSIS

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ROZMIESZCZENIE KAPILAR W MIĘŚNIACH U NIEKTÓRYCH PŁAZÓW

ERRATA

Str.	Fig.	Wiersz od góry	Jest	Powinno być
31	7	7	whait	white
33	8	1	thail	tail
33	8	3	whait	white
34	9	3	whait	white
Table 10	—	4	*Ambystoma maxicanum*	*Ambystoma mexicanum*

G. Czopek — *The distribution of capillaries...*

TORUŃ 1963

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PROBLEM

On account of their function the skeletal muscles have a remarkably intense metabolism. Contact with large amounts of blood, which this involves, is ensured by a well-developed capillary network.

The structure and vascularization of the skeletal muscles have long been the subject of investigations. As long ago as in 1874 Ranvier found that the colour intensity of the muscles depended on the amount of blood vessels. He demonstrated that the number of capillaries on a transverse section through a muscle varied according to the number of muscle fibres on this section.

Muscles may be thin-fibred or thick-fibred, or one muscle may contain both kinds of fibres. Light muscle fibres – poor in sarcoplasm – are distinguished from dark fibres containing abundant sarcoplasm and better vascularized. E.g., in the rabbit the dark muscles have three times as many capillaries as the light ones (Smith and Giovacchini, 1956). Dark fibres contract more slowly than light fibres and are far less liable to fatigue.

A large number of investigators who have dealt with the structure and vascularization of the skeletal muscles may be mentioned, e.g., Spaltholz (1888), Stoel (1926), Paff (1930); it was however Krogh (1919) who first investigated the problem in more detail. He demonstrated that the quantity of functional capillaries in muscles is variable and depends on whether the muscle works or is in resting condition. He also found considerable differences among various muscles in the number of capillaries per unit of cross area on the muscle.

Krogh also demonstrated that the muscles of young individuals were better vascularized than the muscles of older individuals with larger body size. Krogh's studies have contributed a great deal towards increasing other investigators interest in the problems of the structure, vascularization and physiology of skeletal muscles.

A good deal of researches have been carried out, and the literature of the problem has been later collected by Krogh (1930) in a monograph entitled "The anatomy and physiology of capillaries".

A number of interesting items of literature dealing with muscle structure are discussed by Krüger (1952). Most of the researches he mentions have been carried out on ectothermic animals; only a few of them are concerned with amphibians (Schiefferdecker, 1911; Linhard, 1926; Voss, 1932).

The above studies have shown that the number of capillaries per unit of cross area of muscle in amphibians is several times smaller than in ectothermic animals. It should be mentioned that the amphibians have been investigated rather perfunctorily. Only Steudel (1938) studied the problem of the structure and vascularization of the skeletal muscles in amphibians in more detail. He worked out the structure and vascularization of skeletal muscles in eight species of *Salientia* and three species of *Urodela*.

Among other things Steudel calculated the number of capillaries and muscle fibres in 1 mm^2 of cross area as well as the number of capillaries per 100 of fibres and the diameter of the blood vessels. In most species Steudel studied only four muscles, viz., *m. submaxillaris* and three muscles of the hind limb: *m. triceps*, *m. sartorius*, and *m. gastrocnemius*.

As shown by Steudel's study the number of capillaries in the muscle depends on the diameter of the muscle fibres. In thin-fibred muscles the number of capillaries is much larger than in the same area of section through a thick-fibred muscle. The number of capillaries and muscle fibres per unit of cross area increases considerably as the animal is being starved. This is an obvious consequence of the reduction in the diameters of the fibres. Steudel also demonstrated that the muscles in *Salientia* are better vascularized than those in *Urodela*, and that the muscles of toads have 20–30% more capillaries in the same cross area than the muscles of frogs. *M. submaxillaris* in most amphibians has nearly twice as many capillaries as the remaining muscles.

Steudel's researches, though undoubtedly very valuable, need repeating, for the author does not give the number of specimens used for the experiments, their size or weight, and with most species he studied the vascularization of only four muscles. A rather serious shortcoming is his using various methods of injecting the blood vessels of the experimental specimens. Thus e.g. large specimens of *Ranidae* he injected through *v. cutanea magna*, medium-sized amphibians through *v. abdominalis*, and very small ones through the heart. He also tried partial injection, e.g. of hind limbs, through *a. abdominalis*.

The lack of uniformity in the methods of injecting the blood vessels may cause considerable differences in the degree to which the blood vessels in various muscles are filled with dye. Steudel also fails to give the length of muscle capillaries, their surface area and volume per 1 g of mass.

The above reasons induced the author of the present paper to repeat Steudel's experiments using a uniform method of injecting the animals (through the heart), increasing the number of the muscles studied to eight (*Urodela*) or eleven (*Salientia*) and comparing specimens of different weight. The length, surface area and volume of the muscle capillaries per 1 g of muscle mass and per 1 g of body mass were also calculated.

MATERIAL AND METHOD

For the experiments were used 50 specimens of amphibians collected in spring in the years 1954 to 1958. The specimens of *Bombina bombina* (L.), *Bufo calamita* Laur. and *Rana esculenta* L. were found in the neighbourhood of Toruń, those of *Salamandra salamandra* (L.) and *Hyla arborea* (L.) were caught at Kalwaria Lanckorońska (province of Cracow), and *Ambystoma mexicanum* Shaw. and *Xenopus leavis* Daudin were taken from the breeding colony of the Department of General Zoology of Copernicus University.

All the animals were killed by destroying the brain and medulla with a probe, after which they were weighed and injected with Prussian Blue through the truncus arteriosus. The destruction of the brain and medulla was aimed at obtaining a complete vasodilatation.

The injected specimens were fixed in 10% formalin, and after washing in water kept in 75% alcohol. The specimens were skinned and examined under a binocular microscope to see if the muscles were well injected. 19 best injected specimens were selected for further investigations.

The species studied and the weight of the specimens were as follows:
Ambystoma mexicanum (larvae) – 2 specimens, 72 g, 76 g
Ambystoma mexicanum (metamorphosed specimens) – 2 specimens, 24 g and 27 g
Salamandra salamandra – 2 specimens, 28 g and 29 g
Bombina bombina – 2 specimens, 6.9 g and 7.5 g
Xenopus laevis – 2 specimens, 28 g and 40 g
Bufo calamita – 2 specimens, 16 g and 16.5 g
Hyla arborea – 2 specimens, 5.7 g and 6.8 g
Rana esculenta – 5 specimens, 2.65 g, 43 g, 56.5 g, 66 g, 250 g.

The particular species will be discussed in the order given in the list. It should be mentioned that the specimens of *A. mexicanum*, *X. laevis*, *B. calamita* and the specimen of *R. esculenta* weighing 250 g had been previously used by a member of the staff of the Department of General Zoology of Copernicus University for studies on the vascularization of respiratory surfaces.

From the experimental specimens the following muscles were cut out: the arm and forearm muscles (among which the particular muscles were not separated on account of their very small size and the difficulty in isolating them), *m. sartorius*, *m. adductor magnus*, *m. triceps*, *m. gastrocnemius*, *m. tibialis*, *m. peroneus*, *m. longissimus dorsi*, *m. rectus abdominis*, and *m. submaxillaris*. Difficulties were also met with in dissecting out the particular muscles of the hind limbs in *Urodela* and in *B. bombina* and *B. calamita*. Therefore, in these species the muscles of the hind limbs were cut out in only two parts: the thigh and the lower leg muscles. In the *Urodela* also the tail muscle was cut out at its base.

After dehydration and embedding in paraffin the muscles were sectioned 10 μ thick perpendicularly to the run of the muscle fibres, and then every 50th section was selected from the series. The sections were put on slides, and after removing the paraffin slightly stained with eosin, dehydrated and mounted in Canada balsam. The histological slides thus prepared were used for microscopic studies on the vascularization of muscles.

The measurements of the number of capillaries and fibres were carried out under a microscope, whose field of vision was 200 μ in diameter. In each slide all the cross sections of capillaries and muscle fibres lying in the field of vision were counted, and from these data were calculated arithmetical means for each particular muscle. The extreme values of fibres dimensions (the highest and lowest means) were found after examining several (5–10) fields of vision. The results thus obtained were calculated to 1 mm^2. The calculations were carried out as follows: the arithmetical means obtained for each muscle were increased by 27.3%, i.e. in such proportion as the area of a circle must be increased to obtain the area of a square whose side is equal to the diameter of this circle. As the field of vision of the microscope was 200 μ, the result obtained for each muscle was multiplied by 25, for a square whose side measures 200 μ into 1 mm^2 goes 25 times.

For each muscle also measurements were taken of the diameter of the capillaries and muscle fibres, and the number of capillaries per 100 fibres was determined. From the results thus obtained weighted means were calculated for each specimen considering the percentage constituted by the muscles of a given type in the whole of the musculature.

To calculate the length of muscle capillaries for each specimen supplementary measurements and investigations were necessary. The following data had to be found: 1) the muscle mass in the particular specimens, 2) the volume of the muscles after fixation and dehydration, 3) the length of capillaries in 1 mm^3 of these muscles. It was of course impossible to find the muscle mass in specimens from which part of the muscles had been removed for histological slides. Therefore additional specimens had to be used for this purpose.

Each specimen was weighed immediately after killing, and then again after removing the skin, the eyeballs and viscera. After that all the muscles were removed, the skeleton was weighed and the percentage of the body mass constituted by the muscles was calculated. Such measurements were carried out on two specimens from each species, and from the results arithmetical means were calculated. It must be mentioned that the data for *A.mexicanum* and *S.salamandra* have been taken from literature (Welcker, Brandt 1903; Korzhuiev, 1959 et al.) because no material was available, whereas the results given for *B.calamita* have been based on the data obtained for *B.bufo*. The results are presented in the following table.

Species	Muscle mass expressed in % of body mass
A.mexicanum (larva)	54.0
A.mexicanum (metamorphosed individ.)	44.3
S.salamandra	42.6
B.bombina	41.5
X.laevis	54.3
B.calamita	42.4
H.arborea	43.1
R.esculenta	53.4

Knowing the percentage of the body mass constituted by the muscles in the particular species, it was possible to calculate the muscle mass in the experimental specimens.

Then the volume of the muscles after fixation and dehydration had to be calculated, as all the microscopic measurements were carried out on such material. To obtain this it was necessary to calculate the specific volume of the fixed muscles and multiply it by the muscle mass of the specimens investigated. The specific volume is, as we know, the reciprocal of density, which may be easily found by means of a pycnometer. The density of 1 cm^3 of fixed muscles has been found to be 1.3284 g. The specific volume, i.e. the volume of 1 g of fixed muscles is then $\frac{1}{1.3284} = 0.7528$ cm^3. Multiplying the mass of the muscles of the particular specimens by 0.7528 we obtain the volume of these muscles after fixation and dehydration. The density of the muscles was determined only in *R. esculenta* on the assumption that it is approximate in all species investigated.

The length of muscle capillaries in 1 mm^3 was calculated in the following way: it was assumed for simplicity that the length of capillaries in 1 mm^3 of muscle amounted to as many millimetres as there were cross sections of capillaries in 1 mm^2 of muscle. This simplification is admissible on the ground that capillaries in muscles run parallel to the fibres. Only a very small number of capillaries, running perpendicularly to the fibres, are thus not taken into account.

According to Steudel (1938), the number of capillaries running perpendicularly to the fibres is very small: it amounts only to 3 to 8% of the capillaries parallel to the fibres. Knowing the length of capillaries in 1 mm^3, their diameter, the volume of the muscles, their mass and also the body mass, it was possible to calculate for each specimen the length, the surface area and the volume of the capillaries per 1 g of muscle mass and per 1 g of body mass.

Objections might be raised against the fact that from most species only two specimens were studied.

This, however, seems justified for the following reasons: the present research was begun with examining the vascularization of the muscles in three specimens of *R. esculenta* of similar size (43 g, 56.5 g, 66 g). The results, which came very close to one another, induced the author to confine the number of specimens of other species to two. On the other hand, it was decided to increase the number of species investigated from five, as it had been primarily intended, to seven.

For the working out of the vascularization of the muscles in *R. esculenta* (specimens weighing 2.65 g, 66 g and 250 g) were used preparations and some calculations made in the Department of General Zoology of Copernicus University by Mr. J. Sarbinowski.

INTENSITY OF VASCULARIZATION OF MUSCLES

A.MEXICANUM, LARVAL SPECIMEN WEIGHING 72.0 G

The number of capillaries per 1 mm^2 of cross area of muscle ranges from 100.0 to 219.0. The hind limb muscles are vascularized somewhat better than the forelimb ones. While the thigh and lower leg muscles have just a little over 200 cap./mm^2, the arm and forearm muscles do not exceed 180 cap./mm^2. The poorest vascularization is revealed by *m.rectus abdominis*, then by *m.longissimus dorsi* and the tail muscle. The best vascularization is found in *m.submaxillaris*.

The number of muscle fibres in 1 mm^2 is over twice, and in the tail muscle and *m.submaxillaris* even three times that of the capillaries.

The capillary diameter ranges from 10 μ (thigh muscles) to 16.4 μ (tail muscles), whereas the diameter of muscle fibres ranges from 33.2 μ (tail muscle) to 52.2 μ (*m.rectus abdominis*) for mean values (Table 1, Fig. 1, 2).

A.MEXICANUM, LARVAL SPECIMEN WEIGHING 76.0 G

Compared with the former specimen this one shows slight differences in vascularization intensity of some muscles. The largest number of capillaries is found in the thigh muscles and in the arm and forearm muscles, and next in the *m.submaxillaris*. Like in the former specimen, however, the least intensely vascularized muscles are *m.rectus abdominis*, and next *m.longissimus dorsi* and the tail muscle.

The number of muscle fibres per 1 mm^2, like in the former specimen, is largest in *m.submaxillaris*, in the limb muscles and in the tail muscle, and smallest in *m.longissimus dorsi* and in *m.rectus abdominis*.

The number of capillaries per 100 muscle fibres is smallest in the tail muscle and in *m.submaxillaris*. In the remaining muscles this number ranges from 44.0 to 48.2.

The diameter of the capillaries ranges from 10.7 μ to 16.0 μ. The diameter of the muscle fibres is nearly three times as large and ranges from 31.10 μ to 48.7 μ (Table 1, Fig. 1, 2)

A.MEXICANUM, METAMORPHOSED SPECIMEN WEIGHING 24 G

The vascularization intensity in this specimen is slightly lower than in the larval specimens. The largest number of capillaries per 1 mm^2 is found in *m.submaxillaris*, then in the forelimbs and hind limbs muscles. The poorest vascularization occurs in the tail muscle, *m.rectus abdominis* and *m.longissimus dorsi*.

In 1 mm^2 of cross area there are nearly twice as many muscle fibres as capillaries, the fewest fibres occurring in the tail muscle, *m.longissimus dorsi* and *m.rectus abdominis*.

Table 1 – Tabela 1

Ambystoma mexicanum (larvae)

Muscle / Nazwa mięśnia	Specimen weighing 72,0 g					Specimen weighing 76,0 g				
	Number of capillaries in 1 mm² of cross area / Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area / Ilość włókien w 1 mm²	Number of capillaries per 100 fibres / Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ / Średnica kapilar w µ	Mean diameter of muscle fibres in µ / Średnica włókien w µ	Number of capillaries in 1 mm² of cross area / Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area / Ilość włókien w 1 mm²	Number of capillaries per 100 fibres / Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ / Średnica kapilar w µ	Mean diameter of muscle fibres in µ / Średnica włókien w µ
mm. arm – mm. ramienia	179,0	375,4	47,6	11,4	40,9	244,0	546,3	44,6	12,0	35,1
mm. forearm – mm. przedramienia	177,2	426,2	41,6	13,2	39,2	226,0	491,0	46,0	13,7	36,2
mm. thigh – mm. uda	207,2	476,0	43,5	10,0	37,1	245,4	536,4	45,7	11,0	34,3
mm. lower leg – mm. podudzia	203,4	463,8	43,8	12,4	41,0	198,0	410,0	48,2	12,0	37,4
m. longissimus dorsi	114,0	242,0	47,1	12,0	50,9	120,6	268,0	45,0	13,0	48,7
m. rectus abdominis	100,4	246,0	42,2	13,8	52,2	109,7	249,0	44,0	14,0	45,9
m. submaxillaris	219,0	642,0	34,1	11,3	35,0	224,0	614,0	36,4	10,7	31,0
m. tail – m. ogona	127,0	421,0	30,1	16,4	33,2	127,0	400,0	31,7	16,0	35,5
arithmetical mean – średnia arytmetyczna	165,9	411,5	41,2	12,6	41,2	186,8	439,3	42,7	12,8	38,0
weighted mean – średnia ważona	145,5	364,8	40,6	13,1	42,2	161,3	386,6	41,7	13,4	40,0

The number of capillaries per 100 fibres is over 25% greater than in the larval specimens. The smallest number of capillaries per 100 fibres occurs in *m.submaxillaris*, then in *m.rectus abdominis* and in the tail muscle, the largest in the limbs muscles.

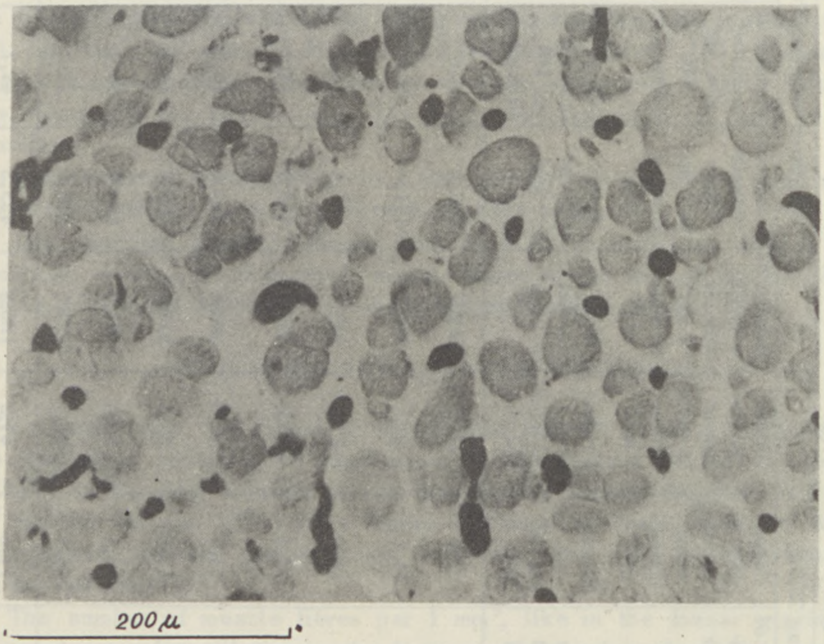

Fig. 1. *A.mexicanum* (larva) – mm. lower leg – mm. podudzia

The diameter of capillaries in the particular muscles varies within rather narrow limits, viz. from 12.5 μ (*m.submaxillaris*) to 15.7 μ (*m.rectus abdominis*). The range of the diameter of muscle fibres is much greater. The thinnest fibres occur in *m.submaxillaris* and in the limbs muscles, the thickest ones in the tail muscle and in *m.longissimus dorsi* (Table 2).

A.MEXICANUM, METAMORPHOSED SPECIMEN WEIGHING 27.0 G

The muscles of this specimen are slightly more intensely vascularized than those of the specimen weighing 24.0 g. The number of capillaries per 1 mm^2 of cross area ranges from 205.4 to 100.8, the poorest vascularization being found, like in the 24.0-g specimen, in the tail muscle, and next in *m.rectus abdominis* and *m.longissimus dorsi*.

The number of capillaries per 100 fibres in the particular muscles is a little higher than in the former specimen.

The diameter of the capillaries and that of the muscle fibres are very similar in both specimens (Table 2).

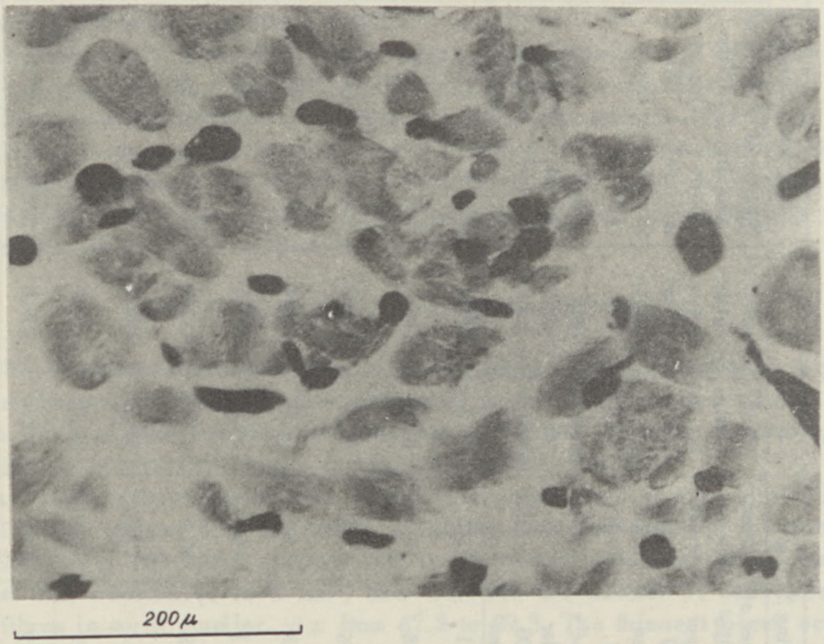

Fig. 2. *A.mexicanum* (larva) – *m. submaxillaris*

The differences in number of capillaries and fibres per 1 mm² of cross area of muscle among the specimens of one species are negligible, and so are the differences in diameter of capillaries and muscle fibres, as it can be seen in the tables (Tables 3–7). Therefore it was considered pointless to discuss each specimen separately.

S.SALAMANDRA, SPECIMENS WEIGHING 28 AND 29 G

The intensity of vascularization of the muscles approximates to that in the metamorphosed specimens of *A.mexicanum*.

The largest number of capillaries per 1 mm² occurs in the forelimb muscles,

Table 2 – Tabela 2

Ambystoma mexicanum (metamorphosed specimens)

Muscle Nazwa mięśnia	Specimen weighing 24,0 g					Specimen weighing 27,0 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ
mm. arm – mm. ramienia	178,0	306,2	58,1	13,6	44,0	200,8	326,2	61,5	14,0	42,0
mm. forearm – mm. przedramienia	175,0	297,4	58,8	14,2	44,5	179,0	313,8	57,0	13,8	43,5
mm. thigh – mm. uda	170,0	244,1	69,6	13,6	43,5	172,6	258,1	66,8	13,8	41,5
mm. lower leg – mm. podudzia	155,0	237,3	65,3	14,7	42,2	159,0	249,3	63,8	14,3	43,1
m.longissimus dorsi	125,8	220,0	57,1	14,9	61,4	132,0	232,0	56,8	14,1	58,6
m.rectus abdominis	120,0	223,0	53,8	15,7	53,3	128,6	229,0	56,1	15,6	57,9
m.submaxillaris	183,4	397,0	46,1	12,5	39,9	205,4	411,1	49,9	12,5	38,2
m. tail – m. ogona	108,8	198,8	54,7	13,0	60,0	100,8	210,8	47,8	14,0	61,1
arithmetical mean – średnia arytmetyczna	152,0	265,5	57,9	14,0	48,6	159,8	278,8	57,5	14,0	48,2
weighted mean – średnia ważona	136,6	232,2	58,6	14,2	53,2	140,2	244,4	56,8	14,2	53,1

in the thigh muscles and in *m. submaxillaris*. The smallest number is found in, like in the metamorphosed specimens of *A.mexicanum*, in the tail muscle, and next in *m.rectus abdominis* and in *m.longissimus dorsi*.

The number of fibres in 1 mm² is smaller than in the larvae of *A.mexicanum*, but larger than in the metamorphosed specimens of this species.

The largest number of fibres occurs in *m.submaxillaris*, and next in the limb muscles. The smallest number of fibres is found in the tail muscle, in *m.rectus abdominis* and in *m.longissimus dorsi*.

The number of capillaries per 100 fibres ranges from 41.0 to 61.8. The range of the diameter of the fibres and capillaries is rather narrow. The thinnest fibres are found in *m.submaxillaris*, the thickest in the tail muscle. The lumen of the capillaries is smallest in the arm muscles, largest in *m.submaxillaris* (Table 3).

Before discussing the structure and vascularization of the skeletal muscles in *Salientia* it must be stated that their muscles are much more intensely vascularized than the muscles of *Urodela*.

B.BOMBINA, SPECIMENS WEIGHING 6.9 G AND 7.5 G

The best vascularized muscle in this species is *m.submaxillaris*. A poorer vascularization is shown by the muscles of the hind limbs and of the forelimbs. The smallest number of capillaries per 1 mm² of cross area of muscle is found in *m.rectus abdominis* and in *m.longissimus dorsi*.

It is interesting to note that in the limb muscles the number of capillaries per 1 mm² is greater than the number of fibres, and, consequently, the number of capillaries per 100 fibres exceeds 100. In the remaining muscles there are more fibres than capillaries in 1 mm², and therefore the number of capillaries per 100 fibres is much smaller, viz. from 67.2 to 89.3. The thinnest fibres occur in *m.submaxillaris* and do not exceed 38.9 μ in diameter. The fibres in the remaining muscles are over 50 μ in diameter, and in *m.rectus abdominis* they even reach 67.8 μ. The diameter of the capillaries ranges from 10.5 μ to 14.7 μ (Table 4, Fig. 3, 4, 5).

X.LAEVIS, SPECIMENS WEIGHING 28.0 G AND 40.0 G

The best vascularized of all the muscles in *X.laevis* is *m.gastrocnemius*. A somewhat less intense vascularization is found in the remaining muscles of the limbs, of which *m.tibialis* and *m.sartorius* have only just over a half of the number of capillaries of the other muscles of the limbs. As already mentioned, the best vascularized muscles are *m.gastrocnemius* and the muscles of the forelimbs. The vascularization of *m.submaxillaris* and that of the hind limbs muscles except *m.gastrocnemius* and *m.sartorius* are similar to each other.

The fewest capillaries per 1 mm² occur in *m.longissimus dorsi*, and next in *m.rectus abdominis*.

The number of fibres per 1 mm² in the particular muscles is on the average 30 to 40% lower than the number of capillaries, and ranges from 95.2 to 213.7

Table 3 – Tabela 3

Salamandra salamandra

Muscle Nazwa mięśnia	Specimen weighing 28,0 g					Specimen weighing 29,0 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ Średnica kapilar w µ	Mean diameter of muscle fibres in µ Średnica włókien w µ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ Średnica kapilar w µ	Mean diameter of muscle fibres in µ Średnica włókien w µ
mm. arm – mm. ramienia	218,5	409,0	53,4	12,5	40,5	220,3	415,0	53,0	12,9	38,1
mm. forearm – mm. przedramienia	201,5	408,8	49,3	13,0	39,9	203,5	390,8	52,3	14,0	41,8
mm. thigh – mm. uda	191,0	308,6	61,8	14,5	43,3	200,2	330,5	60,6	14,9	46,3
mm. lower leg – mm. podudzia	172,1	311,1	55,0	15,6	46,0	183,1	321,3	57,0	14,4	44,0
m. longissimus dorsi	153,6	294,5	53,0	13,0	45,5	148,2	289,0	51,3	12,8	45,9
m. rectus abdominis	138,0	274,0	50,0	13,0	47,5	134,0	281,7	46,8	13,2	45,5
m. submaxillaris	189,1	461,4	41,0	16,0	35,5	186,8	467,1	50,0	16,4	39,5
m. tail – m. ogona	114,7	258,5	44,0	14,3	51,1	115,6	241,5	48,0	14,7	48,7
arithmetical mean – średnia arytmetyczna	172,3	340,9	50,9	13,9	43,7	173,9	342,1	52,4	14,2	43,7
weighted mean – średnia ważona	156,0	301,2	51,6	13,7	46,1	156,8	300,8	51,8	13,9	45,7

Table 4 – Tabela 4

Bombina bombina

Muscle Nazwa mięśnia	Specimen weighing 6,9 g					Specimen weighing 7,5 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ Średnica kapilar w µ	Mean diameter of muscle fibres in µ Średnica włókien w µ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ Średnica kapilar w µ	Mean diameter of muscle fibres in µ Średnica włókien w µ
mm. arm – mm. ramienia	270,4	204,6	132,1	11,5	60,2	275,2	215,2	127,8	11,2	58,0
mm. forearm – mm. przedramienia	237,6	197,7	120,1	13,0	62,0	228,0	193,2	118,0	11,2	61,1
mm. thigh – mm. uda	305,5	225,4	135,5	10,0	56,8	307,2	239,0	128,4	12,2	53,2
mm. lower leg – mm. podudzia	279,0	226,4	123,2	13,0	57,7	289,6	225,8	128,2	11,0	55,9
m. longissimus dorsi	157,9	202,3	78,0	13,0	61,2	160,0	190,8	83,8	12,2	60,8
m. rectus abdominis	108,8	121,8	89,3	14,7	67,8	103,4	123,0	84,0	14,7	61,9
m. submaxillaris	336,0	499,7	67,2	11,0	38,9	349,8	508,2	68,8	10,5	35,8
arithmetical mean – średnia arytmetyczna	242,2	239,7	106,5	12,3	57,8	244,7	242,2	105,6	11,9	55,2
weighted mean – średnia ważona	238,0	200,9	116,2	12,1	62,3	239,1	205,9	113,2	12,4	57,0

per 1 mm² of cross area. The range of the number of capillaries per 100 fibres in those muscles in which there are more capillaries than fibres is slightly narrower. Only in *m. submaxillaris* the number of fibres in 1 mm² slightly exceeds the number of capillaries, and therefore in this muscle there are only 83.3 to 87 capillaries per 100 fibres.

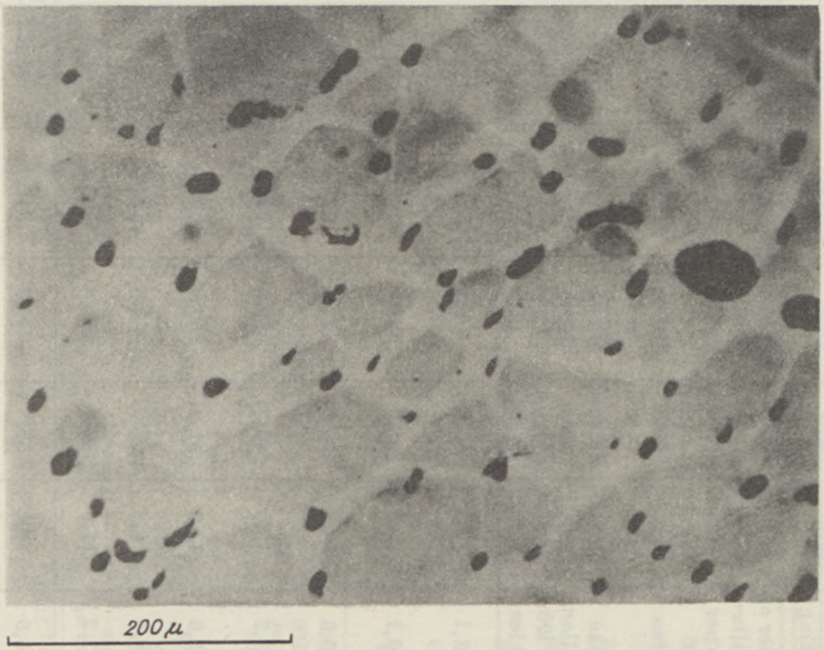

Fig. 3. *B. bombina* – mm. lower leg – mm. podudzia

The diameter of the fibres in *m. submaxillaris* and in the muscles of the forelimbs does not exceed 50 μ, in the remaining muscles it is much larger and ranges from 58.9 μ to 98.2 μ. The variations in the diameter of the capillaries are but very slight. The thinnest capillaries occur in *m. submaxillaris*, the thickest in *m. longissimus dorsi* (Table 5).

B. CALAMITA, SPECIMENS WEIGHING 16.0 AND 16.5 G

This toad has the best vascularized muscles of all amphibians studied so far. The differences in intensity of vascularization of the particular muscles are also greatest in this species. An exceptionally intense vascularization characterizes *m.submaxillaris*. The other muscles have two to four times fewer capillaries. Like in *X.laevis* and *B.bombina*, the number of fibres per 1 mm^2 is

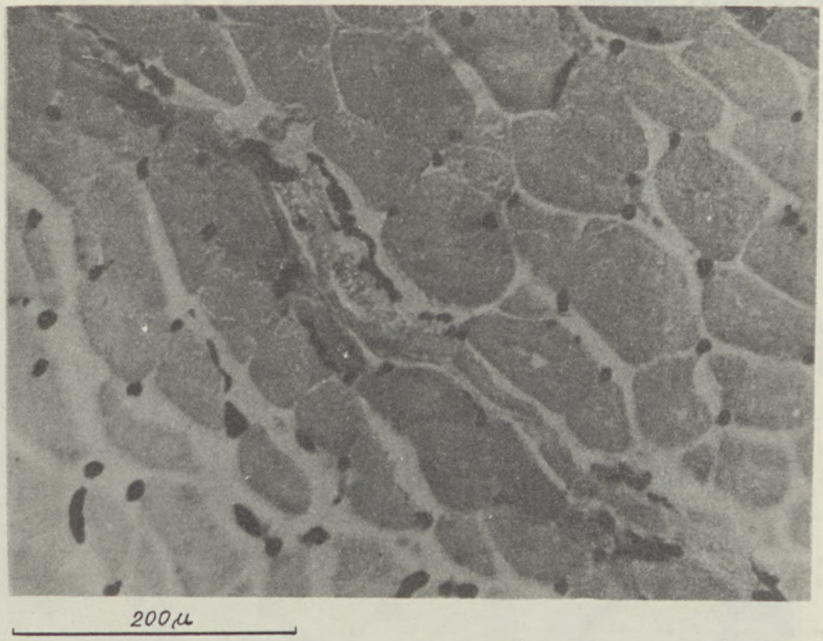

Fig. 4. *B.bombina – m. longissimus dorsi*

smaller than the number of capillaries in this area. Therefore the number of capillaries per 100 fibres exceeds 100. Only *m.submaxillaris* and *m.longissimus dorsi* have more fibres than capillaries in 1 mm^2.

The number of capillaries per 100 fibres is smaller, viz. for *m. submaxillaris* ca 80.0, for *m.longissimus dorsi* ca 70.0. The thinnest fibres occur in *m. submaxillaris*, the other muscles have thicker fibres. The diameter of the capillaries ranges from 5.3 μ to 7.9 μ. (Table 6, Fig. 6).

H.ARBOREA, SPECIMENS WEIGHING 5.7 G AND 6.8 G

In this species the vascularization of the muscles is slightly less intense than in the preceding one, but more intense than in *B.bombina* and in *X.laevis*. The best vascularization is found in *m.submaxillaris*, the poorest in *m.longissi-*

mus dorsi. It is noteworthy that the vascularization of the remaining muscles is similar to one another and very intense.

Like in most *Salientia* studied so far, in the majority of the muscles the number of fibres per 1 mm² is 20 to 30% smaller than the number of capillaries in the same area. In *m.submaxillaris* the number of fibres is much greater than in the remaining muscles.

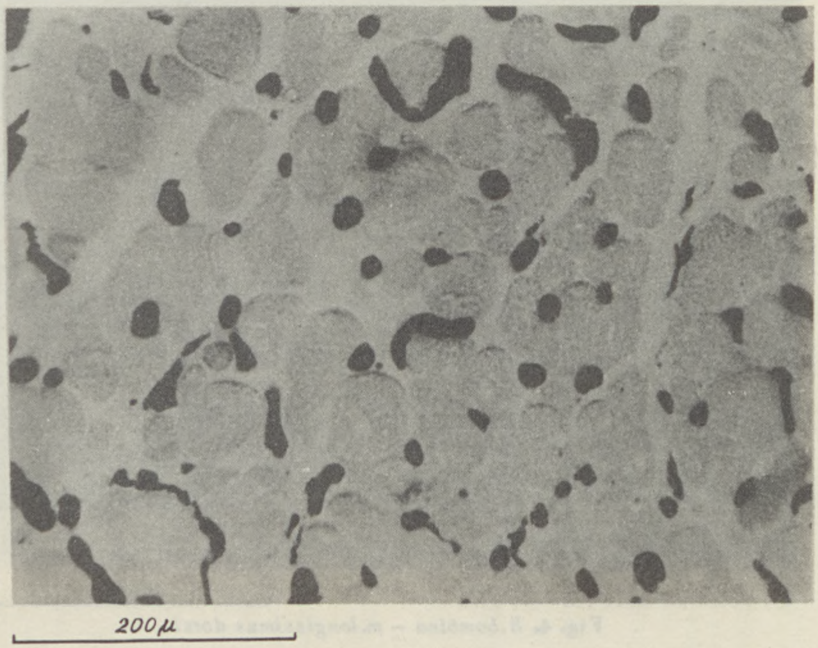

Fig. 5. *B.bombina* – *m.submaxillaris*

The number of capillaries per 100 muscle fibres is similar te to that in *X.laevis* and *B.calamita*.

The diameter of the muscle fibres varies from 33.0 μ to 60.1 μ, it is then somewhat larger than in *B.calamita*, but smaller than in all the other *Salientia*.

R.ESCULENTA

The specimens used in the experiments differ widely in body size. The smallest of them is a freshly metamorphosed individual weighing only 2.65 g.

Table 5 – Tabela 5

Xenopus laevis

Muscle / Nazwa mięśnia	Specimen weighing 28,0 g					Specimen weighing 40,0 g				
	Number of capillaries in 1 mm² of cross area / Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area / Ilość włókien w 1 mm²	Number of capillaries per 100 fibres / Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ / Średnica kapilar w μ	Mean diameter of muscle fibres in μ / Średnica włókien w μ	Number of capillaries in 1 mm² of cross area / Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area / Ilość włókien w 1 mm²	Number of capillaries per 100 fibres / Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ / Średnica kapilar w μ	Mean diameter of muscle fibres in μ / Średnica włókien w μ
mm. arm – mm. ramienia	283,4	204,1	138,8	7,7	48,8	301,0	211,5	142,3	7,3	50,0
mm. forearm – mm. przedramienia	271,0	213,7	126,8	7,8	49,8	288,6	206,3	139,8	8,2	47,6
m. sartorius	191,1	116,4	164,1	7,6	70.0	201,7	125,6	160,5	8,0	70,0
m. adductor magnus	232,5	120,4	193,1	6,9	74,5	239,5	131,6	181,9	7,2	69,5
m. triceps femoris	243,8	146,8	166,0	6,0	70,1	255,8	159,8	160,0	7,0	69,5
m. gastrocnemius	299,2	187,6	159,4	6,8	61,2	313,6	194,8	160,9	7,0	60,3
m. tibialis	169,0	100,2	168,6	6,9	78,9	187,0	102,2	182,9	6,5	81,1
m. peroneus	260,2	158,3	164,3	6,7	58,9	267,8	165,7	161,6	6,1	62,1
m. longissimus dorsi	108,7	95,2	111,8	8,3	89,9	126,3	97,2	129,9	8,7	98,2
m. rectus abdominis	142,9	101,8	140,3	8,5	86,5	151,4	102,2	148,1	8,5	81,1
m. submaxillaris	245,0	279,2	87,7	6,2	45,5	229,0	274,8	83,3	6,6	47,5
arithmetical mean – średnia arytmetyczna	222,4	156,7	147,4	7,2	66,7	232,9	161,0	150,1	7,4	67,0
weighted mean – średnia ważona	218,8	141,5	153,8	7,3	71,8	230,8	147,4	156,3	7,5	71,1

Table 6 – Tabela 6

Bufo calamita

Muscle Nazwa mięśnia	Specimen weighing 16,0 g					Specimen weighing 16,5 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diametef of capillaries in µ Średnica kapilar w µ	Mean diameter of muscle fibres in µ Średnica włókien w µ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in µ Średnica kapilar w µ	Mean diameter of muscle fibres in µ Średnica włókien w µ
mm. arm – mm. ramienia	505,0	362,0	139,5	6,5	43,8	541,5	387,0	139,9	7,1	38,0
mm. forearm – mm. przedramienia	493,0	421,0	117,1	7,7	38,2	487,4	380,8	127,9	7,9	39,8
mm. thigh – mm. uda	486,0	338,1	143,7	7,4	44,1	446,0	317,7	140,3	7,0	41,1
mm. lower leg – mm. podudzia	390,0	281,2	138,6	7,9	45,6	401,3	320,0	125,4	7,8	42,4
m. longissimus dorsi	205,0	282,0	72,6	6,7	43,7	207,4	305,0	68,0	6,7	46,3
m. rectus abdominis	266,0	240,0	110,8	7,6	53,5	296,0	251,2	117,8	7,4	52,9
m. submaxillaris	798,3	973,8	81,9	5,3	29,4	807,6	1000,4	80,4	6,1	29,6
arithmetical mean – średnia arytmetyczna	449,0	414,9	114,9	7,0	42,6	455,3	423,2	114,2	7,1	41,6
weighted mean – średnia ważona	416,8	341,6	122,9	7,3	44,4	417,3	342,8	122,9	7,3	43,1

Table 7 – Tabela 7

Hyla arborea

Muscle Nazwa mięśnia	Specimen weighing 5,7 g					Specimen weighing 6,8 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ
mm. arm – mm.ramienia	320,0	233,0	137,3	7,3	56,2	326,1	240,4	135,6	7,7	53,9
mm. forearm – mm. przedramienia	351,7	283,8	123,9	7,0	52,2	363,5	297,0	122,3	7,5	49,9
m.sartorius	300,3	234,1	128,2	7,4	50,0	314,3	248,1	126,6	8,4	51,0
m.adductor magnus	378,4	279,0	135,6	7,5	45,0	388,8	289,4	134,3	7,9	46,7
m.triceps femoris	325,4	236,8	137,4	7,7	56,6	327,4	238,8	137,1	7,3	58,0
n.gastrocnemius	333,0	233,2	142,7	7,7	56,0	332,6	232,8	142,8	8,1	57,2
m.tibialis	310,0	239,2	129,6	7,5	54,0	311,8	240,8	129,4	7,9	53,4
m.peroneus	312,9	225,0	139,0	7,2	58,5	316,9	221,6	143,0	6,6	59,1
m.longissimus dorsi	235,1	204,3	115,0	6,6	59,5	228,9	198,1	115,5	6,5	60,1
m.rectus abdominis	327,7	272,7	120,2	6,5	42,0	326,3	271,4	120,2	6,9	45,1
m.submaxillaris	581,1	691,0	84,0	7,7	34,8	583,9	693,0	84,1	7,2	33,0
arithmetical mean – średnia arytmetyczna	343,2	284,7	126,6	7,3	51,3	347,3	288,3	126,4	7,5	51,7
weighted mean – średnia ważona	322,9	252,4	128,7	7,1	50,9	325,8	255,4	128,2	7,4	51,8

The largest one, an exceptionally huge specimen, weighs 250 g, i.e. nearly 100 times as much as the former. The weights of the remaining three specimens are approximate to one another. Tables 8 and 9 show that the specimens investigated reveal very considerable differences in the number of capillaries and fibres per 1 mm^2 of cross area of the muscle as well as in the diameter of the muscle fibres. These differences are no doubt connected with the differences in body size of the experimental specimens.

The most intensely vascularized muscles has the specimen weighing 2.65 g. The vascularization of its muscles is only slightly less intense than in *B.calamita*, and more intense than in all the other species.

The largest number of capillaries occurs in *m.submaxillaris*, the smallest in *m.rectus abdominis*. From the remaining muscles the best vascularization is found in *m.peroneus* and *m.gastrocnemius*, which have just over 400 capillaries per 1 mm^2 of cross area.

The number of fibres in 1 mm^2 of cross area is nearly twice the number of capillaries in the same area. The largest number of fibres occurs in *m.submaxillaris*. It is nearly twice as large as the smallest number of fibres, which occurs in the muscles of the forelimb. The number of fibres in the hind limb muscles varies within rather wide limits, the largest number occurring in *m.peroneus*, the smallest in *m.tibialis*. As there are much more fibres than capillaries in 1 mm^2, the number of capillaries per 100 fibres is considerably lower than 100 and varies from 54 to 71.

The diameter of the capillaries ranges from 8.1 μ to 9.6 μ. The thinnest fibres occur in *m.submaxillaris*, next is *m.peroneus*. The other muscles have thicker fibres, their diameter ranging from 20 μ to 26.2 μ (Table 8).

R.ESCULENTA, SPECIMENS WEIGHING 43 G, 56.5 G AND 66 G

These three specimens have much smaller quantities of capillaries and muscle fibres per 1 mm^2 of cross area than the former specimen. The differences in number of capillaries and fibres per 1 mm^2 and in their diameters among these three specimens are but slight, like in other *Salientia* investigated so far, except *X.laevis*, the best vascularized muscle is *m.submaxillaris*.

Also well vascularized is *m.triceps*. The poorest vascularization is found in *m.rectus abdominis*, and next in *m.sartorius*. The vascularization of the remaining muscles ranges from 201.0 cap/mm^2 to 269.0 cap/mm^2.

Unlike in the 2.65 g specimen, the number of fibres per 1 mm^2 of section is considerably smaller than the number of capillaries in this area. Only *m.submaxillaris* has more fibres than capillaries in 1 mm^2. Therefore in this muscle there are only 75 to 90.4 capillaries per 100 fibres, whereas in the remaining muscles this number ranges from 102.0 to 206.0.

Table 8 – Tabela 8

Rana esculenta

Muscle Nazwa mięśnia	Specimen weighing 2,65 g					Specimen weighing 43,0 g					Specimen weighing 56,5 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ
mm. arm – mm. ramienia	372,0	527,0	70,0	8,2	26,2	243,2	159,6	151,9	8,4	61,9	250,3	160,6	156,0	9,2	62,1
mm. forearm – mm. przedramienia	363,0	515,0	70,0	8,1	26,2	258,0	201,1	123,3	8,0	64,5	241,7	196,0	123,3	8,9	63,4
m. sarturius	315,0	585,0	54,0	9,1	21,3	176,8	121,5	146,0	9,2	67,1	172,9	120,0	144,0	9,0	66,5
m. adductor magnus	345,0	605,0	63,0	9,3	22,5	262,7	169,7	153,0	8,7	63,9	252,7	174,4	145,0	9,0	62,6
m. triceps femoris	367,0	671,0	55,0	8,8	20,0	314,4	152,9	205,0	9,1	66,0	311,2	142,2	206,0	8,3	64,6
m. gastrocnemius	412,0	585,0	71,0	9,4	22,5	261,3	168,3	155,0	9,5	63,9	248,7	162,5	153,0	9,0	64,8
m. tibialis	353,0	536,0	66,0	9,3	23,7	203,4	123,0	165,0	8,0	67,9	200,0	120,0	167,0	9,2	68,1
m. peroneus	409,0	710,0	59,0	9,0	15,0	244,6	183,5	133,0	8,9	65,2	266,0	186,2	140,0	9,5	63,9
m. longissimus dorsi	356,0	634,0	57,0	9,1	22,6	201,0	196,0	102,0	8,0	61,1	203,1	183,0	110,8	8,0	62,8
m. rectus abdominis	301,0	549,0	54,0	9,4	25,0	178,2	155,0	114,0	7,9	65,5	196,2	171,0	114,0	8,5	64,6
m. submaxillaris	614,0	953,0	65,0	9,6	12,5	463,1	512,0	90,4	9,7	32,9	386,2	506,1	87,2	9,7	33,2
arithmetical mean – średnia arytmetyczna	382,5	624,5	62,2	9,0	21,6	255,1	194,8	139,9	8,7	61,8	248,1	192,9	140,6	8,9	61,5
weighted mean – średnia ważona	362,6	594,0	62,6	9,0	22,8	245,9	167,3	148,3	8,7	64,1	243,5	164,2	148,0	8,8	63,7

The diameter of the muscle fibres is three times as large as in the freshly metamorphosed individual and ranges from 46.7 μ to 72.2 μ. Only in *m.submaxillaris* the fibres are much thinner and their diameter does not exceed 28.0 to 33.2 μ. The diameters of the capillaries in the three specimens investigated are similar and range from 7.9 to 10.0 μ (Tables 8 and 9).

R.ESCULENTA, SPECIMEN WEIGHING 250 G

This large specimen has even fewer capillaries and fibres per 1 mm^2 of cross area of muscle than the medium-sized specimens.

The best vascularization is found, like in the other specimens, in *m.submaxillaris*. The remaining muscles are vascularized much less intensely.

The number of muscle fibres in 1 mm^2 of cross area varies from 69 to 388. The highest value, like in all hitherto studied species, occurs in *m.submaxillaris*. In all the muscles of the hind limb the number of fibres is under 100. The largest number is found in *m.gastrocnemius*, then is in *m.peroneus*, *m.triceps*, and *m.adductor magnus*. The smallest number in *m.tibialis*. The remaining muscles have 100 or just over 100 fibres per 1 mm^2 of cross area.

The diameter of the fibres is much larger compared with the former specimens. It ranges in the particular muscles from 76.5 μ to 121.1 μ, except *m.submaxillaris*, whose fibres are thinner (Table 9).

As indicated by the above data, the muscle fibres in the 250-g specimen are over four times as thick as the fibres in the freshly metamorphosed specimen, and nearly one and a half as thick as in the medium-sized specimens.

The number of capillaries per 100 fibres is highest in the muscles of the hind limbs. Next in turn are the muscles of the forelimbs, then *m.longissimus dorsi*, *m.rectus abdominis* and *m.submaxillaris*.

The diameters of capillaries in all the specimens of *R.esculenta* are much alike; their means range from 8.7 to 9.2 μ (Tables 8 and 9).

LENGTH, SURFACE AREA AND VOLUME OF MUSCLE CAPILLARIES

The figures (weighted means) in Table 10 show that there are no great differences in the length, surface area and volume of capillaries per 1 g of muscle mass among the particular species of *Urodela*. Very distinct differences, however, appear between the *Urodela* and the *Salientia* and among the particular species of *Salientia*.

A.MEXICANUM

In the larvae there are 109.53 to 121.43 m of capillaries per 1 g of muscle mass. The surface area of these capillaries ranges from 45.07 to 51.10 cm^2,

Table 9 — Tabela 9

Rana esculenta

Muscle Nazwa mięśnia	Specimen weighing 66,0 g					Specimen weighing 250,0 g				
	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ
mm. arm — mm. ramienia	267,0	177,0	151,0	8,4	68,0	146,0	118,0	123,0	8,8	89,2
mm. forearm — mm. przedramienia	243,0	193,0	127,0	8,5	64,0	160,0	137,0	118,0	8,5	81,0
m. sartorius	205,0	121,0	169,0	9,1	72,2	146,0	85,0	173,0	9,7	102,0
m. adductor magnus	251,0	171,0	147,0	9,8	68,0	157,0	87,0	178,0	9,0	82,9
m. triceps femoris	310,0	152,0	205,0	8,3	63,7	140,0	87,0	160,0	8,6	99,9
m. gastrocnemius	260,0	173,0	151,0	10,0	68,0	139,0	94,0	167,0	10,2	121,1
m. tibialis	192,0	112,0	170,0	9,0	70,7	118,0	69,0	172,0	9,2	97,7
m. peroneus	269,0	199,0	135,0	9,0	46,7	161,0	90,0	180,0	9,0	97,7
m. longissimus dorsi	204,0	167,0	114,0	9,0	55,2	121,0	100,0	121,0	9,2	76,5
m. rectus abdominis	180,0	173,0	105,0	9,6	46,7	140,0	129,0	109,0	8,8	80,7
m. submaxillaris	405,0	529,0	75,0	9,3	28,0	279,0	388,0	74,0	10,0	34,0
arithmetical mean — średnia arytmetyczna	253,3	197,0	140,8	9,1	59,2	155,2	125,8	143,2	9,2	87,5
weighted mean — średnia ważona	246,8	169,9	147,8	9,2	62,8	144,8	102,7	149,6	9,1	93,2

their volume from 14.76 to 17.13 mm³. Calculated to 1 g of body mass this will amount to 59.15–65.57 m, 24.34–27.60 cm² and 7.97–9.25 mm³ respectively.

In the metamorphosed specimens the length of the capillaries per 1 g of muscle mass in only a little less than in the larvae (102.83 to 105.54 m); their surface area and volume are similar as well (45.87–47.08 cm² and 16.28–16.71 mm³).

There are much greater differences between the larvae and the metamorphosed specimens in the length of capillaries per 1 g of body mass. The metamorphosed specimens have only 45.54 to 46.75 m of capillaries per 1 g of body mass, i.e., nearly 25% less than the larvae. This drop is caused to a large extent by a decrease in the ratio of muscle mass to body mass in the metamorphosed specimens. While in larvae the muscles constitute 54% of the body mass, in metamorphosed individuals they do not exceed 45%. The surface area of the muscle capillaries per 1 g of body mass in metamorphosed individuals amounts to 20.32–20.85 cm², their volume to 7.21–7.40 mm³.

S.SALAMANDRA

The figures obtained for this species are a little higher than those for metamorphosed specimens of *A.mexicanum*. The length of capillaries, their surface area and their volume per 1 g of muscle mass are: 117.44–118.04 m, 50.54–51.53 cm² and 17.30–17.91 mm³ respectively. The respective values per 1 g of body mass are: 50.04–50.27 m, up to 22 cm² and 7.37–7.63 mm³.

B.BOMBINA

B.bombina has over 50% more capillaries per 1 g of muscle mass than the *Urodela* (179.16 to 179.98 m). The surface area of the muscle capillaries amounts to 68.10–70.09 cm², and their volume to 20.60–21.71 mm³. The figures per 1 g of body mass are as follows: length of capillaries 74.26–74.63 m, surface area 28.23–29.06 cm², volume 8,54–9.00 mm³.

X.LAEVIS

X.laevis has nearly the same length of capillaries per 1 g of muscles as *B.bombina* (164.72 to 173.75 m). Their surface area is nonetheless nearly twice smaller (37.77 to 30.93 cm²), and their volume even three times smaller (6.83 to 7.66 mm³) than in *B.bombina*. This is accounted for by the fact that the diameter of the capillaries in *X.laevis* averages 7.3 to 7.5 μ, whereas in *B.bombina* it exceeds 12 μ. Notwithstanding that the length of capillaries per 1 g of muscle mass in *B.bombina* and *X.laevis* is much alike, the latter has nearly 20% more muscle capillaries per 1 g of body mass (89.42 to 94.34 m). In *X.laevis* the muscles constitute 54% of the body mass, whereas in *B.bombina* they do not exceed 42%. The surface area of capillaries per 1 g of body mass ranges from 20.50 to 22.23 cm², and their volume from 3.74 to 4.16 mm³.

BUFO CALAMITA

This species has the most intensely vascularized muscles of all amphibians studied so far (Fig. 6). In *B.calamita* there are 313.71 to 314.14 m of capillaries per 1 g of muscle mass, i.e., almost three times as much as in the *Urodela*

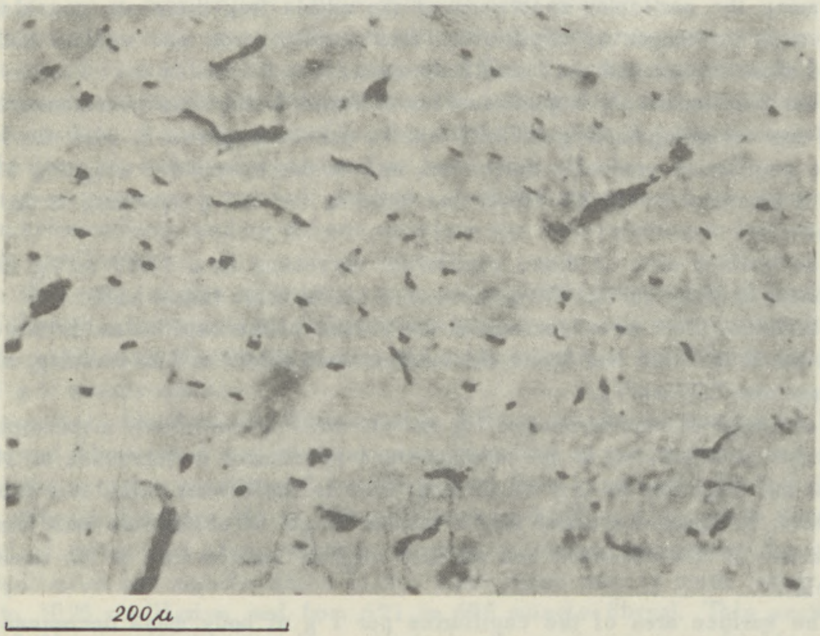

Fig. 6. *B.calamita* – mm. lower leg – mm. podudzia

and about twice as much as in most *Salientia*. The surface area of these capillaries amounts to 72 cm^2/g, and their volume is just over 13 mm^3/g. As the muscles in *B.calamita* constitute less than 43% of the body mass, both the length of muscle capillaries and their surface area and volume attain much lower values when calculated per 1 g of body mass, and the differences in this respect between *B.calamita* and the other species are smaller. The length of capillaries is ca 133 m/g, the surface area is just over 30 cm^2/g, and the volume 5.55 mm^3/g.

H.ARBOREA

In *H.arborea* there are 243.09 to 245.19 m of capillaries per 1 g of muscles, i.e. nearly 1/3 less than in the former species, but more than in the remaining *Salientia* except the freshly metamorphosed *R.esculenta*.

The surface area of the capillaries ranges from 54.21 to 56.98 cm², and their volume from 9.62 to 10.55 mm³. The respective values per 1 g of body mass are: 104.91 to 105.65 m, 23.29 to 24.55 cm² and 4.15 to 4.54 mm³.

R.ESCULENTA

Among the particular specimens of the edible frog there are considerable differences in length of capillaries, their surface area and volume both per 1 g of muscle mass and per 1 g of body mass.

Most capillaries per 1 g of muscles is found in the freshly metamorphosed specimen weighing 2.65 g (272.97 m). As the body grows in size the length of the capillaries gradually decreases, and in the specimens weighing 43 and 66 g it amounts to 183.31–185.79 m, while in the 250-g specimen it drops to 109.01 m.

The surface area of these capillaries decreases from 77.17 cm²/g (2.65-g specimen) to 31.15 cm²/g (250-g specimen), i.e. by more than a half.

Likewise, there is a decrease in the volume of the capillaries. In the small specimen it is 17.36 mm³/g, in the medium ones 10.99 to 12.34 mm³/g, and in the large one 7.09 mm³/g.

The length of capillaries per 1 g of body mass in the freshly metamorphosed specimen is 146.27 m, in the medium-sized specimens it decreases to 100 m, and in the large one to only 58.21 m/g. This is the lowest value ever found in *Salientia*. It should be noted that a similar length of capillaries was found in the larvae of *A.mexicanum*, and an only slightly smaller one in the remaining *Urodela*.

The surface area of the capillaries per 1 g of body mass decreases from 41.35 cm² (small specimen) to 16.64 cm² (large specimen), while the volume of the capillaries drops from 9.30 mm³ (small specimen) to 3.78 mm³ (large specimen).

DISCUSSION OF RESULTS

As already mentioned in the introduction, the inwestigations of the vascularization of muscles in amphibians have been few and rather perfunctory. It was only Steudel (1938) who dealt with this problem in more detail. He demonstrated that the number of capillaries per 1 mm² of cross area in the particular muscles of *Urodela* varied from 133 (*m.intermandibularis* in *A.mexicanum*) to 309 (*m.supracoracoideus* in *S.salamandra*). In *Salientia* it ranges from 286 (*m.gastrocnemius* in *R.esculenta*) to 652 capillaries (*m.submaxillaris* in *R.temporaria*).

Steudel found that *Urodela* had nearly twice as many fibres as capillaries in 1 mm^2 of cross area, whereas in *Salientia* there were 50 to 100% more capillaries than fibres. An exception to this is *m.submaxillaris*, in which there are about 40% more fibres than capillaries and *m.obliquus oculi inferior*, in which the number of fibres in 1 mm^2 of cross area exceeds five times that of the capillaries. According to Steudel, in *Urodela* the number of capillaries per 100 muscle fibres does not exceed this number, while in *Salientia* it is much larger (except *m.submaxillaris* and *m.obliquus oculi inferior*).

Steudel's data come fairly close to the results presented in this paper, but it must be remembered that the two are difficult to compare, since Steudel does not give the weight of the specimens he has studied, and, as demonstrated by our studies, the vascularization intensity in muscles and the dimensions of muscle fibres depend to a large extent on body size.

In most species Steudel studied only three muscles of the appendages and *m.submaxillaris*, and he did not calculate any data referring to the length of muscle capillaries.

In this work, on the other hand, 8 muscles in the *Urodela* and 11 in most of the *Salientia* were examined. Calculations have been made of the length of the muscle capillaries, their surface area and volume both per 1 g of body mass and per 1 g of muscle mass.

Steudel found in amphibians large differences in the number of capillaries and fibres per 1 mm^2 of cross area depending on sex, season, and above all on the nutritive condition of the individual. Thus in normally fed individuals of *B.calamita* there are 443 to 710 capillaries and 300 to 613 muscle fibres per 1 mm^2 of cross area of *m.sartorius*, whereas in starved specimens the number of capillaries and muscle fibres in the same cross area is much larger (from 963 to 1025 capillaries and from 621 to 675 muscle fibres). This section of Steudel's results has not been checked: all specimens were freshly caught and immediately prepared.

Significant differences in the vascularization of the particular muscles have been noted also in fishes. Thus in the eel (*Anguilla anguilla L.*) *m.subcutaneus* has 1065 cap/mm^2, while *m.parietalis* only 97 cap./mm^2. In the trout (*Salmo trutta f.fario L.*) *m.subcutaneus* has 400 cap/mm^2, *m.parietalis* 123 cap./mm^2 (Pollak, 1955, 1960).

The muscles in mammals are much better vascularized, e.g. in the horse there are 1350 cap/mm^2, in the dog 2630 cap/mm^2, in the guinea pig 4000 cap/mm^2 (Krogh, 1930).

The results obtained in this work have revealed that in amphibians there are significant differences in vascularization intensity of various muscles, also in the number of muscle fibres per 1 mm^2 of cross area and in the number of muscle capillaries per 100 fibres. From the differences in vascularization intensity of the particular muscles inferences can be made on the metabolism and efficiency of these muscles.

In *Salientia* the best vascularization is found in *m.submaxillaris*: from

279 cap/mm² (*R.esculanta*, 250 g) to 807 cap/mm² (*B.calamita*). This muscle has on the average 80 to 100% more capillaries than the limb muscles, and twice to four times as many capillaries as *m.longissimus dorsi* and *m.rectus abdominis.* Only in *X.laevis* the vascularization of *m.submaxillaris* is slightly less intense than that of the limb muscles, but this is accounted for by the fact that the movements of the mouth floor in this species are weaker than in other *Salientia*, for the air exchange mechanism in the lungs takes advantage of the pressure excercised on the animal by the surrounding water. *R.esculenta* in a temperature of 17°C performs on the average 73 movements with its mouth, while *X.laevis* at 25°C performs 44 to 55 such movements (Herter, 1941).

The best vascularized muscles among *Salientia* have *B.calamita* and *H.arborea.* It is noteworthy that while in *B.calamita* the differences in vascularization intensity among various muscles are very great, in *H.arborea* they are negligible (Table 6–7). This may be explained as follows: the difference in the amount of work performed by various muscles in the terrestrial and burrowing *B.calamita* will certainly be greater than in the tree-dwelling *H.arborea;* this leads to differentiation in the vascularization of the muscles in the toad.

Observations have shown that *S.salamandra* and *A.mexicanum* exhibit but faint movements of the mouth (J. Czopek – results unpublished). *M.submaxillaris* in these species is also poorly vascularized: it has 183 to 224 cap/mm² (Table 1–3).

The comparatively poor vascularization of *m.submaxillaris* in *Caudata* is certainly associated with low efficiency of the gular pump, which again is conditioned by the small size of the head (Schmalhausen, 1957). In lungless salamanders the *m.submaxillaris* will certainly be much better vascularized than in the remaining *Urodela*, for the former perform very vigorous movements with their mouth floor. At 17°C the rate of these movements is 300 per minute (Herter, 1941).

This vigorous ventilation of the mouth indicates that it plays a greater part in gaseous exchange than in other species. This hypothesis is supported by morphological studies of the vascularization of the respiratory surfaces in amphibians. The capillaries of the mouth constitute in the *Plethodontidae* up to 10% of the total length of the respiratory capillaries, while in the remaining amphibians they never exceed 1–3% (Czopek, 1955 a, b, 1957, 1959, 1960, 1961; G. Czopek, J. Czopek, 1959).

The vascularization of other muscles is also much poorer in the *Urodela* than in the *Salientia.* The vascularization of the tail muscle is on the average one half that of the limb muscles, viz. from 100 to 127 cap/mm². A somewhat better vascularization than in the tail muscle is found in *m.rectus abdominis* and in *m.longissimus dorsi* (100 to 153 cap/mm²).

It is noteworthy that in all *Salientia m.submaxillaris* has 15 to 30% more fibres than capillaries. In 100 fibres in this muscle there are 67 to 90 capillaries. Besides *m.submaxillaris*, the number of fibres slightly exceed that of the capillaries in *m.longissimus dorsi* (*B.bombina*, *B.calamita*) and *m.rectus* *abdominis* (*B.bombina*). All the other muscles in *Salientia* have 20 to 100% more capillaries than fibres per 1 mm² of cross area, which means that the number of capillaries per 100 fibres exceeds this figure and ranges from 102 – *m.longissimus dorsi* (*R.esculenta*, 43-g specimen) to 206 – *m.triceps* (*R.esculenta*, 43, 56.5 and 66-g specimens).

The *Urodela*, on the other hand, have on the average 70 to 100% more fibres than capillaries per 1 mm² of cross area. The number of capillaries per 100 fibres does not exceed this figure and varies from 30 to 69 (Table 1–3).

The above-described differences in the number of capillaries per 100 fibres that exist in amphibians both among the muscles of one species and among various species are accounted for chiefly by the differences in thickness of the fibres: the thickness of the connective tissue surrounding the muscle fibres shows no significant deviations from standard in any species and averages from 6 to 10 μ.

The diameter of the fibres in *m.submaxillaris* is in *Salientia* 1/2 to 1/5, and in *Urodela* about 1/2 the fibre diameter in the remaining muscles. The weighted mean of the thickness of muscle fibres calculated separately for each species is in *Caudata* 40 to 53 μ. Muscle fibres of comparable thickness are found in *B.calamita* and *H.arborea*; in the remaining *Salientia* the muscle fibres are 20 to 50% thicker (Table 10, Fig. 7).

The vascularization of the muscles per unit cross area in *H.arborea* and *B.calamita* exceeds two or three times that in the *Urodela*, and by 40 to 80% that in the remaining *Salientia*. The comparatively thin muscle fibres in these two species will thus be certainly better supplied with blood, and more efficient than in other amphibians.

Details concerning the thickness of the muscle fibres in the particular species are presented in Tables 1 to 9.

The length of muscle capillaries per 1 g of muscle in the particular species of the *Urodela* varies within rather narrow limits, viz. from 102 to 121 m. The *Salientia* have significantly more capillaries and the interspecific differences with them are much greater.

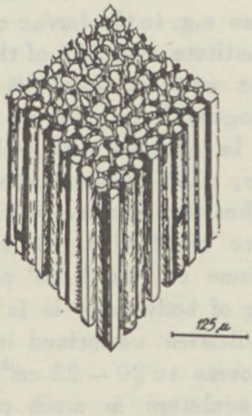

Fig. 7. Vascularization of *m.submaxillaris* of *Bufo calamita* of 16.5 g– Unaczynienie *m.submaxillaris* u *Bufo calamita* o wadze 16,5 g
Muscle fibres whait, capillaries black. Dimensious of the cube 250 μ × 250 μ – Włókna mięsne białe, kapilary czarne. Wymiary sześcianu 250 μ × 250 μ

The fewest capillaries are found in *X.laevis*: 164 to 173 m/g. This water-dwelling species uses up less energy for moving than other, partly terrestrial, species, and, consequently, its muscles do not need so abundant vascularization. Somewhat more capillaries has the predominantly aquatic *B.bombina* (c. 180 m/g), and most capillaries have the decidedly terrestrial *B.calamita* (314 m/g) and *H.arborea* (243 to 245 m/g).

The above data show that in the *Salientia* there are 50 to 300% more capillaries per 1 g of muscle than in the *Caudata*. The surface area of these capillaries ranges in the *Salientia* from 38 to 77 cm^2, their volume from c. 7 to over 17 mm^3.

In the *Caudata* the surface area of the capillaries ranges from 45 to 51 cm^2/g, their volume from 15 to 18 mm^3/g (Table 10). So in spite of considerable differences in the length of muscle capillaries their surface area in the urodeles and *Salientia* is much alike, and the volume of the capillaries is even larger in the urodeles. This is accounted for by the fact that the blood cells of the urodeles are much larger (Herter, 1941), and the diameter of their capillaries is 70 to 100% larger than that of the *Salientia* (Table 10). It must not therefore be assumed that the volume of capillaries in 1 mm^3 of muscles informs about the working conditions of the muscle.

The relation of muscle mass to body mass varies according to species. Thus e.g. in the larvae of *A. mexicanum*, in *X. laevis* and *R. esculenta* the muscles constitute over 54% of the body mass, while in *S. salamandra*, *H. arborea* or *B. bombina* no more than 43% of the body mass is muscles. This ratio varies during ontogeny (Korzhuiev et al., 1959).

In species with well-developed musculature the length of muscle capillaries, their surface area and volume per 1 g of body mass are comparatively higher than in species with poorer musculature (Table 10). Thus e.g. in *X. laevis* there are 164 to 173 m of capillaries, whose surface area is 38 to 41 cm^2 and volume c. 7 to 8 mm^3 per 1 g of muscles. The length of muscle capillaries per 1 g of body mass is in this species 89 to 94 m, that is more than a half of the capillaries comprised in 1 g of muscles. The surface area of these capillaries amounts to 20 – 22 cm^2, and their volume to about 4 mm^3. In *B. bombina*, whose musculature is much poorer, the length of capillaries per 1 g of muscles is about 180 m, their surface area 68 to 70 cm^2, and their volume 20 to 21 mm^3. The length of muscle capillaries per 1 g of body mass in the same species is 74 m, i.e. much less than a half of the quantity of capillaries per 1 g of muscles. Their surface per 1 g of body mass is 28 to 29 cm^2, their volume 8.5 to 9 mm^3 (Table 10).

Metamorphosis produces rather essential changes in the muscles, viz. their fibres become thicker. It does not, however, affect the intensity of vascularization of the muscles. The fibres in the larvae of *A. mexicanum* are 31 to 51 μ in diameter, the thinnest fibres being found in *m. submaxillaris* and in the tail muscle (31 to 35 μ). In the metamorphosed specimens the diameter of the muscle fibres varies from 38 μ (*m. submaxillaris*) to 61 μ (tail muscle). The muscle fibres in *m. submaxillaris* gain less in thickness than those in the trunk and tail muscles. In the larvae the weighted mean of the thickness of the fibres is 40–42 μ, in the metamorphosed specimens it increases to 53 μ (Fig. 8).

In consequence of the change to terrestrial habits the muscles of the metamorphosed specimens must no doubt perform a greater amount of work and their

Table 10 – Tabela 10

Specimen Gatunek	Species, weight and sex of the specimen Waga ciała w g oraz płeć okazu	Number of capillaries in 1 mm² of cross area Ilość kapilar w 1 mm²	Number of muscle fibres in 1 mm² of cross area Ilość włókien w 1 mm²	Number of capillaries per 100 fibres Ilość kapilar na 100 włókien	Mean diameter of capillaries in μ Średnica kapilar w μ	Mean diameter of muscle fibres in μ Średnica włókien w μ	Weight of muscles in g Waga mięśni w gramach	Volume of fixed muscles in cm³ Objętość mięśni po utrwaleniu w cm³	Length of capillaries in meters per 1 g of muscle Długość kapilar w m przypadająca na 1 g mięśni	The surface area of capillaries in cm² per 1 g of muscle Powierzchnia kapilar w cm² na 1 g mięśni	Volume of capillaries in mm³ per 1 g of muscle Objętość kapilar w mm³ na 1 g masy mięśni	Length of capillaries in meters per 1 g of weight of specimen Długość kapilar w metrach na 1 g masy ciała	Surface area of capillaries in cm² per 1 g of weight of specimen Powierzchnia kapilar w cm² na 1 g masy ciała	Volume of capillaries in mm³ per 1 g of weight of specimen Objętość kapilar w mm³ na 1 g masy ciała	Length of** respiratory capillaries in meters per 1 g of weight of specimen Długość kapilar oddechowych w m na 1 g masy ciała	Ratio of respiratory capillaries to muscle capillaries Stosunek kapilar oddechowych do kapilar mięśni
Ambystoma mexicanum (larvae)	*72,00 ♂	145,5	364,8	40,6	13,1	42,2	38,88	29,269	109,53	45,07	14,76	59,15	24,34	7,97	6,226	1 : 9,50
	*76,00 ♀	161,3	386,6	41,7	13,4	40,0	41,04	30,895	121,43	51,10	17,13	65,57	27,60	9,25	6,340	1 : 10,34
Ambystoma maxicanum (metamorphosed specimens)	*24,00 ♀	136,6	232,2	58,6	14,2	53,2	10,63	8,002	102,83	45,87	16,28	45,54	20,32	7,21	11,492	1 : 3,96
	*27,00 ♂	140,2	244,4	56,8	14,2	53,1	11,96	9,003	105,54	47,08	16,71	46,75	20,85	7,40	11,760	1 : 3,98
Salamandra salamandra	28,00 ♂	156,0	301,2	51,6	13,7	46,1	11,93	8,981	117,44	50,54	17,30	50,04	21,53	7,37	9,133	1 : 5,48
	29,00 ♂	156,8	300,8	51,8	13,9	45,7	12,35	9,297	118,04	51,53	17,91	50,27	21,95	7,63	9,133	1 : 5,50
Bombina bombina	6,90 ♂	238,0	200,9	116,2	12,1	62,3	2,86	2,153	179,16	68,10	20,60	74,26	28,23	8,54	14,620	1 : 5,08
	7,50 ♂	239,1	205,9	113,2	12,4	57,0	3,11	2,341	179,98	70,09	21,71	74,63	29,06	9,00	14,620	1 : 5,10
Xenopus laevis	*28,00 ♂	218,8	141,5	153,8	7,3	71,8	15,20	11,443	164,72	37,77	6,88	89,42	20,50	3,74	16,241	1 : 5,50
	*40,00 ♀	230,8	147,4	156,3	7,5	71,1	21,72	16,351	173,75	40,93	7,66	94,34	22,23	4,16	13,724	1 : 6,87
Bufo calamita	*16,00 ♂	416,8	341,6	122,9	7,3	44,4	6,78	5,103	313,71	71,93	13,10	132,93	30,48	5,55	25,034	1 : 5,31
	*16,50 ♀	417,3	342,8	122,9	7,3	43,1	6,99	5,262	314,14	72,03	13,12	133,09	30,51	5,56	24,785	1 : 5,37
Hyla arborea	5,70 ♀	322,9	252,4	128,7	7,1	50,9	2,46	1,852	243,09	54,21	9,62	104,91	23,39	4,15	45,990	1 : 2,28
	6,80 ♂	325,8	255,4	128,2	7,4	51,8	2,93	2,205	245,19	56,98	10,55	105,65	24,55	4,54	45,990	1 : 2,30
Rana esculenta	2,65	362,6	594,0	62,6	9,0	22,8	1,42	1,069	272,97	77,17	17,36	146,27	41,35	9,30	44,830	1 : 3,26
	43,00 ♀	245,9	167,3	148,3	8,7	64,1	22,96	17,284	185,11	50,59	10,99	98,84	27,01	5,87	17,870	1 : 5,53
	56,50 ♀	243,5	164,2	148,0	8,8	63,7	30,17	22,712	183,31	50,66	11,14	97,88	27,05	5,95	17,870	1 : 5,48
	66,00 ♀	246,8	169,9	147,8	9,2	62,8	35,24	26,529	185,79	53,69	12,34	99,20	28,67	6,59	17,870	1 : 5,55
	*250,00 ♀	144,8	102,7	149,6	9,1	93,2	133,50	100,499	109,01	31,15	7,09	58,21	16,64	3,78	11,000	1 : 5,29

*Specimens used in previous studies of the vascularization of respiratory surfaces – okazy służące do badań nad unaczynieniem powierzchni oddechowych

**After Andrzejewski and al., 1962; Czopek 1955, 1957, 1959, 1960; Czopek G., Czopek J. 1959; Strawiński S. 1956.

fibres consequently become thicker and stronger. The length of muscle capillaries per 1 g of muscle in the larvae and in the metamorphosed specimens is much the same and ranges from 102 to 125 m. Nevertheless the oxygen supply will certainly be much better in the metamorphosed specimens, for the larvae have just over 6 m of respiratory capillaries per 1 g of body mass, whereas the metamorphosed specimens have nearly twice that quantity (Czopek, 1957).

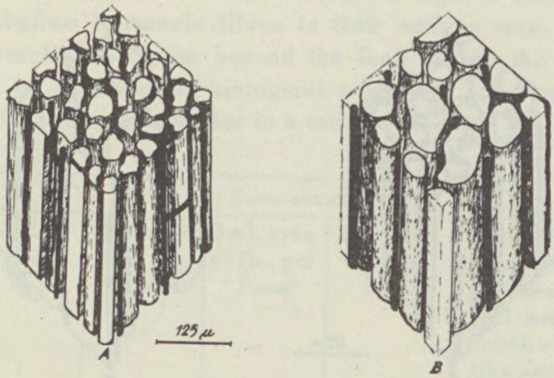

Fig. 8. The vascularization of the thail muscles in *Ambystoma mexicanum* – Unaczynienie mięśni ogona u *Ambystoma mexicanum*

Muscle fibres whait, capillaries black. Dimensious of the cube 250 μ × 250 μ × 250 μ – Włókna mięsne białe, kapilary czarne. Wymiary sześcianu 250 μ × 250 μ × 250 μ

A – neotenic larva – okaz nieprzeobrażony; B – metamorphosed specimen – okaz przeobrażony

There is a very intimate correlation in amphibians between the vascularization intensity of the muscles and the size of the muscle fibres on the one hand and the growth of the body on the other. Parallel to body growth goes a significant decrease in vascularization intensity of the muscles. In the freshly metamorphosed individual of *R. esculenta* (weight 2.65 g) there are from 301 (*m. rectus abdominis*) to 614 (*m. submaxillaris*) capillaries per 1 mm² of cross area. In the 43 to 66-g specimens the quantity of capillaries in the muscles varies from 173 to 463, in the extremely large specimen weighing 250 g it is just over one third (118 to 279) of the quantity found in the freshly metamorphosed specimen. This drop in vascularization in the specimens weighing from 44 to 250 g is closely correlated with the decrease in quantity of the respiratory capillaries per 1 g of body mass (Andrzejewski et al., 1962). Consequently, the ratio of respiratory to muscular capillaries remains the same notwithstanding the growth of the body (Table 10). A similar decrease in vascularization intensity associated with the increase in body size has been stated in mammals by Krogh (1919) and by Paff (1930).

The growth of the body in amphibians is associated with a decrease in the quantity of muscle fibres per 1 mm² of cross area and with their becoming considerably thicker. The freshly metamorphosed *R. esculenta* has on the average

594 fibres per 1 mm², the 43 to 66-g specimens have about 170 fib/mm², and the 250-g specimen has only 102 fib/mm². In the medium-sized, specimens, and even more in the large one, the fibres with the largest cross area are found in the jumping muscles, while the thinnest ones are in the *longissimus dorsi*, *rectus abdominis* and *submaxillaris*. The diameter of the fibres increases from 22.8 μ (freshly metamorphosed specimen) to 93.2 μ (250-g specimen). (Fig. 9).

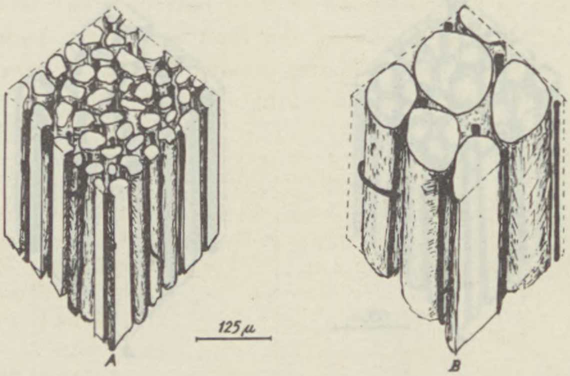

Fig. 9. The vascularization of *m.tibialis* of *Rana esculenta* – Unaczynienie *m.tibialis* u *Rana esculenta*

Muscle fibres whait, capillaries black. Dimensious of the cube 250 μ × 250 μ × 250 μ – Włókna mięsne białe, kapilary czarne. Wymiary sześcianu 250 μ × 250 μ × 250 μ

A – specimen weighing 2.65 g – okaz o wadze 2,65 g; B – specimen weighing 250.0 g – okaz o wadze 250,0 g

The above results lend support to Davison's (1955) conclusions. This worker measured the surface area of the muscles in amphibians and found that the animal's growth within the muscles was effected solely through enlargement of the cells. It is noteworthy that in the freshly metamorphosed specimen the diameter of the muscle fibres in various muscles is much the same, which may testify to a still low degree of specialization of the particular muscles. In large frogs, on the other hand, the jumping muscles must perform more work because the whole body has gained in weight, and this in consequence leads to the fibres becoming thicker. It may be also induced from the above observations that the growth in thickness of the fibres is a direct result of the amount of work performed.

Steudel (1938) thinks that there is a correlation between the increase in the diameter of the fibre and the increase in the quantity of blood vessels. This is associated with the heightened metabolism of the thickening fibres. In fact, while for supplying the thin fibres in the freshly metamorphosed frog a smaller number of blood vessels (54 to 71 vessels per 100 fibres) is needed, in large frogs this number is 102 to 206 per 100 fibres. If we assume that the supply of muscle fibres is proportional to the number of capillaries per 100 fibres, then a doubled diameter of the fibres will require a fourfold increase in the number of capillaries. Accordingly, in the 250-g specimen of *R. esculenta*, whose muscle fibres are four times as thick as those in the freshly metamorphosed specimen, the number of capillaries per 100 fibres ought to be 864 to 1136, i.e. 6–8 times as many as there actually are.

It seems therefore that D a v i s o n (1955) is right in claiming that the factor limiting metabolism in muscle fibres is their surface area. An increase in the number of muscle capillaries beyond the limit set by the surface area of the fibres would be deprived of biological sense. In this connection it seemed interesting to compare certain data in a table:

Rana esculenta							
Weight of specimen in g waga w g	Diam. of fibres in μ Śred. włók. w μ	Quant. of fib. per 1 mm² Ilość włókien w 1 mm²	Surf. area of fib. per 1 mm² Pow. włók. w 1 mm²	Volume of fib. per 1 mm³ Objęt. włók. w mm³	Ratio of surf. area of fibres per 1 mm³ to vol. of fibr. per 1 mm³ Stos. pow. włók. w 1 mm³ do obj. włók. w 1 mm³	Surface area of capil. per 1 g of muscle mass Powierzchnia kapilar na 1 g masy mięśni	Length of capil. per 1 g of muscle mass in m/g Długość kapilar na 1 g masy mięśni w m/g
2.65	22.8	594.0	42.525	0.242	171	77.17	272.9
250.00	93.2	102.7	30.050	0.681	44	31.15	109.0

The above table gives only the results obtained for the largest and the smallest individual, for the intermediate specimens showed intermediate values.

It follows from the table that parallel to the growth in body size the surface area of the fibres contained in 1 mm³ of muscle decreases, and so does the ratio of the surface area of the fibres to their volume.

The decrease in the surface area of the fibres is however comparatively much lower than it would be implied by the fact that the diameter of the fibre increased in the same time from 22.8 to 93.2 μ. This is understandable considering that the amount of contractile substance in 1 mm³ of muscle in a small individual is rather small (0.242 mm³), a large part of the cross area being occupied by the connective tissue, whereas in a large individual the amount of connective tissue becomes markedly smaller, and the amount of contractile substance increases to 0.681 mm³. Therefore, the surface area of the fibres per 1 mm³ of tissue does not diminish in the course of growth to such an extent as might be expected.

There is, however, a very marked deterioration of the relation between the surface area of the fibres and their volume. This quotient drops from 171 to 44. A comparison of these values with the decrease in the surface area of the capillaries per 1 mm^3 leads to the conclusion that the decrease in the number of capillaries in the muscle does not keep up with the decrease in the surface area of the fibres. The thickening of the fibres as the animal grows must result in a gradual deterioration of the blood supply conditions of the muscle irrespective of the density of the capillaries.

Schmidt-Nielsen and Pennycuik (1961), working on mammals, put forward the hypothesis that the density of vascularization of muscles depends to a large extent on the dimensions of the muscle fibres. According to these workers, however, the dimensions of the muscle fibres depend not only on the size of the animal: of great significance is also the type of the muscle and the way it works.

The efficiency of the muscles will certainly greatly depend on their supply with oxygen, and, consequently, on the intensity of vascularization of the respiratory surfaces. Though the presence of oxygen is not required during contraction, it is indispensable during relaxation, when takes place the re-synthesis of certain substances, in the first place of the lactic acid, produced during contraction, into glycogen.

Studies on the vascularization of the respiratory surfaces in amphibians have demonstrated that there are significant differences among species in the length of respiratory capillaries per 1 g of body mass (Czopek, 1955 a, b; 1957, 1959, 1960, 1961; G. Czopek, J. Czopek, 1959; Strawiński, 1956; Andrzejewski et al. - 1962). The fewest respiratory capillaries are found in larvae of *A.mexicanum* (over 6 m/g), *S.salamandra* (9 m/g) and metamorphosed specimens of *A.mexicanum* (about 12 m/g).

The *Salientia* have significantly more respiratory capillaries. E.g. *B.bombina* has about 15 m/g, *B.calamita* 25 m/g, and *H.arborea* nearly 46 m/g. The length of the respiratory capillaries becomes greatly reduced in the course of growth of the animal. While the freshly metamorphosed edible frog has nearly 45 m of respiratory capillaries per 1 g of body mass, the 43 and 66-g specimens have only about 18 m of these vessels, and the 250-g specimen has hardly 11 m/g (Table 10).

The great variations in the length of respiratory capillaries occuring in *Amphibia* may result in differences in the supply of oxygen to the muscles among various species, even though the vascularization of muscles in those species is of similar intensity. Thus the larvae of *A.mexicanum* have 59 to 65 m of muscle capillaries per 1 g of body mass, and the ratio of the lengths of respiratory capillaries to that of the muscle capillaries is about 1:10. The metamorphosed specimens of this species have a little fewer muscle capillaries (45 to 46 m), but in consequence of the considerable length of respiratory capillaries the relation of their length to the length of the muscle capillaries is over twice more favourable, viz. 1:3.98. Therefore, in spite of the slightly better vascularization of the muscles in the larvae, the conditions of gaseous exchange will be much better in the muscles of the metamorphosed specimens. This will ensure a higher efficiency of the muscles. The most favourable relation of the length of respiratory capillaries to that of the muscle capillaries is found in *H.arborea* (1:2.30). This frog, even in resting condition, generally finds itself in a position requiring a steady expenditure of energy, being suspended on a support by means of adhesive pads (Czopek, and Szarski, 1954). It may be therefore assumed that its muscles have an increased call for oxygen.

In the remaining species the relation in question is much the same, viz. from 1:5.08 (*B.bombina*) to 1:6.87 (*X.laevis*). Notwithstanding the fact that e.g. in *S.salamandra*, *R.esculenta* and *B.calamita* the ratio of the length of respiratory capillaries to that of muscle capillaries is much alike (about 1:5.5), the supply of oxygen to the muscles in these species will certainly vary. The worst conditions of supply of oxygen to the muscles exist in the salamander, which has only 9 m/g of respiratory capillaries. The best conditions on the other hand are found in *B.calamita*, in which there are 25 m/g of respiratory capillaries (Table 10).

It should be kept in mind that the efficiency of the muscles is determined not only by their vascularization and the length of respiratory capillaries per 1 g of body mass: of great significance are also other factors, as the number of erythrocytes per 1 mm^3 of blood, the varying capacity of hemoglobin of combining with oxygen and giving it up, differences in innervation etc.

The *Salientia*, as we know, possess significantly more erythrocytes in 1 mm^3 of blood than the *Urodela*; they also have a higher hemoglobin content (Herter, 1941). The quantity of erythrocytes and the amount of hemoglobin in *Amphibia* are subject to seasonal variations; they also depend on the degree of desiccation of the animals (Zepp, 1923; Heesen, 1924; Czopek, 1956) and on the stage of ontogeny (Korzhuiev et al., 1959).

Also metabolism in *Amphibia* is subject to great seasonal variations (Fromm & Johnson, 1955). The motor efficiency of the muscles in *Amphibia* is certainly reduced owing to the fact that 80% of the lactic acid produced while the muscle is working is retained in the muscle, where subsequently, under anaerobic conditions, it retransforms into glycogen. In mammals all the lactic acid penetrates with the blood to the liver, and there it is converted into glycogen (Bladergroen, 1955). The major part of the lactic acid produced during contraction of muscles remaing in them and their vascularization being poor, the muscles of *Amphibia* will certainly need a rather long period of rest to convert the lactic acid into glycogen.

All those factors collectively determine the efficiency of the muscles in *Amphibia* and the level of metabolism of the muscular tissue. It seems therefore obvious that to estimate muscular efficiency solely on the base of morphological studies would mean an oversimplification of the problem. Conclusions based on such studies should be regarded with reserve, for they require verification by apropriate physiological studies.

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STRESZCZENIE

Zbadano intensywność unaczynienia mięśni u kilku okazów 2 gatunków płazów ogoniastych i 5 gatunków płazów bezogonowych. Obliczono także dla tych gatunków długość kapilar mięśniowych, ich powierzchnie i objętość przypadającą na 1 g masy mięśni oraz na 1 g masy ciała.

Najsilniejsze unaczynienie u płazów bezogonowych ma mięsień podszczękowy: od 279 kapilar/mm² (*R. esculenta* o wadze 250 g) do 807 kap/mm (*B. calamita*). Mięsień ten posiada na jednostkę powierzchni niemal dwukrotnie więcej kapilar niż mięśnie odnóży, a dwu- do czterokrotnie więcej niż m. grzbietu długi i m. brzucha prosty.

U płazów ogoniastych unaczynienie m. podszczękowego jest prawie równe lub nieco słabsze niż mięśni odnóży i waha się od 183 do 224 kap/mm². Mięsień ogonowy ma przeciętnie o połowę słabsze unaczynienie niż mięśnie odnóży. Wynosi ono niewiele ponad 100 kap/mm². Nieco silniejsze unaczynienie posiada m. grzbietu długi i m. brzucha prosty (od 100 do 153 kap/mm²).

Płazy ogoniaste mają w poszczególnych mięśniach prawie dwukrotnie więcej włókien niż kapilar. Płazy bezogonowe posiadają natomiast na jednostkę powierzchni 20 do 100% więcej kapilar niż włókien. Wyjątkiem jest m. podszczękowy, u którego przypada 15 do 30% więcej włókien niż kapilar. Ilość kapilar i włókien przypadająca na jednostkę powierzchni przekroju zmniejsza się u płazów w miarę wzrostu ciała, powiększa się natomiast znacznie średnica włókien.

Długość kapilar przypadająca na 1 g masy mięśni jest u wszystkich badanych gatunków płazów ogoniastych zbliżona i waha się od 102 do 121 m. Płazy bezogonowe mają znacznie więcej kapilar mięśniowych, duże są także u nich różnice międzygatunkowe (od 164 m u *X. laevis* do 314 m u *B. calamita*). Dlugość kapilar mięśniowych, jaka

przypada na 1 g masy ciała, jest zależna od stopnia umięśnienia gatunku. Długość ta u gatunków słabiej umięśnionych wynosi więcej niż połowę długości kapilar przypadających na 1 g mięśnia, natomiast u gatunków słabiej umięśnionych jest wyraźnie mniejsza.

Mimo że *Salientia* mają znacznie więcej kapilar niż *Caudata* zarówno na 1 g masy mięśni, jak i na 1 g masy ciała, powierzchnia tych naczyń u obu rzędów jest do siebie zbliżona, a ich objętość jest wyraźnie większa u płazów ogoniastych. Płazy ogoniaste mają bowiem przeciętnie 70 do 100% większą średnicę kapilar niż płazy bezogonowe.

Cena zł 9,—