VASCULARIZATION IN THE BRAINS OF REPTILES
V. NOTES ON SOME SNAKES AND LIZARDS

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The occasion of the twenty-fifth anniversary of the Institute of Biology of the National University of Mexico is one for congratulation and for the most cordial expressions of comradeship towards both the members of the Institute and the people of Mexico of whose National University it forms a part. It is a welcome privilege to be able to mark the occasion by contributing, in however small and inadequate a manner, to the volume published in its honour.

A series of previous publications (Craigie 1941a, 1941b, 1941c, 1942) has been devoted to certain aspects of the morphology of the bloodvessels of the reptilian central nervous system and to quantitative measurements of vascular richness in the brains of a turtle, of Sphenodon, and of an alligator. For various reasons these were considered the most important representatives of the reptiles for study as part of the general survey of cerebral vascularity carried on by the writer during several decades.

Nevertheless, in a class so large and so diverse as the Reptilia, it does seem desirable to have some information regarding the state of affairs in the largest living order, the Squamata. Furthermore, the existence in this one order of two radically different types of cerebral vascular morphology rouses curiosity as to the quantitative relations in the possessors of mechanisms of these two types.

So long ago as 1878, Schöbl described the peculiar arrangement of the vessels in the brain-tissue of lizards, this tissue being penetrated by pairs of closely-applied vessels, which branch repeated-

ly in a strictly parallel manner to end finally in numerous hairpin loops without any anastomosis between the branches of one pair of vessels and those of another (Fig. 1). This arrangement appears to be an elaboration of a system of simple vascular loops found in the

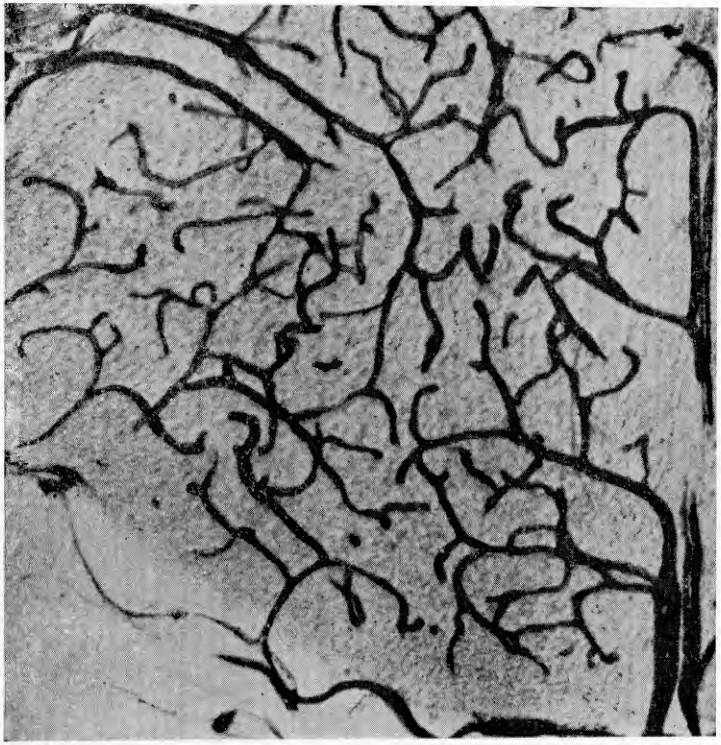

Fig. 1.—Photomicrograph of part of a transverse section of the medulla oblongata of a lizard, **Anolis carolinensis**, with injected bloodvessels, showing the arrangement of these in closely associated pairs terminating in hairpin loops and not anastomosing. Thickness 150 micra. Magnification × 100

brains of tailed amphibians (Schöbl, 1882; Sterzi, 1904; Craigie, 1938a) and coecilians (Craigie, 1940b). It is practically identical with that occurring in marsupial mammals (Wislocki and Campbell, 1937; Craigie, 1938b; Scharrer, 1939; Sunderland, 1941) and contrasts with the more usual arrangement found in other vertebrates, including the snakes, where the tissue of the brain, like that of other organs,

contains a continuous spongy network of capillaries supplied by numerous arteries and drained by numerous veins which are not closely associated with corresponding arteries (Fig. 2). An attempt to trace out the phylogenetic relations of these two types of vascular mechanism has been discussed by the present writer (1945).

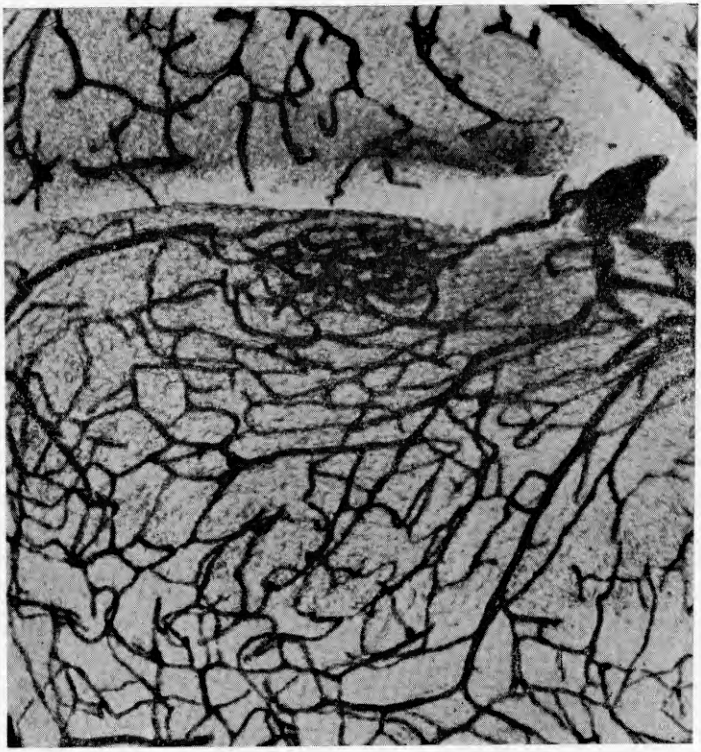

Fig. 2.—Photomicrograph of part of a transverse section of the medulla oblongata of a snake, **Sistrurus catenatus**, with injected blood-vessels, showing the arrangement of the capillaries in a spongy network connected with separate arteries and veins. Thickness 150 micra. Magnification × 100

Even within the suborder Sauria or Lacertilia, the lizards, the morphology is not constant, there being a few representatives of this group which have vascular networks (Schöbl, Sterzi) or show intermediate conditions (Craigie, 1941c; 1945). Material of these adequate for quantitative measurements has not been available in the present study, however.

MATERIAL AND METHODS

The material used in preparing these notes consists of four brains of the lizard **Anolis carolinensis** injected with carmine gelatine and cut into serial transverse sections after imbedding in celloidin and four brains of snakes prepared in the same way. The snakes belonged to three species, there being one common garter snake, **Thamnophis sirtalis sirtalis** (28 inches long); two massasaugas, **Sistrurus catenatus catenatus** (25-½ and 24 inches); and one water moccasin, **Agkistrodon piscivorus** (15-½ inches). In each case, every eleventh section was cut 150 micra thick for use in checking the completeness of injection, and the rest of the sections, including all in which measurements of the lengths of the capillaries were made, were 20 micra thick.

The measurements were made with a square-ruled eye-piece micrometer, all the instruments being the same which have been used throughout the author's studies in this field.

Unfortunately measurements of shrinkage were not made on these specimens. An approximate coefficient for correction for shrinkage (Craigie, 1924) was obtained from another garter snake brain. This coefficient was 0.76.

For identification of the regions in which measurements were made, series of sections stained with cresyl violet and by the method of Weil were employed for comparison. The publications of Crosby and Woodburne (1940), Frederikse (1931), Kappers, Huber and Crosby (1936), Warner (1931, 1935), and Weston (1936) among others were useful.

The use of so few specimens and particularly the inclusion of three different species of snakes make the observations open to some criticism. However, it being impracticable to extend the material at present, the results obtained have been deemed sufficient to justify their publication.

OBSERVATIONS

Richness of the capillary supply

Snakes.

The measurements of length of the capillaries in a unit volume of tissue with their averages before and after correction for shrinkage are recorded in table 1. The probable errors have not been recorded as the number of specimens is so small as to make these of little

value. Only the larger differences can be regarded as significant. No obvious differences between the three species of snakes represented are observed.

Nevertheless, plotting of the values and comparison with those for the turtle and alligator, which were represented by larger numbers of specimens, show that most of the relations are rather closely parallel so it is probable that they are reasonable approximations to the truth (Fig. 3).

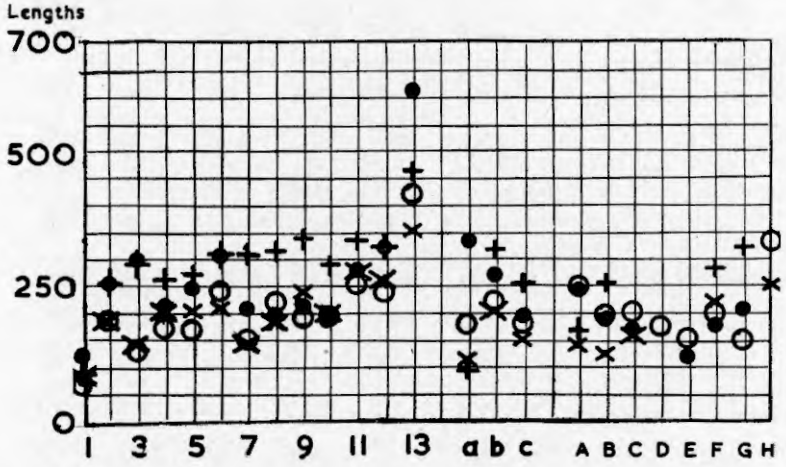

Fig. 3.—Graph showing the relative lengths in micra of the capillaries in 100^3 cubic micra of fresh tissue in various parts of the brain. ♀ snakes; + lizard (Anolis); X turtle (Chrysemys); O alligator. 1, fasciculus longitudinalis medialis; 2, nucleus motorius dorsalis X; 3, nucleus XII; 4, nucleus motorius VII; 5, nucleus motorius V; 6, nucleus fasciculi solitarii; 7, nucleus spinalis V; 8, cerebellum; molecular layer; 9, nucleus sensibilis principalis V; 10, cerebellum: granular layer; 11, cerebellum: lateral nucleus; 12, nucleus vestibularis ventrolateralis; 13, nucleus cochlearis; a, primordial nucleus supraopticus; b, nucleus mamillaris lateralis; c, nucleus hypothalamicus ventromedialis; A, hippocampus (cell layer in H_3); B, parahippocampal cortex (cell layer); C, primordium neopallii; D, primordium neopallii, molecular layer; E, pyriform cortex (cell layer); F, palaeostriatum; G, neostriatum; H, richer lateral portion of neostriatum

It is interesting to note that the excess in vascular richness of the cochlear nucleus, while occurring in all cases, is greater in the snakes than in other reptiles studied. The hypoglossal nucleus is relatively more richly vascular than in the reptiles with less mobile tongues.

In general, the order of magnitude of the values is not widely different from those in turtle and alligator though the snakes tend

TABLE 1. TOTAL LENGTH OF CAPILLARIES IN ½ × 189² × 200 C. MICRA BRAIN TISSUE OF SNAKES ON THE SLIDE AND CORRECTED VALUES

	Sn. 19 Thamnophis sirtalis sirtalis	Sn. 20 female Sistrurus catenatus catenatus	Sn. 21 male Sistrurus catenatus catenatus	Sn. 23 Agkistrodon piscivorus	Average length of capillaries in ½ × 189² × 200c. micra on slide.	Average length corrected for shrinkage (coef. 0.76)	Length in 100³ c. micra of fresh tissue
Fascic. long. medialis	407	470	772	786	609	461	129
Nucleus XII	1241	1477	1532	1538	1447	1100	307
Nuc. mot. X	1239	1163	1141	1279	1206	917	257
Nuc. mot. VII	1059	1062	945	956	1006	765	214
Nuc. mot. V	1095	1306	1223	1081	1176	894	250
Nuc. fasc. solit.	1243	1436	1507	1624	1452	1104	309
Nuc. spin. V	995	926	1116	904	985	749	210
Cerebel.: molecular	1125	770	1010	856	940	714	200
Nuc. sens. princ. V	818	1248	895	1123	1021	776	217
Cerebel.: granular	941	916	867	928	913	696	195
Cerebel.: nuc. lateralis	1194	1454	1295	1435	1345	1022	286
Nuc. vestib. ventrolat.	1569	1592	1604	1448	1553	1181	331
Nuc. cochlearis	2680	2703	3130	2996	2877	2186	612
Primord. nuc. supraopticus	1491	1485	1392	1981	1587	1206	337
Nuc. mam. lat.	1148	1415	1321	1290	1294	983	275
Nuc. hypothal. ventromed.	802	903	921	1094	930	707	198
Hippocampus (cell layer)	1045	1393	1166	1103	1176	894	250
Parahippocampal cortex	799	1005	960	929	923	701	196
Primord. neopallii	639	993	769	820	805	612	171
Pyriform cortex	714	930	652	1041	584	444	124
Palaeostriatum (mesostriatum)	778	834	786	1069	867	658	184
Neostriatum	916	887	1072	1210	1021	776	217

TABLE 2. TOTAL LENGTH OF CAPILLARIES IN ½ × 189² × 200 C. MICRA BRAIN TISSUE OF LIZARDS **(ANOLIS CAROLINENSIS)** ON SLIDE, AND CORRECTED VALUES

	Anolis 3	Anolis 4	Anolis 5	Anolis 6	Average length in ½ × 189² × 200 c. micra on slide.	Average length in ½ × 189² × 200 c. micra fresh tissue (correction coef 0.76)	Average length in 100³ c. micra fresh tissue
Fasc. log. medialis	405	564	409	338	429	326	91
Nucleus XII	1642	1368	1253	1249	1378	1047	293
Nuc. mot. X	1174	1254	1325	1038	1198	910	255
Nuc. mot. VII	1280	1326	1134	——	1247	948	265
Nuc. mot. V	1264	1427	1192	1261	1286	977	273
Nuc. fasc. sclit.	1776	1149	1344	1583	1463	1112	311
Nuc. spin. V	1453	1628	1558	1131	1443	1097	307
Cerebel.: molecular	1736	977	1505	1746	1491	1133	317
Nuc. sens. princ. V	1393	1614	1820	1607	1608	1222	342
Cerebel.: granular	1501	1175	1614	1239	1382	1050	294
Cerebel.: nuc. lateralis	1508	1685	1601	1495	1572	1195	335
Nuc. vestib. ventrolat.	1645	1687	1412	1398	1536	1167	327
Nuc. cochlearis	2026	2685	2021	2046	2195	1668	467
Primord. nuc. supraopticus	352	783	237	435	452	344	96
Nuc. mam. lat.	1264	1698	1469	1583	1504	1143	320
Nuc. hypothal. ventromed.	1492	1063	1144	1074	1193	907	254
Hippocampus (cell layer)	834	932	818	611	799	607	170
Parahippocampal cortex	1029	1297	1218	1306	1213	922	258
Palaeostriatum (mesostriatum)	1480	1552	1590	826	1362	1035	290
Neostriatum	1403	1867	1749	1119	1535	1167	327

to be a little richer in most regions. This tendency, observed in the actual measurements, has been accentuated by the different coefficients for correction for shrinkage.

The apparent richness of the primordial supraoptic nucleus is notable, suggesting an advance in the snakes in a direction paralelling that in which mammals have gone much further.

In the cellular layers of the cerebral cortex the identity of conditions with those in the alligator may be noticed.

Lizards.

The corresponding results for **Anolis carolinensis** are presented in table 2 and are also represented graphycally in figure 3.

The difference in the fundamental morphology of the vascular mechanism makes the value of a direct comparison of the measurements open to question but, no way to allow for this difference having yet been suggested, the total length of the capillaries has been recorded irrespective of their arrangement. It would appear, however, that, with an equal total length of capillaries, diffusion through the tissues must go further in lizards than in animals with a spongy network of vessels.

In most parts of the brain studied, the supply of vessels is a little richer in lizards than in snakes. The cochlear nucleus is a notable exception to this, that of the lizard approaching that of the alligator.

The relative richness of the hypoglossal nucleus seen in snakes is again visible, confirming the hypothesis of its relation to lingual mobility. The cerebellum is also relatively vascular (in relation to rapidity of movement?), as are the sensory trigeminal centres.

The primordial supraoptic nucleus is weakly developed. The poverty of its vascular supply is probably significant though the accuracy of the value obtained may be questioned since the nucleus appears only as a line of scattered cells.

In the cerebral hemisphere, a thinning of the dorsolateral part of the pallium in Anolis (Craigie, 1936) has nearly obliterated the pyriform cortex, so that no useful measurements could be made therein nor could the primordium neopallii be identified with sufficient certainty for use.

Calibre of the capillaries

The diameters of fifty capillaries selected at random were measured in each of six of the regions studied and the averages are set down in tables 3 and 4. In table 3 the individual measurements are given lest there should be differences between the three species of snakes represented, but this does not seem to be the case.

In lizards, the two vessels associated as a pair usually differ a little in calibre. Hence the diameters of the narrower and the wider members are tabulated separately, as was done in the studies on Necturus (Craigie, 1940a) and on Sphenodon (Craigie, 1941b).

The cerebral capillaries of the snakes appear to be a little wider than those of Anolis and though the differences are not great they are rather consistent. They are a little narrower than those in young alligators (5.5 micra) and considerably narrower than those in the small turtle, Chrysemys (7.1 micra).

TABLE 3. DIAMETERS IN MICRA, AREAS OF WALLS, AND VOLUMES OF GELATIN-INJECTED CAPILLARIES IN BRAINS OF SNAKES

	Sn. 19 Thamnophis sirtalis	Sn. 20 Sistrurus catenatus	Sn. 21 Sistrurus catenatus	Sn. 23 Agkistrodon piscivorus	Average diameter in snake brains on the slide.	Average diameter in fresh tissue.	Area in sq. micra of capillary walls in 1003 cu. micra of fresh tissue.	Volume in cu. micra of capillaries in 1003 cu. micra of fresh tissue.	Area in sq. mm. to which 1 cu. mm. of blood is exposed.
Fasc. long. med.	4.0	4.8	4.5	4.4	4.4	5.1	2066	2634	785
Nucleus XI	4.2	4.8	5.2	4.7	4.7	5.4	5207	7031	741
Cerebel.: molecular	4.4	4.6	4.4	4.3	4.4	5.1	3204	4084	785
Cerebel.: granular	4.4	4.7	4.3	4.4	4.4	5.1	3124	3982	785
Hippocampus	4.9	4.5	4.5	4.1	4.5	5.2	4083	5309	769
Palaeostriatum	4.6	5.3	4.6	4.6	4.8	5.5	3173	4370	727
Average					4.5	5.2			765

TABLE 4. DIAMETERS IN MICRA, AREAS OF WALLS, AND VOLUMES OF GELATIN-INJECTED CAPILLARIES IN BRAINS OF LIZARDS **(ANOLIS CAROLINENSIS)**

	Average diameter of narrower capillaries	Average diameter of wider capillaries	Average diameter of all capillaries on the slide	Average diameter of all capillaries in fresh tissue	Area in sq. micra of walls of capillaries in 1003 cu. micra of fresh tissue.	Volume in c. micra of capillaries in 1003 cu. micra of fresh tissue.	Area in sq. mm. to which 1 cu. mm. of blood is exposed.
Fasc. long. med.	4.0	4.8	4.4	5.1	1457	1858	785
Nucleus XII	3.7	4.5	4.1	4.7	4326	5084	851
Cerebel.: molecular	4.0	4.7	4.3	5.0	4979	6223	800
Cerebel.: granular	3.6	4.3	4.0	4.6	4248	4884	870
Hippocampus	3.7	4.4	4.1	4.7	2509	2949	851
Palaeostriatum	3.9	4.8	4.4	5.1	4646	5923	785
Average			4.2	4.8			824

It should perhaps be reiterated that such measurements of gelatin-injected capillaries always show their calibre to be less than the diameter of an erythrocyte and that blood-distended capillaries would be wider.

Volumes of the capillaries and areas of their walls

The volumes of the capillaries in a unit volume of tissue and the areas of their walls in the six representative regions are recorded in Tables 3 and 4 and in Figures 4 and 5 they are shown graphically in comparison with the corresponding dimensions for the turtle and the alligator.

It is evident that the order of magnitude of the dimensions in question and the general relations between the parts in these respects are not widely different in the various reptiles. The snakes have slightly smaller areas than the lizards in some parts, larger in others,

and similarly both have smaller areas than turtle or alligator in some parts and larger in others. The same general statement is true regarding the volumes.

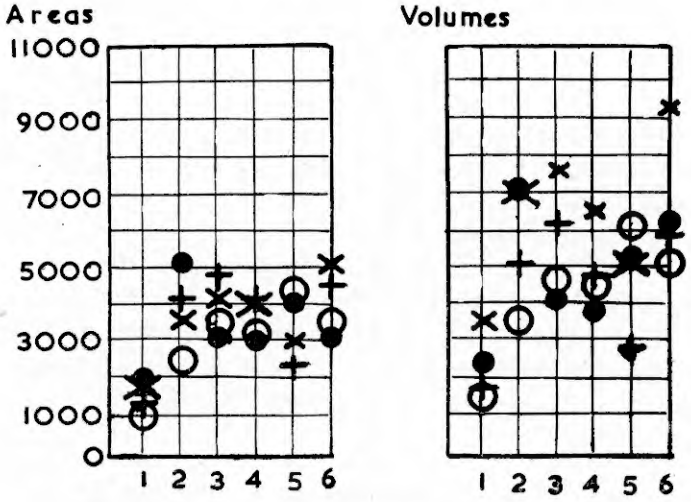

Fig. 4.—Graph showing the areas in square micra of the walls of the capillaries contained in 100^3 cubic micra of fresh tissue in six parts of the brain. ° snakes; + lizard (Anolis); X turtle; O alligator. 1, fasciculus longitudinalis medialis; 2, nucleus XII; 3, cerebellum: molecular layer; 4, cerebellum: granular layer; 5, hippocampus; 6, palaeostriatum. Fig. 5.—Graph showing the volume in cubic micra of the capillaries contained in 100^3 cubic micra of fresh tissue in six parts of the brain. Symbols as in figure 4

The rather high length of the vessels in the hypoglossal nucleus is reflected, though less markedly, in the areas but the volumes of the vessels are not correspondingly great.

The area of the wall which would be covered by a unit volume of blood if the vessels were not distended by the blood within them is indicated in the last column of tables 3 and 4. This area in the snakes is almost identical with that in the alligator (average 726) and markedly larger than that in the turtle (average 564). The corresponding area in the lizard is a little greater than in any of these other reptiles.

In comparing alligator and turtle (Craigie, 1942) it was suggested that a consistently smaller volume of blood in the former is partly compensated by the greater efficiency gained by spreading it over a larger surface. Such a relation is less evident in the present com-

parison and would require more extensive measurements to demonstrate it if it exists. Reference may again be made to the statement of Benedict (1932) that the metabolic rate is similar in alligators, snakes, and lizards and is higher in turtles.

SUMMARY

1. The total length of the capillaries in a unit volume of tissue in each of twenty-two regions of the brain has been measured in four snakes and in four lizards (Anolis). The fundamental difference in the morphology of the vessels in lizards, which have branched, non-anastomosing loops instead of the spongy capillary network of most animals, has not been considered in making this quantitative study.

2. The lengths of the capillaries in snakes are generally comparable with those in alligator and turtle though tending to be a little greater. They are definitely greater in lizards in most parts of the brain studied.

3. The cochlear nucleus is particularly well supplied with capillaries, especially in the snakes, and the hypoglossal nucleus also is notably richer in snakes and lizards than in the other reptiles. The cerebellum is also relatively highly vascular in the lizards.

4. The calibre of the capillaries is slightly greater in the snakes than in the lizard but is less than in the young alligator or the small turtle previously studied.

5. The areas of the walls of the capillaries and the volumes of these vessels show no consistent differences. The area over which a unit volume of blood is spread is about the same in the snakes and alligators, apparently a little greater in the lizards.

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