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The Morphology of the Carotid Labyrinth in *Bufo bufo*  
and *Leiopelma hochstetteri*

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*Abstract*

THE internal architecture of the carotid labyrinth in *Bufo bufo* and *Leiopelma hochstetteri*, as shown by wax-plate reconstruction, is described and illustrated. Each comprises a deep internal carotid rete, fed from a main chamber which is prominent in *Bufo* but inconspicuous in *Leiopelma*. The moderately complex and sharply recurrent external carotid rete in both species receives blood from the internal carotid rete, and, in *Bufo*, also direct from the main chamber.

IN previous papers (1955, 1967) I have drawn attention to the fact that in amphibians with a carotid labyrinth the origin of the external carotid is recurrent. Chowdhary (1958) claimed that in *Bufo bufo*, which has a labyrinth, the external carotid does not arise recurrently. Whereas Chowdhary did not reconstruct the labyrinth, the present description of the internal structure of the organ in *Bufo bufo* is based on wax-plate reconstructions. The most striking example of the recurrent origin of the external carotid artery in Anura is shown by the primitive *Leiopelma hochstetteri*, and the labyrinth in this species is also described.

MATERIAL AND METHODS

Both carotid labyrinths from single specimens of *Bufo bufo* and *Leiopelma hochstetteri* were reconstructed from  $10\mu$  serial histological sections using the wax-plate method, at  $75\times$  and  $150\times$  for *Bufo* and  $150\times$  and  $300\times$  for *Leiopelma*. Serial sections of the labyrinths of further specimens of *Bufo* (2) and *Leiopelma* (3) were studied to confirm the findings.

RESULTS

*Bufo bufo*

The carotid labyrinth (Fig. 1), in the fixed specimen, is a swelling about 1.3mm long with an oval cross-section  $800\mu \times 600\mu$ . Its long axis is directed dorsally, rostrally and laterally. Its proximal (ventral) pole receives the common carotid

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artery caudally and gives rise to the external carotid rostrally. The recurrent origin of the external carotid is clearly marked externally, in the angle between the common and external carotids, by bulges produced by the convex aspects of the medial and lateral caudal roots of origin of the external carotid.

The *common carotid artery* (which has a bore of about  $200\mu$ ) dilates in the proximal third of the labyrinth to form the *main chamber*. This chamber,  $500\mu$  long and  $300\mu$  across, is placed eccentrically towards the caudal aspect of the organ, and is drained distally by four openings, two directed dorsally to the internal carotid rete and two rostrally to the external carotid rete.

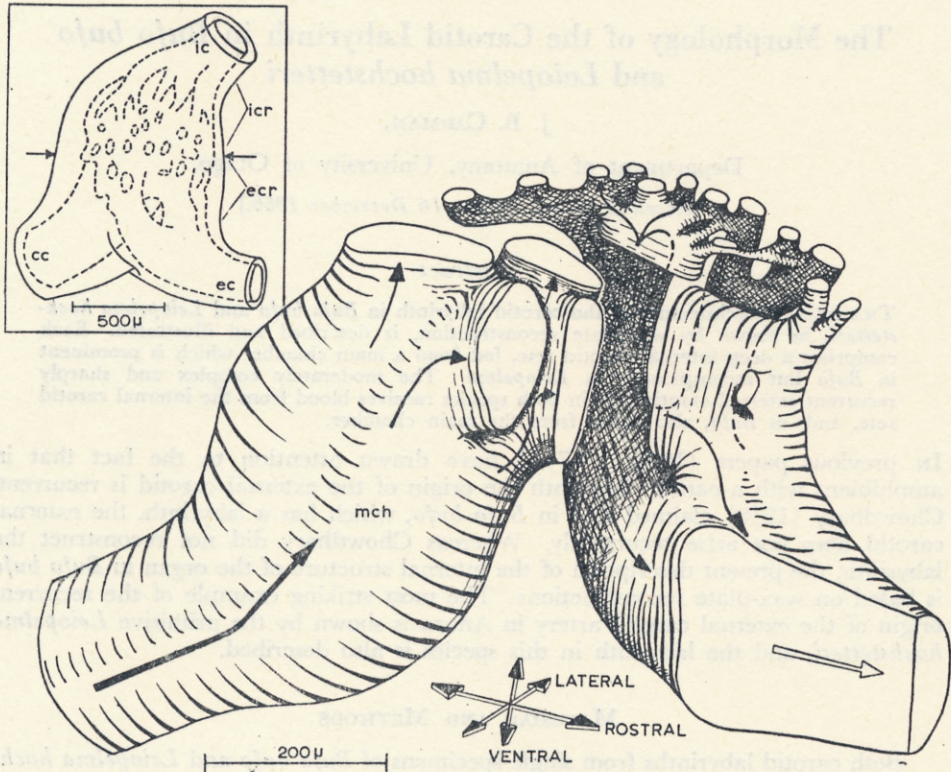


FIG. 1.—A cast of the interior of the proximal half of the carotid labyrinth in *Bufo bufo*. The cast of the whole interior is shown ghosted within the labyrinth in the inset; proximal (ventral) is below and the common carotid (cc) enters from the left. The main drawing illustrates that part of the interior of the organ below the arrows in the inset. The common carotid and main chamber (mch) have been detached from the rest of the cast and withdrawn slightly caudally to reveal the four openings leaving the dorsal part of the main chamber. The remainder of the cast is of the lateral half of the external carotid rete (ecr) and the commencement of the external carotid artery (ec) which has been sectioned longitudinally where the medial half of the external carotid rete has been removed. The uppermost parts of the cast represent the commencement of the internal carotid rete (icr) which can be seen feeding the internal carotid artery (ic) in the inset. The arrows in the main drawing represent the direction of blood flow.

The *external carotid rete* is a simple one, comprising three or four major roots. One or two of these arise directly from the rostral aspect of the main chamber and turn back quite sharply to run a short recurrent course before opening into the dorsal wall of the external carotid artery. These rostral roots communicate by a few small channels with the internal carotid rete. Arising from the medial and

lateral parts of the proximal surface of the internal carotid rete are one or two rootlets which lead away recurrently (ventrally), caudal to the rostral roots and, turning rostrally, enter the caudal wall of the external carotid artery. Blood entering these roots from the main chamber must pass through the most proximal parts of the internal carotid rete. The *external carotid artery* is formed by the fusion of the main channels of the external carotid rete in the proximal pole of the labyrinth; it has a bore of about  $120\mu$ .

The *internal carotid rete* occupies the distal (dorsal) half of the labyrinth. It comprises, primarily, a mass of short anastomosing capillary-sized channels which are drained peripherally by a series of progressively enlarging vessels. These large channels unite in the distal pole to form the *internal carotid artery*, which has a bore of about  $180\mu$ .

The three carotid arteries have a typical musculo-elastic media and a substantial fibrous adventitia. The main chamber and the channels of the external carotid rete have thinner musculo-elastic walls containing considerable collagenous tissue. The trabeculae of the capillary portion of the internal carotid rete comprise delicate collagenous tissue containing numerous cells, many of which appear to be modified smooth muscle cells. The peripheral wall of this part of the rete and the walls of the larger channels in its distal part are collagenous. The internal carotid artery has a surprisingly thin musculo-elastic media and a substantial fibrous adventitia.

### *Leiopelma hochstetteri*

The carotid labyrinth in *Leiopelma* (Fig. 2), when fixed, is about  $700\mu$  long and the greatest diameter of its oval cross-section is about  $500\mu$ . The long axis of the organ is directed laterally and somewhat dorsally. The *common carotid artery*, which has a bore of about  $110\mu$ , enters the caudal half of the proximal (medial) pole of the labyrinth and enlarges very slightly to form an inconspicuous *main chamber*, which is drained at its distal pole through four large openings leading directly to the *internal carotid rete*. This rete comprises a complex of intercommunicating capillary-sized vessels which occupies the distal half of the organ, and, at the distal pole, a number of very short larger vessels uniting to form the *internal carotid artery*, which has a bore of about  $90\mu$ . The *external carotid rete* arises from the proximal aspect of the internal carotid rete, where it surrounds the main chamber, by some 20 channels, ranging from  $10\mu$  to  $40\mu$  across. These unite to form an annular channel encircling the termination of the common carotid artery in the proximal pole of the labyrinth. From the rostral part of this annular channel the external carotid artery, with a bore of about  $100\mu$ , passes medially, parallel to the terminal part of the common carotid artery, with which it shares a common wall for a distance of  $400\mu$  or more, before turning rostrally into the floor of the mouth. The blood flow in the common carotid is, of course, directed *laterally* towards the labyrinth, whereas the flow in the external carotid rete and artery is directed *medially* and *recurrently* away from the organ. Allowing for the more delicate nature of the connective tissues associated with the small size of the organ in this animal, the labyrinth in *Leiopelma* is histologically similar to that in other species.

In the case of *Leiopelma* it is possible to measure with reasonable accuracy the cross-sectional area of the parts of the labyrinth. Taking the area of the common carotid ( $0.0095\text{ mm}^2$ ) as one unit, the area of the openings leaving the main chamber is about 4 units ( $0.0385\text{ mm}^2$ ), of the internal carotid rete 6 units ( $0.0563\text{ mm}^2$ ) and of the external carotid rete 3.5 units ( $0.0345\text{ mm}^2$ ), giving a maximum section of 9.5 units, and of the internal carotid 0.6 units ( $0.0064\text{ mm}^2$ ) and of the external carotid 0.8 units ( $0.0076\text{ mm}^2$ ), a total of 1.4 units.

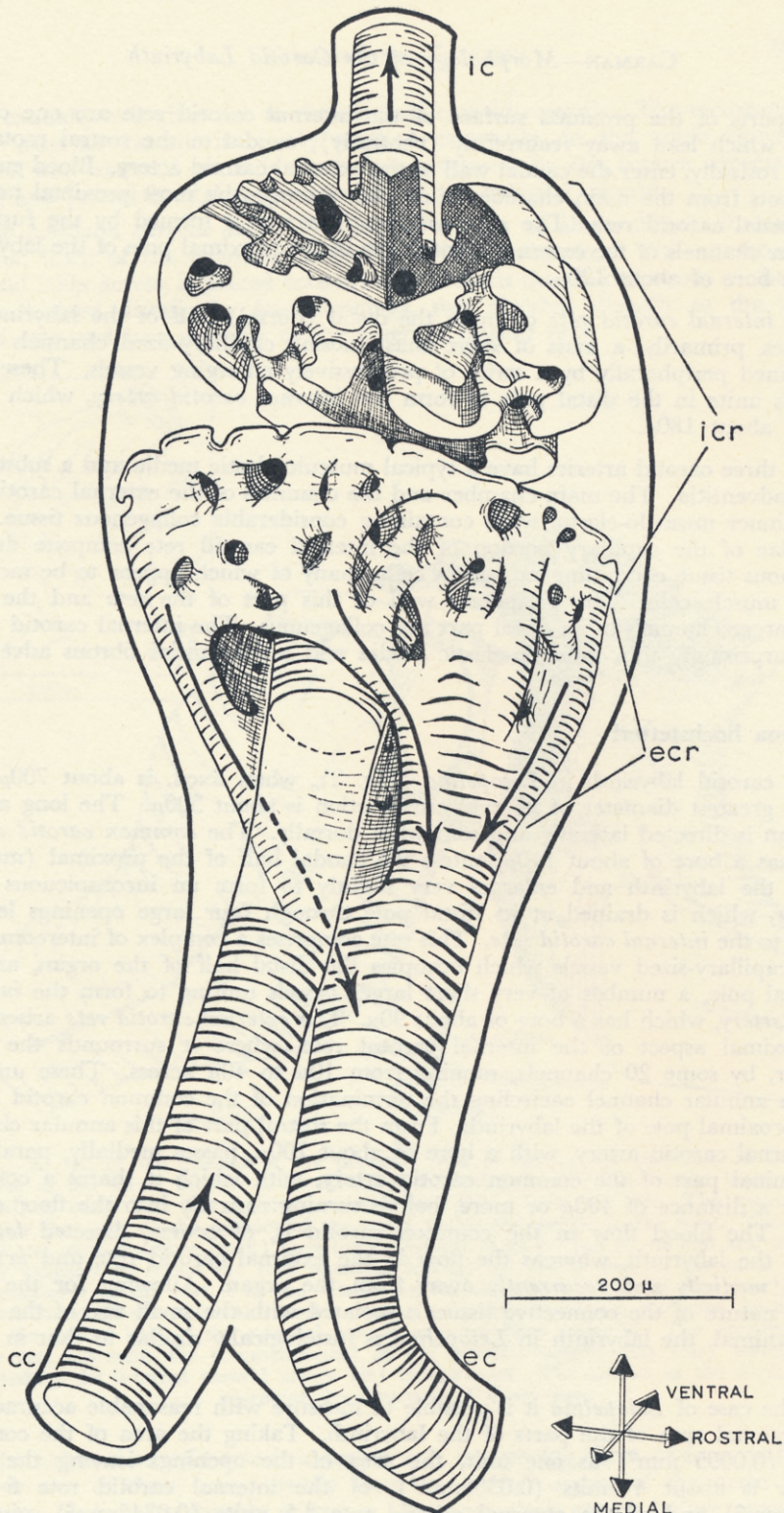


FIG. 2.—A cast of the interior of the carotid labyrinth in *Leiopelma hochstetteri*. Proximal (medial) is below. The small main chamber at the termination of the common carotid (cc) is obscured by the complex, annular external carotid rete (ecr) which is drained by the external carotid (ec). The middle portion of the internal carotid rete (icr) was not reconstructed but was similar to the distal part which can be seen draining into the internal carotid artery (ic). The arrows represent the direction of blood flow.

## DISCUSSION

The origin of the external carotid artery, the external carotid rete, is sharply recurrent in both *Bufo bufo* and *Leiopelma hochstetteri*. In the six labyrinths from three specimens of *Bufo bufo* I have been unable to confirm Chowdhary's claim, also based on the study of serial sections but without reconstruction, that the external carotid in this species does not arise recurrently. My findings in *Bufo bufo* are very similar to those described for *B. vulgaris* (Ishida, 1954) and *B. marinus* (Rogers, 1966).

*Leiopelma* shows the recurrent nature of the external carotid artery very strikingly. Because the long axes of all the principal channels were approximately parallel in the example reconstructed, a reasonably accurate measurement of the total cross-sectional areas of these passages was possible. The combined cross-sectional area of the internal and external carotid retia is nine times that of the common carotid, and of the external and internal carotid arteries 1.4 times. These measurements allow an approximate estimate of the flow rates and velocities in the various parts of the organ.

If the velocities in two vessels are equal then the flows are proportional to their cross-sectional areas. Unless there is a significant difference in the resistances of the capillary beds fed by the external and internal carotids, the blood velocity in the internal carotid is unlikely to appreciably exceed that in the external carotid, as the fall of pressure through the deep and complex internal carotid rete is almost certainly greater than that in the external carotid rete. Thus, using the areas of the internal and external carotids as a guide, it is reasonable to suggest that the flow in the internal carotid artery is most unlikely to exceed 40% of the flow in the common carotid. As the cross-section of the internal carotid rete is some six times as great as that of the common carotid artery, the velocity in the rete may well be as low as 1/15th or less of that in the common carotid. The significance of this profound slowing of the blood flow in the internal carotid rete deserves careful consideration.

Attention has been drawn to the similarity between the labyrinths in *Leiopelma* and the urodeles (Carman, 1964; Wislang, 1964) and these and other aspects of the form and function of the amphibian carotid labyrinth have been fully reviewed in a recent paper in this Journal (Carman, 1967).

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In the urodeles as two vessels are equal and the flow is proportional to their cross-sectional areas. Unless there is a significant difference in the diameter of the vessels, both led by the external and internal carotids, the blood flow in the internal carotid is unlikely to appreciably exceed that in the external carotid, as the fall of pressure through the deep and complex internal carotid artery is almost certainly greater than that in the external carotid artery. Thus, while the area of the internal and external carotids as a guide to its resistance to water flow, the flow in the internal carotid artery is most unlikely to exceed 50% of the flow in the common carotid. As the cross-section of the internal carotid artery is less than one-quarter of that of the common carotid artery, the velocity in the internal carotid will be at least as high as 1/16th or less of that in the common carotid. The significance of this profound slowing of the blood flow in the internal carotid artery is worthy of careful consideration.

A number of papers have been written on the similarity between the labyrinth in *Xenopus* and the urodeles (Carmann 1964; Wislang 1964) and there and other aspects of the form and function of the amphibian carotid labyrinth have been fully reviewed in a recent paper in this journal (Carmann 1967).

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