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VASCULARIZATION OF RESPIRATORY SURFACES IN SOME *PLETHODONTIDAE*

by

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INTRODUCTION

Comparatively little research has been devoted to the vascularization of the respiratory surfaces in the Urodela. So far the vascularization of the skin, lungs and mouth has been investigated in *Triturus cristatus* (LAUR.), *T. alpestris* (LAUR.), *T. vulgaris* (L.), *Ambystoma mexicanum* (COPE) and *Salamandra salamandra* (L.) (CZOPEK, PUGACZEWSKA, SOPOĆKO 1954, BRODOWA 1956, CZOPEK 1957, 1959 a, b, 1960). The above-mentioned investigations have shown that most respiratory capillaries per gram of body mass are found in newts (15 to 17 m./gm.), less in metamorphosed individuals of *A. mexicanum* (about 12 m./gm.), and still less in *S. salamandra* (a little over 9 m./gm.). A particularly small quantity of respiratory capillaries is found in the large neotenic larvae of *A. mexicanum* (a little over 6 m./gm.). A considerable part in the gas exchange of the species mentioned is played by the lungs: the lung capillaries constitute in newts over 20 per cent, and in the European salamander even about 60 per cent of the total amount of respiratory capillaries.

It was no doubt interesting to study the vascularization of respiratory surfaces in lungless amphibians. Although there exist studies on vessels in the *Plethodontidae*, dealing with the structure of the skin and mouth, or with the intensity of gas exchange (BETHGE 1898, NOBLE 1925, MC COURT 1954, LÜDIKE 1955), they contain no particular data on the vascularization of respiratory surfaces. They lack such data as the length of respiratory capillaries per one gram of body mass in the particular species, the number of capillary meshes in 1 mm^2. of skin, or mouth etc. It was the aim of the present study to investigate the vascularization of the skin and mouth in the *Plethodontidae* and to supply the above-mentioned data.

MATERIAL AND METHOD

The material was collected and injected in 1959 by Prof. Dr. H. Szarski, who in that time stayed in the U.S.A. on a Rockefeller Foundation grant. He was helped in collecting and determining the material by the following American scientists: J. D. Anderson, Ch. M. Bogert, H. C. Dalton, H. A. Dundee C. J. Goin, M. K. Hecht, W. J. Riemer, R. C. Stebbins, E. P. Volpe, and R. G. Zweifel. To all of them I am greatly indebted. All the specimens were injected with Prussian blue through the truncus arteriosus. Out of a larger number 33 specimens were selected, 24 of which were studied in detail. Of each species were selected specimens differing widely in size of the body. This was aimed at revealing the possible differences in vascularization of respiratory surfaces within the particular species in connection with growth.

One species belonging to the *Desmognathinae* subfamily and six species of the *Plethodontinae* subfamily were studied. The species studied and the number and weight of the particular specimens are as follows:

Desmognathus fuscus (GREEN) — two specimens (1.87 gm., 6.16 gm.)

Plethodon glutinosus (GREEN) — five specimens (3.40 gm., 3.85 gm., 3.96 gm., 5.50 gm., 6.80 gm.)

Plethodon jordani metcalfi BRIMLEY — two specimens (2.20 gm., 2.86 gm.)

Batrachoseps attenuatus (ESCHOLTZ) — four specimens (0.51 gm., 0.62 gm., 0.63 gm., 0.69 gm.)

Aneides flavipunctatus (STRAUCH) — three specimens (3.17 gm., 3.77 gm., 7.37 gm.)

Aneides lugubris (HALLOWELL) — four specimens (1.30 gm., 1.38 gm., 2.96 gm., 13.60 gm.)

Eurycea longicauda (GREEN) — four specimens (1.43 gm., 1.54 gm., 1.65 gm., 3.85 gm.).

The above species will be discussed in the paper in the same systematic order.

The method applied was the same as the one used and described in detail in the author's previous works (CZOPEK 1955).

STRUCTURE OF THE SKIN

The skin shows considerable differences in structure depending on the species. The differences concern the number of layers in the epidermis and its thickness, as well as the thickness of the corium, the number of glands and their distribution. It should be noted that these differences occur not only among species, but also among the particular regions of the skin in individuals.

Desmognathus fuscus. The skin is covered with an epidermis consisting on the average of 4 to 6 layers of cells, and the weighted mean of its thickness is 25.8 μ. The epidermis is somewhat thicker on the ventral side of the body (25 to 26 μ) than on the dorsal side (22 to 23 μ). It is still thicker on the tail (30 μ). The corium, conversely, is thicker on the dorsal side (110 to 120 μ), and thinner on the ventral side (70 to 80 μ). It is very thick on the tail (250 μ). The weighted mean of the thickness of the corium amounts to 132 μ. 1 mm.² of skin contains an average of 84 glands, the skin on the posterior part of the body containing fewer glands than on the anterior. Fewest glands occur in the tail (table 1).

Table 1

Desmognathus fuscus

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	4-5	22	110	90
Posterior part of back	4-5	23	120	86
Anterior part of belly	5-7	25	80	92
Posterior part of belly	4-7	26	70	86
Tail	4-8	30	250	76
The weighted mean	4-6	25.8	132.0	84.0

Table 2

Plethodon glutinosus

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	4-5	25	200	76
Posterior part of back	4-5	26	230	72
Anterior part of belly	4-6	36	120	88
Posterior part of belly	4-6	38	150	83
Tail	4-7	39	440	68
The weighted mean	4-6	35.5	235.0	74.3

Plethodon glutinosus has an epidermis consisting, on the average, of 4 to 6 layers of cells. The epidermis on the back is 25 to 26 μ thick, on the belly and tail it is 36 μ and 39 μ thick. The thickness of the corium

ranges from 200 to 230 μ on the back, from 120 to 150 μ on the belly, and amounts to 440 μ on the tail. The average number of glands in 1 mm.² of skin is 74 (table 2).

Plethodon jordani metcalfi. The weighted mean of the thickness of the epidermis is 25.2 μ, that of the corium 130 μ. The epidermis on the dorsal side of the trunk is thin (19 to 20 μ), on the ventral side and the tail it is much thicker (26 to 30 μ). Like in *P. glutinosus*, the tail has the thickest corium (260 μ). The corium on the trunk ranges in thickness from 70 to 100 μ. The number of glands averages 82 per 1 mm². (table 3).

Table 3

Plethodon jordani metcalfi

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	4-5	19	95	81
Posterior part of back	4-5	20	100	77
Anterior part of belly	4-5	26	70	98
Posterior part of belly	4-5	26	75	90
Tail	4-7	30	260	78
The weighted mean	4-5	25.2	130.0	82.0

Table 4

Batrachoseps attenuatus

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	3-5	12	30	87
Posterior part of back	3-5	13	34	83
Anterior part of belly	3-5	14	38	84
Posterior part of belly	3-5	15	40	78
Tail	3-6	18	48	75
The weighted mean	3-5	14.8	39.2	78.1

Batrachoseps attenuatus has the thinnest skin of all amphibian species studied so far. The epidermis on the back ranges in thickness from 12 to 13 μ, on the belly and tail it is somewhat thicker — from 14 to 18 μ.

The thickness of the corium ranges from 30 to 40 μ on the trunk, and reaches 48 μ on the tail. The average number of glands is 78 per 1 mm.² of skin (table 4).

Aneides flavipunctatus. The thickness of the epidermis is 20 μ on the back, and 23 to 25 μ on the belly and tail. In the skin of this species there is a particularly well developed pigment layer composed mainly of melanophores. They form in the corium an almost uniform layer constituting three-fourths its entire thickness on the belly, and seven-eights on the back, so that only a thin layer adjacent to the subdermal tissue is devoid of pigment cells. The corium, like in the preceding species, is thickest on the tail (250 μ), much thinner on the back (180 to 190 μ), and thinnest on the belly (100 to 110 μ). The weighted mean of its thickness is 175 μ. There are 75 glands per 1 mm.² of skin (table 5).

Table 5

Aneides flavipunctatus

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	4-5	20	180	80
Posterior part of back	3-5	20	190	77
Anterior part of belly	4-5	23	100	84
Posterior part of belly	3-5	24	110	76
Tail	4-5	25	250	72
The weighted mean	4-5	22.8	175.0	75.2

Table 6

Aneides lugubris

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	3-5	18	90	80
Posterior part of back	3-4	18	92	74
Anterior part of belly	3-5	19	85	78
Posterior part of belly	3-5	20	88	67
Tail	3-5	24	130	67
The weighted mean	3-5	20.2	98.6	70.0

Aneides lugubris has a somewhat thinner epidermis and corium than the former species. The weighted mean of the thickness of the epidermis is 20.2 μ, that of the corium — 98.6 μ. Differently from the species discussed above, the differences in the thickness of the corium between the back and the belly are small (85 and 92 μ). The corium of the tail is also comparatively thin (130 μ). The mean number of glands in 1 mm.² of skin is 70 (table 6).

Eurycea longicauda is distinguished by particularly great differences in the thickness of epidermis between the dorsal and ventral side of the trunk. The thickness of the epidermis averages 16 to 18 μ on the back, and 36 to 37 μ on the belly. Differently from the species discussed above, the corium is much thicker on the belly than on the back (belly — 100 μ, back — 60 to 65 μ). The weighted mean of the thickness of the epidermis is 30.5 μ, that of the corium 96 μ. The average number of glands in 1 mm.² of skin is 91. (table 7).

Table 7

Eurycea longicauda

Investigated parts of the body	Number of layers of epidermis	Thickness of epidermis in μ	Thickness of corium in μ	Number of glands in 1 mm.² of skin
Anterior part of back	3-4	16	60	100
Posterior part of back	3-4	18	65	93
Anterior part of belly	4-5	36	100	104
Posterior part of belly	4-5	37	100	93
Tail	4-6	38	130	85
The weighted mean	4-5	30.5	96.0	91.3

VASCULARIZATION OF THE SKIN

The vascularization of the skin in the Urodela is distinguished from that in the Salientia by its lack of special arteries and veins exclusively for the supply of the skin. The subepidermal capillaries of the skin form a network, the density of which depends not only on the region of the body and on the species, but also on the size of the body of the specimen. Small individuals have a better developed network of skin capillaries than large individuals of the same species (fig. 1 to 3).

Desmognathus fuscus. The mean number of capillary meshes in 1 mm.² of skin is 106 to 109. The anterior part of the trunk is better vascularized than its posterior part. The tail has a poorer developed capillary network

Table 8

Specimen	Weight of body in grams and sex	Number of meshes of capillary-net per 1 mm.² of skin					
		Anterior part of back	Posterior part of back	Anterior part of belly	Posterior part of belly	Tail	The weighted mean
D. fuscus	1.87 ♂	128	113	123	98	94	109.2
	6.16 ♂	121	100	128	100	94	106.7
P. glutinosus	3.40 ♂	110	110	108	102	109	109.6
	3.85 ♀	115	110	112	110	106	112.4
	3.96 ♀	123	112	119	111	105	112.0
	5.50 ♂	126	120	112	112	117	118.3
	6.80 ♀	117	110	112	108	105	109.5
P. jordani metcalfi	2.20 ♂	125	119	112	105	112	116.0
	2.86 ♀	118	113	119	108	108	112.1
B. attenuatus	0.51 ♀	69	60	68	64	63	64.3
	0.62 ♀	60	61	71	65	62	63.3
	0.63 ♂	66	64	65	60	66	64.6
	0.69 ♀	68	66	66	63	64	65.0
A. flavipunctatus	3.17 ♀	87	104	90	85	81	87.6
	3.77 ♂	87	96	91	84	78	85.2
	7.37 ♀	71	85	70	70	66	71.0
A. lugubris	1.30 ♂	88	81	88	76	71	78.6
	1.38 ♂	87	78	80	77	72	77.3
	2.96 ♂	68	60	61	58	56	59.5
	13.60 ♀	56	51	49	46	45	48.4
E. longicauda	1.43 ♂	94	87	87	72	70	78.9
	1.54 ♀	88	85	86	78	73	79.3
	1.65 ♂	93	87	82	75	71	78.8
	3.85 ♂	83	76	83	74	74	76.9

(table 8). The specimen weighing 1.87 gm. has 13.992 m. of skin capillaries per gram of body mass, while the specimen weighing 6.16 gm. has only 9.122 m./gm. This difference is due mainly to the fact that the relation of body surface to body mass becomes less favourable as the body grows in size, and not to a decrease in intensity of the vascularization of the skin. For, the number of capillary meshes in 1 mm.² in both specimens is similar, whereas the ratio of body surface (in cm².) to body mass (in gm.) deteriorates; the respective ratios are 6.69 and 4.41 (table 9 and 10). The diameter of the capillaries varies from 6-16 μ in the small specimen (mean 10.8 μ) to 7-20 μ in the large one (mean 12.5 μ).

Plethodon glutinosus. The weighted mean of the number of meshes in 1 mm.² of skin varies from 109 to 118. The intensity of vascularization of the particular regions of the skin is much like that in *D. fuscus*. The

Table 9

Specimen	Weight of body in grams and sex	Length of body in mm.	Surface of skin in mm.²	Length of skin capillaries in meters per 1 gm. of body mass	Surface of the mucous membrane of mouth cavity in mm.	Number of meshes of capillary net per 1 mm.²	Length of mouth cavity capillaries in meters per 1 gm. of body mass
D. fuscus	1.87 ♂	78	1 252	13.992	72	121	1.186
	6.16 ♂	117	2 720	9.122	170	125	1.110
P. glutinosus	3.40 ♂	95	1 875	11.547	126	110	0.994
	3.85 ♀	102	2 110	11.618	136	104	0.936
	3.96 ♀	110	2 080	11.114	134	112	0.931
	5.50 ♂	118	2 590	10.247	180	96	0.833
	6.80 ♀	127	2 980	9.168	196	92	0.719
P. jordani metcalfi	2.20 ♂	94	1 490	14.588	108	110	1.235
	2.86 ♀	102	1 880	13.857	124	104	1.101
B. attenuatus	0.51 ♀	63	516	16.229	24	81	0.932
	0.62 ♀	67	624	16.023	28	83	0.888
	0.63 ♂	68	628	16.029	28	83	0.873
	0.69 ♀	69	662	15.466	30	82	0.866
A. flavipunctatus	3.17 ♀	103	2 050	12.106	108	77	0.777
	3.77 ♂	116	2 180	10.674	120	75	0.716
	7.37 ♀	127	2 940	6.726	172	72	0.515
A. lugubris	1.30 ♂	65	948	12.922	88	76	1.533
	1.38 ♂	67	990	12.612	100	74	1.618
	2.96 ♂	88	2 120	11.044	136	74	1.027
	13.60 ♀	140	4 285	4.385	154	70	0.246
E. longicauda	1.43 ♂	86	1 124	13.959	64	77	0.863
	1.54 ♀	90	1 180	13.654	70	72	0.848
	1.65 ♂	93	1 196	12.873	70	72	0.791
	3.85 ♂	117	2 160	9.841	100	67	0.467

length of skin capillaries ranges from 11.547 m./gm. (specimen weighing 3.40 gm.) to 9.168 m./gm. (specimen weighing 6.80 gm.). The range of variation is smaller than in *D. fuscus*, because the differences in body size are also smaller. The ratio of body surface to body mass decreases from 5.51 to 4.38 (table 8, 9 and 10). The differences in the diameter of skin capillaries are fairly considerable. Its mean in the specimen weighing 3.40 gm. is 12.5 μ. The diameter of the capillaries becomes somewhat larger with the growth of the body and in the specimen weighing 6.80 gm. it amounts to 14 μ.

Plethodon jordani metcalfi is much smaller than the former species, and therefore its relation of body surface to body mass is more favourable (2.20 gm. specimen — ratio 6.77, 2.86 gm. specimen — ratio 6.57). The specimens have 116 and 112 capillary meshes in 1 mm.^{2} of skin, and the length of these capillaries per gram of body mass amounts to 14.588 m. and 13.857 m. (table 8 and 9). The diameter of the capillaries varies from 8 to 19 μ, and averages 13.5 μ.

Batrachoseps attenuatus. The average number of capillary meshes in 1 mm.^{2} of skin in this species is 63 to 65, i. e. just over a half their number in the species described above. The front of the body is better vascularized than its back (table 8). The elongated shape of the body and its low weight are responsible for the outstandingly favourable relation of its surface to its mass (ratio from 9.59 to 10.12). Therefore, in spite of the relatively poorly developed network of skin capillaries, this species has more skin capillaries per gram of body mass than any other species of the *Plethodontidae* (16.229 m./gm. to 15.466 m./gm). The diameter of the capillaries averages 13 μ.

Aneides flavipunctatus. Two small specimens, weighing 3.17 g. and 3.77 g. and a large one, weighing 7.37 g. were investigated. In consequence of the considerable differences in body size the ratio of surface to mass decreases from 6.47 (3.17 g. specimen) to 3.99 (7.37 g. specimen). The number of capillary meshes in 1 mm.^{2} of skin amounts to 87.85 and 71 respectively, and the length of skin capillaries per gram of body mass in the three specimens studied is 12.106 m., 10.674 m., and 6. 726 m. (table 8, 9 and 10). The diameter of the capillaries in the small specimens averages 16 μ, in the large one 18.3 μ.

Aneides lugubris. The specimens of this species vary in size of body to a very considerable extent: the largest specimen is more than 10 times the weight of the smallest one. Owing to this circumstance we observe in *A. lugubris* greater differences in intensity of vascularization of the skin than in the other species. The weighted mean of the number of capillary meshes in 1 mm.^{2} of skin decreases with the growth of the body from 78 (small specimen) to 48 (large specimen). The length of skin capillaries falls from 12.922 m./gm. to 4.385 m./gm., and the ratio surface/mass decreases from 7.29 to 3.15 (tables 8 and 10). The diameter of the capillaries, on the other hand, increases from 9-21 μ in the small specimens (mean 14.5 μ) to 10-34 μ in the large one (mean 21 μ).

Eurycea longicauda. The specimens studied do not much vary in size of the body. The ratio surface/mass decreases from 7.86 to 5.61. The number of capillary meshes in 1 mm.^{2} of skin averages from 76 to 79, and the length of the capillaries falls from 13.959 m./gm. (1.43 — gm. specimen) to 9.841 m./gm. (3.85 gm. specimen) (tables 8, 9 and 11). The

Table 10

Specimen	Weight of body in grams. Sex	Total length of capillaries of respiratory organs in meters per 1 gm. of body mass	Total surface of capillaries of respiratory organs in cm^2 per 1 gm. of body mass	Ratio of surface of skin (in cm^2) to body weight (in gm.)	Length of capillaries of respiratory organs in per cent of total		Surface of capillaries of respiratory organs in per cent of total	
					Skin	Mouth cavity	Skin cavity	Mouth
D. fuscus	1.87 ♂	15.178	5.286	6.69	92.19	7.81	89.78	10.22
	6.16 ♂	10.232	3.992	4.41	89.15	10.85	89.70	10.30
P. glutinosus	3.40 ♂	12.541	4.954	5.51	92.07	7.93	91.50	8.50
	3.85 ♀	12.554	4.958	5.48	92.54	7.46	91.99	8.01
	3.96 ♀	12.045	4.758	5.25	92.27	7.73	91.70	8.30
	5.50 ♂	11.080	4.859	4.71	92.48	7.52	92.73	7.27
	6.80 ♀	9.887	4.337	4.38	92.73	7.27	92.97	7.03
P. jordani metcalfi	2.20 ♂	15.793	6.730	6.77	92.37	7.63	91.93	8.07
	2.86 ♀	14.958	6.361	6.57	92.64	7.36	92.39	7.61
B. attenuatus	0.51 ♀	17.161	6.991	10.12	94.57	5.43	94.80	5.20
	0.62 ♀	16.911	6.890	10.06	94.75	5.25	94.98	5.02
	0.63 ♂	16.902	6.886	9.97	94.83	5.17	95.06	4.94
	0.69 ♀	16.332	6.653	9.59	94.70	5.30	94.93	5.07

Specimen	Weight of body in grams. Sex	Total length of capillaries of respiratory organs in meters per 1 gm. of body mass	Total surface of capillaries of respiratory organs in cm^2 per 1 gm. of body mass	Ratio of surface of skin (in cm^2) to body weight (in gm.)	Length of capillaries of respiratory organs in per cent of total		Surface of capillaries of respiratory organs in per cent of total	
					Skin	Mouth cavity	Skin	Mouth cavity
A. flavipunctatus	3.17 ♀	12.883	6.450	6.47	93.97	6.03	94.33	5.67
	3.77 ♂	11.390	6.037	5.78	93.71	6.29	94.42	5.58
	7.37 ♀	7.241	4.110	3.99	92.89	7.11	94.09	5.91
A. lugubris	1.30 ♂	14.455	6.488	7.29	89.39	10.61	90.72	9.28
	1.38 ♂	14.230	6.380	7.17	88.63	11.37	90.05	9.95
	2.96 ♂	12.071	5.433	7.16	91.49	8.51	92.58	7.42
	13.60 ♀	4.631	3.078	3.15	94.69	5.31	96.23	3.77
E. longicauda	1.43 ♂	14.822	6.390	7.86	94.18	5.82	94.70	5.30
	1.54 ♀♂	14.502	6.252	7.66	94.15	5.85	94.67	5.33
	1.65 ♂	13.664	5.890	7.25	94.21	5.79	94.74	5.26
	3.85 ♂	10.308	4.814	5.61	95.47	4.53	96.20	3.80

differences in the diameter of the capillaries among the specimens are but slight. The diameter of the capillaries varies from 9 to 21 μ, averaging 15 μ.

In no one of the *Plethodontidae* studied so far does the surface of the capillaries in 1 mm². of skin exceed 1 mm.², and it ranges from 0.650 mm.² (*B. attenuatus*) to 0.940 mm.² (*A. lugubris* — specimen weighing 13.60 gm.).

VASCULARIZATION OF THE MOUTH

In the study of the vascularization of the mouth only the mucous membrane of the palate was examined in detail. It has been assumed for simplicity that the surface of the whole mouth is twice the surface of the palate, and that the intensity of vascularization of the floor of the mouth and that of the palate are similar.

The meshes of the capillary network vascularizing the mucous membrane of the mouth widely vary in size, also the density of the network is subject to variation depending on the region of the mouth. The best vascularization is noted in the region of the choanae, the poorest in the region of the mucous membrane covering the parasphenoid. The capillary walls have more or less developed digitiform diverticulae. In *B. attenuatus* and *E. longicauda* these are but poorly developed, so that they increase the surface of the vessels by no more than 10 per cent. In *P. jordani metcalfi* the increase in vessel surface induced by the diverticulae is twice as large, and in *P. glutinosus*, *A. flavipunctatus* and *A. lugubris* it averages 30 per cent (fig. 4 and 5). In *D. fuscus* there are only few diverticulae, but the vessels are sinuous; less so in the specimen weighing 1.87 gm., and more so in the one weighing 6.15 gm.

The intensity of vascularization of the mouth in all species studied is similar to that of the skin. The number of meshes in 1 mm.² of mucous membrane averages 67 to 125 (table 9). It should be noted that the small specimens of a given species have more capillaries per gram of body mass than the large ones. This is accounted for by the large size of the head in proportion to the whole body in small specimens. Thus in the *A. lugubris* specimen weighing 1.30 gm. there are 1.533 m. of mouth capillaries per gram of body mass, whereas the specimen weighing 13.60 gm. has only 0.246 m./gm. of these vessels (table 9). The mouth capillaries constitute only 5 to 10 per cent of the total amount of respiratory capillaries. The diameter of the mouth capillaries in the particular species is very much like the diameter of the skin capillaries.

SUMMARY OF RESULTS AND DISCUSSION

The skin of the species investigated is covered with a thin epidermis, which undoubtedly favours the penetration of oxygen to the subepidermal

capillaries. Only in *E. longicauda* and *P. glutinosus* does the weighted mean of the thickness of the epidermis exceed 30 μ. In the remaining species the epidermis is thinner: from 20.2 μ in *A. lugubris* to 25.8 μ in *D. fuscus*. It is thinnest (14.8 μ) in *B. attenuatus*. The claim of some writers (BERNSTEIN 1953) that the epidermis in the *Plethodontidae* is thinner than in any other amphibian is in fact unfounded, for a similarly thin epidermis is found in such species as *B. bombina*, *T. alpestris*, *T. vulgaris* (CZOPEK 1955, 1959a, BRODOWA 1956). The epidermis varies in thickness depending on the region of the body. It is thicker on the belly than on the back. These differences are particularly great in *E. longicauda*: they exceed 100 per cent. In the remaining species they range from 10 to 30 per cent. The epidermis is thickest on the tail (tables 1 to 7). The weighted mean of the thickness of the corium varies from 39 μ (*B. attenuatus*) to 235 μ (*P. glutinosus*). The corium on the tail is from 20 to 150 per cent thicker than on the back. The corium of the ventral side of the body is much thinner than that of the dorsal side. Only in *B. attenuatus* and *E. longicauda* both the corium and the epidermis are thicker on the belly.

The *Plethodontidae*, with their thin epidermis, small size and strongly elongated shape of the body, more than any other amphibians are exposed to desiccation. This is prevented by the secretion of the very numerous skin glands. In those *Plethodontidae* which permanently stay in water the mucus layer protects the organism against excessive penetration of water from the medium. As demonstrated by the experiments of DINESMAN (1948), mucus remarkably impedes the penetration of water through the skin in amphibians.

The number of glands in the particular species varies from 70 (*A. lugubris*) to 91 (*E. longicauda*) in 1 mm.^{2} of skin, which means that it is two or three times as great as in other amphibian species with the exception of *Hyla arborea*, which has 97 glands per mm.^{2}. The dimensions of the glands are variable, depending on the region of the body. Large glands usually occur on the tail and laterally, and the diameter of the largest of them may exceed 450 μ (in *P. glutinosus*).

The intensity of the vascularization of the skin varies depending on the region of the body. The posterior part of the body has a poorer vascularization than the anterior part, the poorest vascularization is noted on the tail. The number of capillary meshes per 1 mm.^{2} of skin varies from 48 (*A. lugubris*) to 118 (*P. glutinosus*) (table 8). The number of meshes per mm.^{2} of skin decreases with the growth of the body: the greater the difference in size of the body of the specimens the more pronounced the decrease. Thus the *A. lugubris* specimen weighing 1.30 gm. has an average of 78 meshes per 1 mm.^{2}, while the specimen weighing 13.60 gm. has only 48. As the growth of the body is associated with a gradual deterioration

of the relation of surface to mass, the large specimens have a very small amount of skin capillaries per gram of body mass; this amount is the smaller the larger are the differences in body size among the specimens of one species. Thus the *A. lugubris* weighing 1.30 gm. has 12.922 m./gm. of capillaries, while the 13.60 gm. specimen has only 4.385 m/g. The ratio of body surface (in cm.^{2}) to body mass (in m./gm.) in these specimens is 7.29 and 3.15 respectively. In the remaining species the differences are not so great (tables 9 and 10). A particularly large amount of skin capillaries (15.466 m/gm. to 16.229 m./gm. and a favourable ratio of surface to mass (9.59 to 10.12) characterize *B. attenuatus* (weight of specimens from 0.51 to 0.69 gm.). It should be stressed that in all other amphibian species investigated the decrease in length of skin capillaries per gram of body mass associated with body growth is much less pronounced than in the *Plethodontidae*. Thus in *S. salamandra* weighing 1.18 gm. there are 8.607 m./gm. of skin capillaries, while the 38.00 gm. specimen has 3.777 m./gm. of these capillaries (CZOPEK 1960). A freshly metamorphosed *R. esculenta* weighing 1.74 gm. has 15.81 m./gm. of skin capillaries, and a specimen weighing 53.00 gm. has 6.140 m./gm. of them (STRAWIŃSKI 1957, CZOPEK 1955). Similar results have been obtained with *R. temporaria* and *R. terrestris* (ANDRZEJEWSKI, MACIASZEK 1960.)

As the body grows in size, we observe in the *Plethodontidae* a gradual increase in the diameter of the skin capillaries. The increase is slight in the species in which the individual differences in body size are small (e. g. in *P. glutinosus* it is 10 per cent), it may, however, exceed 50 per cent, when the specimens studied differ considerably from one another in body size (as in *A. lugubris*). The increase in the diameter of the capillaries accounts for the fact that the differences in capillary surface per gram of body mass among the specimens of one species are much smaller than the differences in their length (table 10). Thus with *A. lugubris* the 1.30 gm. specimen has 14.455 m./gm. of respiratory capillaries, and the 13.60 gm. specimen has only 4.631 m./gm. i. e. four times less. The surface of these capillaries in the small specimen amounts to 6.488 cm.^{2}/gm., whereas in the large one it is smaller only by one half (3.078 cm.^{2}/gm.). The increase in diameter of the skin capillaries is undoubtedly a factor capable of compensating to a certain extent the limitation of the vascularization of the skin associated with body growth and deterioration of the surface/mass ratio.

It is noteworthy that the epidermis in the large specimens is much thicker than in the smaller ones belonging to the same species. Thus in *S. salamandra* weighing 1.18 gm. the epidermis of the skin does not exceed 20 μ in thickness, while in the specimen weighing 38.00 gm. it amounts to 59 μ (CZOPEK 1960). The penetration of oxygen to the subepidermal

capillaries will therefore be impeded in large specimens. In consequence of the increase in diameter of the capillaries the rate of the blood flow will be slowed down and so the oxygenation of the blood will improve. In some amphibians a seasonal increase in capillary diameter has been described. Thus in *T. vulgaris* the diameter of skin capillaries increases in the breeding season by an average of 25 per cent, while the epidermis of the skin becomes markedly thinner. These changes are probably an adaptation to the organism's increased oxygen demand (CZOPEK 1959 a).

As already mentioned in the chapter discussing the vascularization of the skin, the capillary surface per 1 mm.^{2} of skin in the *Plethodontidae* does not exceed 1 mm.^{2}, and ranges from 0.650 mm.^{2} (*B. attenuatus*) to 0.940 mm.^{2} (*A. lugubris* — specimen weighing 13.60 gm.). This lends support to the author's hypothesis (CZOPEK 1959 c) that an increase in capillary surface to the extent that it would exceed the surface of the skin through which the penetration of oxygen takes place would be of no avail. In such a case part of the capillaries would be unable to perform respiratory functions and would prove superfluous.

The intensity of vascularization of the mouth in the particular species is similar to that of the skin. The capillaries of the mucous membrane of the mouth have digitiform diverticulae, developed to various degrees in the particular species. They increase the respiratory surface by 10 to 30 per cent. Only in *D. fuscus* the vessels form but few diverticulae, but have a pronouncedly sinuous course instead. Considering that the mouth surface is very small in proportion to the skin surface, respiration through the mouth will probably be of little importance in gas exchange. An evidence of this is the small length of mouth capillaries per gram of body mass: from 0.246 m./gm. (A. lugubris weighing 1.30 gm.) to 1.533 m./gm (*A. lugubris* weighing 13.60 gm) which constitutes from 5 per cent to about 11 per cent of all respiratory capillaries. In most *Plethodontidae* the mouth capillaries constitute only 5 to 7 of respiratory capillaries. Their part in gas exchange is therefore small as compared with that of the skin capillaries. MCCOURT (1954) also claims that it is the skin, not the mouth, that plays the main role in gas exchange in the *Plethodontidae*. In other Urodela, as well as in the Salientia, the mouth capillaries constitute in most cases from 1 per cent to 3 per cent of all respiratory capillaries (CZOPEK 1955, 1957, 1959, BRODOWA 1956), that is, even less than in the *Plethodontidae*. According to VOS (1936), the gular movements of the mouth floor in amphibians are of no, or very little, importance in gas exchange. These movements are associated with the organ of smell rather than with respiration (MATTHES 1924, ELKAN 1955).

Similar lengths of respiratory capillaries as the *Plethodontidae* have been found in newts (15.090 m./gm. to 16.814 m./gm.) and in metamorphosed spe-

cimens of *A. mexicanum* (11.492 m./gm. to 11.760 m./gm.). More respiratory. capillaries per gram of body mass occur in the genus *Rana* (17.870-18.650 m./gm.), in the genus *Bufo* (19.680-25.034 m./gm.),and in *H. arborea* (45.990 m./gm.). The reason for the better vascularization of respiratory surfaces in the Salientia is the presence of well developed lungs, the capillaries of which constitute 62.5 to 74.7 per cent of all respiratory capillaries. (CZOPEK, PUGACZEWSKA, SOPOĆKO 1954, CZOPEK 1955, 1957, 1959a, BRODOWA 1956, G. CZOPEK, J. CZOPEK 1959).

SUMMARY

The vascularization of the respiratory surfaces has been studied in seven species of the *Plethodontidae*. It has been found that the length of respiratory capillaries per gram of body mass gradually decreases as the body grows, the decrease being the more pronounced, the larger the interindividual differences in body size.

As the body grows, the number of capillary meshes per mm². of skin decreases, while the diameter of the skin capillaries becomes from 10 to 50 per cent larger. The increase in the diameter of the capillaries is undoubtedly capable of compensating to a certain extent the limitations associated with the deterioration of the surface/mass ratio in the course of the animal's growth. It induces an increase in the diffusion surface of the vessels, slows down the rate of the blood current and so contributes to its better oxygenation.

The length of the respiratory capillaries varies in the particular species from 17.161 m./gm. (*B. attenuatus*) to 4.631 m./gm. (large specimen of A. *lugubris*). The capillary surface ranges from 6.991 cm²./gm. (*B. attenuatus*) to 3.078 cm²./gm. (large specimen of *A. lugubris*).

Nearly 90 to 95 per cent of respiratory capillaries are situated in the skin, the mouth capillaries constitute only 5 to 10 per cent of all respiratory capillaries.

UNACZYNIENIE POWIERZCHNI ODDECHOWYCH U *PLETHODONTIDAE*

STRESZCZENIE

Zbadano unaczynienie powierzchni oddechowych u siedmiu gatunków płazów. Wykazano, że długość kapilar oddechowych jaka przypada na 1 g masy ciała obniża się stopniowo w miarę wzrostu ciała i to tym wyraźniej, im większe są różnice w wielkości ciała badanych okazów.

W miarę wzrostu ciała zmniejsza się ilość oczek kapilar przypadających na 1 mm² skóry, zwiększa się natomiast od 10% do 50% średnica kapilar skórnych. Powiększenie średnicy kapilar jest niewątpliwie czynnikiem zdolnym do pewnej kompensacji ograniczeń związanych z pogarszającym się w miarę wzrostu ciała stosunkiem powierzchni do masy. Powoduje wzrost powierzchni dyfuzyjnej naczyń, zmniejsza chyżość prądu krwi i przyczynia się do lepszego jej natlenienia.

Długość kapilar oddechowych waha się u poszczególnych gatunków w granicach od 17.161 m/g (*B. attenuatus*) do 4.631 m/g (wielki okaz *A. lugubris*). Powierzchnia kapilar wynosi od 6.991 cm²/g (*B. attenuatus*) do 3.078 cm²/g (wielki okaz *A. lugubris*).

Niemal 90 do 95% kapilar oddechowych przypada na skórę, kapilary jamy gębowej stanowią zaledwie od 5 do 10% wszystkich kapilar oddechowych.

REFERENCES

Andrzejewski, H. J., Maciaszek, M., 1960: Unaczynienie powierzchni oddechowych u młodych okazów żaby trawnej (*Rana temporaria* L.), żaby moczarowej (*Rana terrestris* Andrz.) i rzekotki drzewnej (*Hyla arborea* L.). Zesz. Nauk. Uniw. M. Kopernika, Biol., 5, 17-28.

Bernstein, H., 1953: Structural modifications of the amphibian skin. Proc. Pennsylvania Acad. Sci., 27, 204-211.

Bethge, E., 1898: Das Blutgefässsystem von *Salamandra maculata*, *Triton taeniatus* und *Spelerpes fuscus*, mit Betrachtungen über den Ort der Athmung beim lungenlosen *Spelerpes fuscus*. Zeit. wiss. Zool., 63, 680-707.

Brodowa, G., 1956: Unaczynienie powierzchni oddechowych traszki górskiej (*Triturus alpestris* Laur.). Stud. Soc. Scient. Tor., 3, 85-93.

Dinesman, L. G., 1948: Adaptation of amphibia to varying conditions of air humidity. Zool. Zhurnal, 27, 231-239. (in Russian).

Elkan, E., 1955: The buccal and pharyngeal mucous membrane in urodeles. Proc. Zool. Soc. London, 125, 685-692.

Czopek, G., Czopek, J., 1959: Vascularization of respiratory surfaces in *Bufo viridis* Laur. and *Bufo calamita* Laur. Bull. Acad. Polon. Sci. Série sci. biol., 7, 39-45.

Czopek, J., 1955: The vascularization of respiratory surfaces of some Salientia. Zool. Pol., 6, 101-134.

Czopek, J., 1957: The vascularization of respiratory surfaces in *Ambystoma mexicanum* (Cope) in ontogeny. Zool. Pol., 8, 131-149.

Czopek, J., 1959 a: Skin and lung capillaries in European Common Newts. Copeia, 2, 91-96.

Czopek, J., 1959b: Vascularization of respiratory surfaces in *Salamandra salamandra* L. in ontogeny. Bull. Acad. Polon. Sci. Série sci. biol., 7, 473-478.

Czopek, J., 1959c: Surface of skin and lung capillaries of amphibians. Bull. Acad. Polon. Sci. Série sci. biol., 7, 479-484.

Czopek, J., 1960: Unaczynienie powierzchni oddechowych u salamandry plamistej (*Salamandra salamandra* L.) w rozwoju ontogenetycznym. Zesz. Nauk. Uniw. M. Kopernika, Biol., 5, 3-16.

CZOPEK, J., PUGACZEWSKA, H., SOPOĆKO, I., 1954: Unaczynienie powierzchni oddechowych u traszki grzebieniastej (*Triturus cristatus* LAUR.). Folia Morph., 5, 93-104.

LÜDIKE, R., 1955: Über den Respirationsapparate verschiedenen Urodelen und seine Beziehungen zum Herzen. Z. Morph. u. Ökol. Tiere, 43, 578-615.

MATTHES, E., 1924: Das Geruchsvermögen von Triton beim Aufenthalt unter Wasser. Z. vgl. Physiol., 1, 57-83.

MC COURT, R., P., 1954: The comparative morphology and physiology of the respiratory system of the lungless salamanders (*Plethodontidae*). The Ohio State University, Dissertation.

NOBLE, G. K., 1925: The integumentary, pulmonary, and cardiac modifications correlated with increased cutaneous respiration in amphibia: A solution of the "hairy frog" problem. J. Morphol., 40, 341-416.

STRAWIŃSKI, S., 1956: Vascularization of respiratory surfaces in ontogeny of the edible frog, *Rana esculenta*. Zool. Pol., 7, 327-365.

VOS, H. J., 1936: Über die Atembewegungen und den Schnüffelmechanismus (Kehloszillationen) bei Reptilien und Amphibien. Zool. Anz., 115, 142-144.

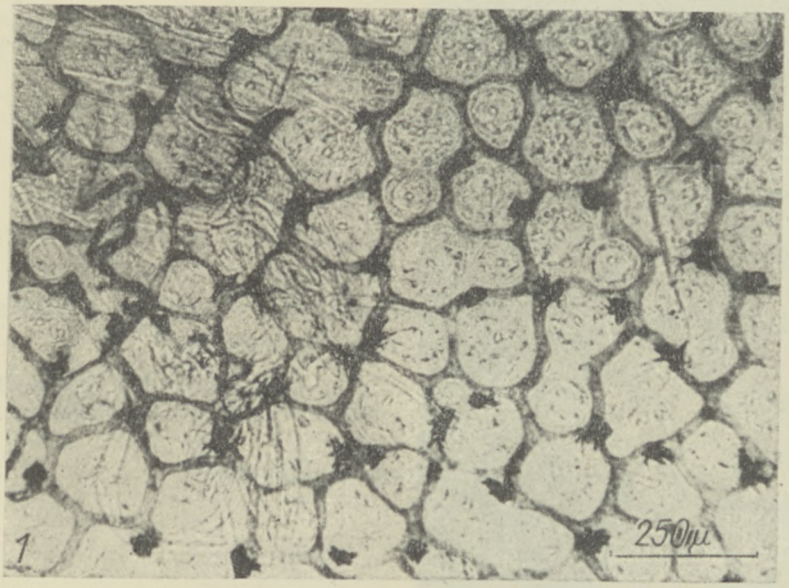

Fig. 1. Capillaries of the skin in *Aneides lugubris* (Hallowell) weighing 1.30 gm.

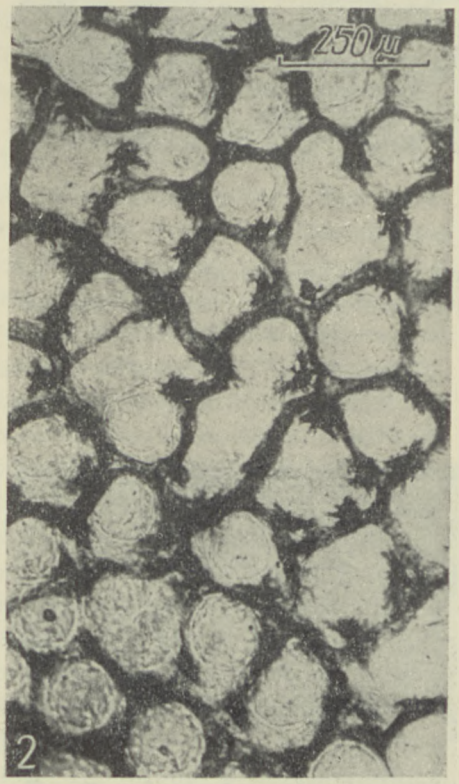

Fig. 2. Capillaries of the skin in *Aneides lugubris* (Hallowell) weighing 13.60 gm.

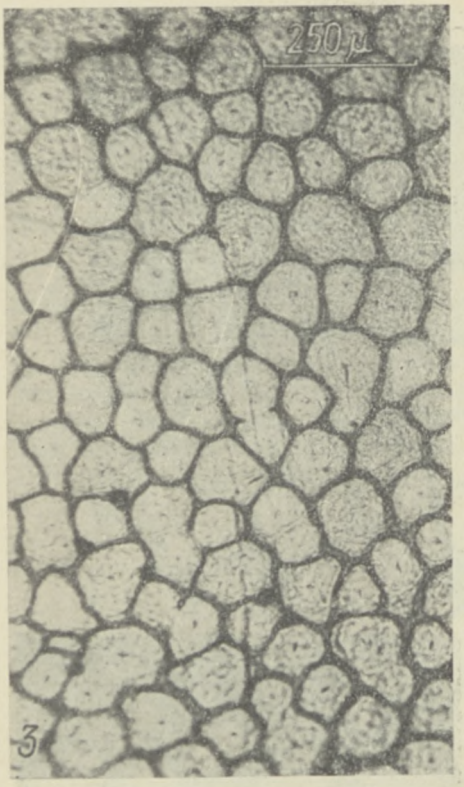

Fig. 3. Capillaries of the skin in *Plethodon jordani metcalfi* Brimley weighing 2.00 gm.

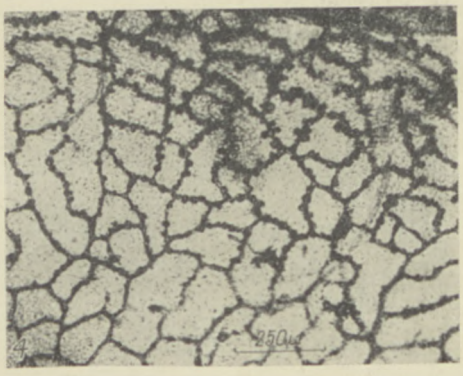

Fig. 4. Capillaries of the palate in *Plethodon glutinosus* (Green) weighing 6.80 gm.

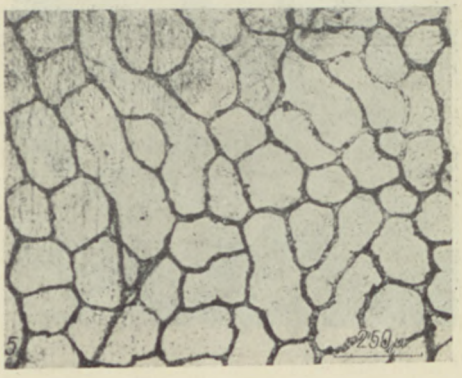

Fig. 5. Capillaries of the palate in *Eurycea longicauda* (Green) weighing 3.85 gm.