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The Carotid Labyrinth in the Anuran *Breviceps mossambicus*

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Abstract

THE carotid labyrinth (the presence of which in Amphibia may be related to the mode of origin of the external carotid artery in the gilled, aquatic larva) is described in an anuran, *Breviceps mossambicus*, which lacks a tadpole stage. Despite this modified life history the labyrinth is present, showing the same basic features as in other Urodela and Anura. The common carotid artery ends within the organ in an enlarged *main chamber*. From this, the internal carotid artery arises through a plexus, the *internal carotid rete*, which, compared with other species, is very simple. The external carotid artery arises *recurrently*, through an *external carotid rete*, which in *Breviceps* is relatively complex. The histology is also described. It is suggested that the terms "main chamber", "internal carotid rete" and "external carotid rete" should be used for the three essential components of the organ in future descriptions. Attention is drawn to the fact that in all species in which the labyrinth is present and has been studied by reconstruction techniques, the external carotid artery arises recurrently, while in the Gymnophiona and some salamanders (*Plethodon*, *Desmognathus*) the external carotid arises in a simple, non-recurrent way and the labyrinth is absent.

INTRODUCTION

THE amphibian carotid labyrinth, a swelling at the carotid bifurcation, has received relatively little detailed investigation until recently and none of the hypotheses put forward to account for it is entirely satisfactory. Hyrtl (1838) and Boas (1883)—contrary to later statements (e.g., Pischinger, 1934) that they considered the organ simply as an accessory heart—clearly associated the labyrinth with the remarkable sharply recurrent origin of the external carotid artery in Anura and Urodela. The commencement of the external carotid in these animals forms an angle with the common carotid which is considerably *less than* a right angle, a condition which is most unusual at arterial bifurcations, where the angle between a branch and its supplying vessel is almost always *equal to or greater than* a right angle. Referring to this feature, Hyrtl wrote: "desshalb in diesem Falle gewiss eine bedeutende Hemmung der Circulations-Geschwindigkeit in diesem Gefässe Statt finden müsste, wenn nicht die selbstthätigen Zusammenziehungen jenes Nebenbulbus eine Ausgleichung bewirkten". Whereas Hyrtl believed that active muscular contractions of the labyrinth assist the blood into the external carotid, Boas considered that the

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process is passive and results from recoil of the walls of the distended labyrinth following ventricular systole. The internal configuration of the carotid labyrinth in *Hyla aurea* strongly suggested to me also (Carman, 1955) that the organ was well shaped to turn blood back into the recurrent origin of the external carotid and that the function of the organ might be largely or entirely related to the peculiar mode of origin of this vessel. Boas (1882; 1883) pointed out that the labyrinth is absent in the Gymnophiona where the origin of the external carotid is not recurrent and Nitecki (1965) has shown that in the lungless salamanders *Plethodon glutinosus* and *P. cinereus* where the external carotid artery forms an acute angle with the internal carotid there is no carotid labyrinth.

The peculiar recurrent origin of the external carotid in those Anura and Urodela in which it occurs results from the vascular arrangements in the gilled, aquatic larva. While the gill circulation is present the external carotid arises from the efferent artery of the first gill arch: in urodeles from that portion of the vessel leaving the base of the gill to pass towards the aorta (Boas, 1882; Schmalgauzen, 1953), and in anurans from the ventral end of the efferent vessel (Marshall, 1893; Pischinger, 1934; Schmalgauzen, 1953). In both cases, the external carotid, running ventrally to reach the floor of the mouth, passes close to the proximal part of the first afferent branchial artery with which it communicates by a few small anastomoses. The blood flows in opposite directions in the two vessels, passing ventrally in the external carotid and dorsally in the afferent artery. With the loss of gills at metamorphosis the external carotid comes to arise from the afferent vessel—now the common carotid—in the region of the anastomosis, but because of the larval relations its origin remains sharply recurrent. It is at this stage that the carotid labyrinth develops (Maurer, 1888; Marshall, 1893; McMullen, 1938; Witschi, 1949).

In view of the intimate relationship between the larval gill circulation and the development of the carotid labyrinth, those Amphibia which do not possess a free-living tadpole and in which the gills show substantial reduction (Archev, 1922; de Villiers, 1929; Lynn, 1942) are of considerable interest. The labyrinth in one such anuran, the primitive New Zealand frog, *Leiopelma hochstetteri*, has already been described briefly (Carman, 1955; 1964). The labyrinth in this species shows considerable differences from the organ in other Anura, although it has a number of similarities to the urodelan organ (Wislang, 1964; 1965). This paper describes the results of a study of the carotid labyrinth in another anuran, *Breviceps mossambicus*, which also has no tadpole stage and completes its larval development and metamorphosis within the egg, but which is phylogenetically advanced (see Noble, 1931), to determine whether the reduction in gills in this type of development can be correlated with any special features of the internal structure of the labyrinth.

MATERIAL AND METHODS

Breviceps mossambicus (Family Brevicipitidae, Suborder Diplasiocoela—Noble, 1931) has a striking appearance, with a globular body, a small head, and short hind limbs. Two specimens (body lengths 2.7cm and 2.4cm) were used. The axillary regions of the larger specimen were dissected under a stereoscopic microscope to display the great vessels and associated structures; the labyrinths were then serially sectioned transversely in paraffin at 5μ and stained with haematoxylin-eosin, iron-haematoxylin, and picro-fuchsin, and azan. The anterior one-half of the smaller specimen was serially sectioned transversely in paraffin at 10μ and stained with haematoxylin-eosin. Graphic reconstructions ($15\times$ and $50\times$) were made of the great vessels and surrounding structures to ascertain their detailed relationships. Two wax-plate reconstructions, one of the walls and one of the lumina, were made of each labyrinth in this specimen, at $300\times$ for the left and $150\times$ for the right.

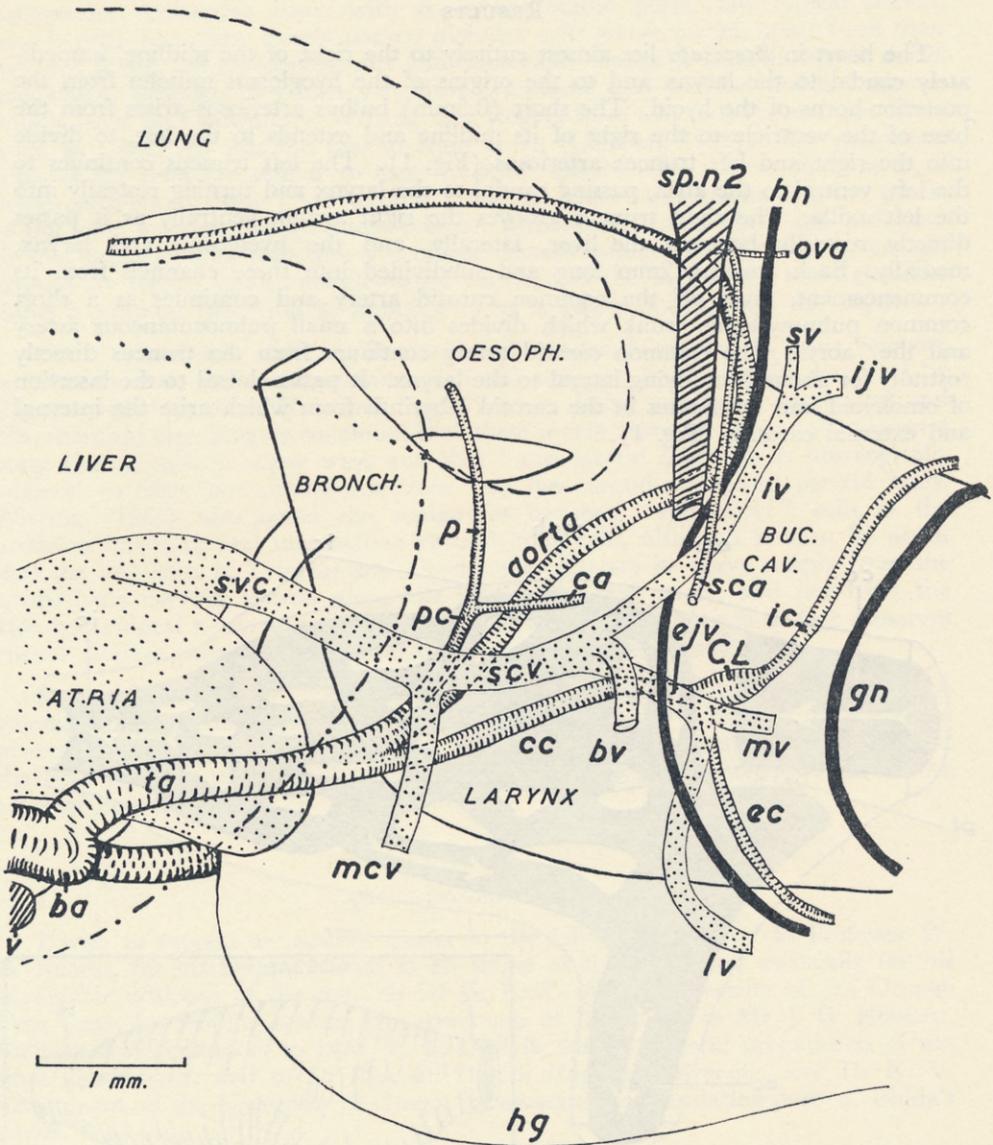


FIG. 1.—The great vessels and nerves of the right axillary region, seen from laterally. Graphic reconstruction; dorsal is above and rostral to the right; the right lung lies lateral to the oesophagus, and the liver lies lateral to the lung and heart.

LIST OF ABBREVIATIONS

ba, bulbus arteriosus; BRONCH., bronchus; BUG. CAV., buccal cavity; bv, brachial vein; ca, cutaneous artery; cc, common carotid artery; CL, carotid labyrinth; e, endothelial cells; ec, external carotid artery; ecr, external carotid rete; ejv, external jugular vein; el, elastic fibres; epith, epithelioid cells; f, fibrocytes; gn, glossopharyngeal nerve; hg, hyoglossus; hn, hypoglossal nerve; ic, internal carotid artery; icr, internal carotid rete; ijv, internal jugular vein; iv, innominate vein; lv, lingual vein; mch, main chamber; mcv, musculo-cutaneous vein; mv, mandibular vein, OESOPH., oesophagus; ova, occipito-vertebral artery; p, pulmonary artery; pc, pulmo-cutaneous artery; pf, proximal foramen; s, septum; sca, subclavian artery; scv, subclavian vein; sm, smooth muscle; sp.n 2, spinal nerve 2; sv, subscapular vein; svc, superior vena cava; ta, truncus arteriosus; v, ventricle.

RESULTS

The heart in *Breviceps* lies almost entirely to the right of the midline, immediately caudal to the larynx and to the origins of the hyoglossus muscles from the posterior horns of the hyoid. The short (0.5mm) bulbus arteriosus arises from the base of the ventricle to the right of its midline and extends to the left, to divide into the right and left truncus arteriosus (Fig. 1). The left truncus continues to the left, ventral to the atria, passing caudal to the larynx and turning rostrally into the left axilla. The right truncus grooves the right atrium ventrally as it passes directly rostrally between the liver, laterally, and the hyoglossus and larynx, medially. Each truncus, 2mm long and subdivided into three channels from its commencement, gives off the common carotid artery and continues as a short common pulmosystemic trunk which divides into a small pulmocutaneous artery and the aorta. The common carotid artery continues from the truncus directly rostrally for about 3mm, lying lateral to the larynx. It passes dorsal to the insertion of omohyoid and terminates in the carotid labyrinth from which arise the internal and external carotids (Fig. 1).

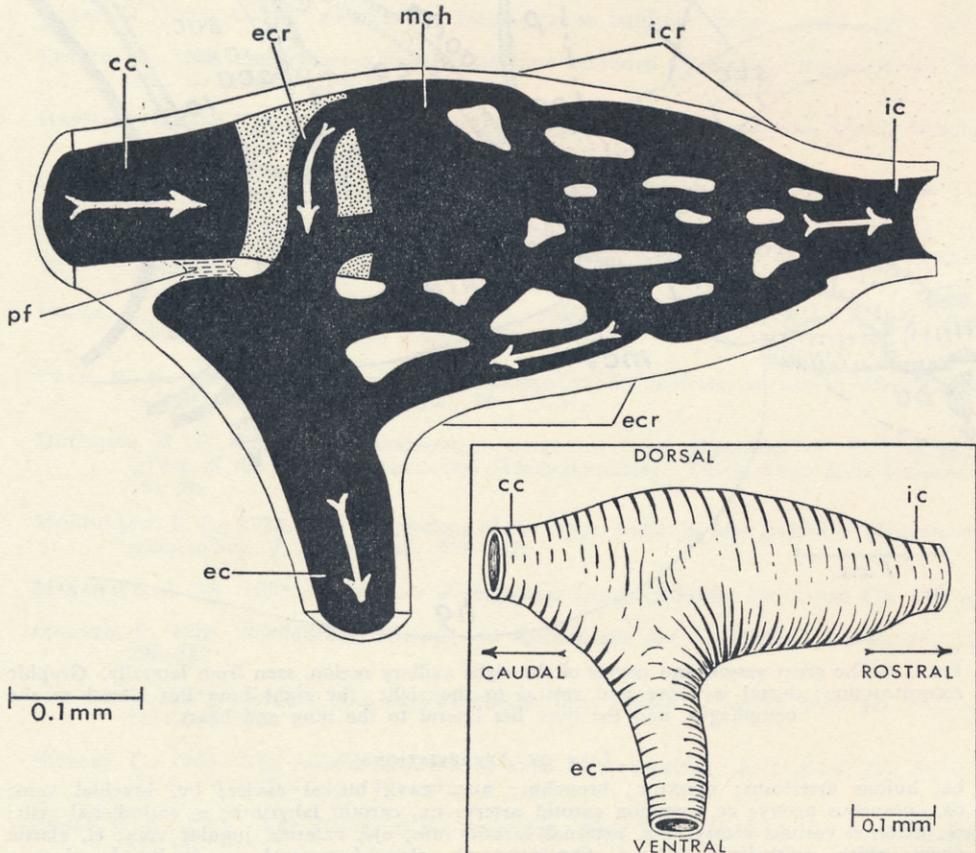


FIG. 2.—A schematic representation of the carotid labyrinth in *Breviceps*, using the conventions of Ishida ('54) and Adams ('58). The common carotid artery (cc), main chamber (mch), external carotid rete (ecr) and external carotid artery (ec), and internal carotid rete (icr) and internal carotid artery (ic) are shown schematically. The white arrows indicate the direction of blood flow. Inset: an external view of the labyrinth, showing its orientation.

The hypoglossal nerve (spinal nerve I) courses ventrally lateral to the petrohyoideus II and anterior to the subclavian artery. It passes medial to the internal jugular vein, lateral to the termination of the common carotid artery with the external jugular vein intervening, and then turns rostrally ventral to the external carotid into the floor of the mouth. The glossopharyngeal nerve (cranial nerve IX) leaves the IX-X nerve complex just lateral to the point where the internal carotid artery turns medially across the roof of the buccal cavity. It curves ventrally and caudally close to the anterior horn of the hyoid bone and anterior to the internal carotid; it then turns forwards into the floor of the mouth running dorsolateral to the external carotid artery (Fig. 1).

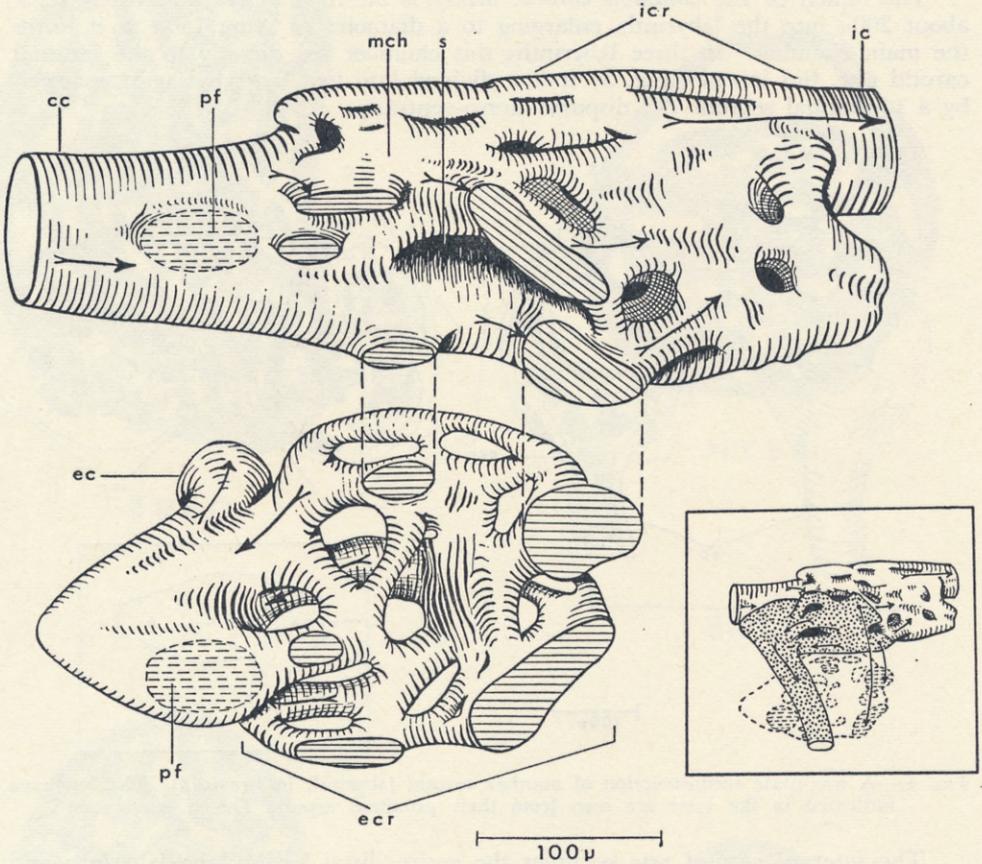


FIG. 3.—A cast (prepared by wax-plate reconstruction) of the vascular channels of one carotid labyrinth in *Breviceps*, seen from ventro-medially. Proximal is on the left, dorsal is above and behind. The external carotid rete has been cut away from the ventral aspect of the main chamber—which in this case was largely subdivided by a septum (s)—and turned laterally, as shown in the inset, so that it is seen from dorsally. The proximal foramen (pf) present in this specimen is shown in interrupted hatching.

The carotid labyrinth (Fig. 1; Fig. 2, inset) is an elongate, fusiform swelling 0.6mm long and 0.25mm across with its long axis rostro-caudal. The common carotid artery reaches it at its caudal (proximal) pole and the internal carotid leaves its rostral (distal) pole. The external carotid arises from its ventral aspect, close to the proximal pole, forming an angle of about 105° with the common

carotid artery; it passes ventrally, and slightly medially and forwards, before turning rostrally into the floor of the mouth (Fig. 1). Externally there is no evidence of the complicated internal configuration of the labyrinth.

The common carotid artery terminates (Fig. 2) in the proximal half of the labyrinth as a slightly dilated cavity—the *main chamber* (mch)—which feeds distally into a number of channels which form a rete—the *internal carotid rete* (icr)—leading to the internal carotid artery. Openings in the ventral, medial and lateral walls of the main chamber lead to an irregular plexus of channels—the *external carotid rete* (ecr)—which lies ventrally in the proximal part of the organ and passes recurrently to the commencement of the external carotid artery (Fig. 2).

The lumen of the *common carotid artery* is 90–100 μ across and extends for about 200 μ into the labyrinth, enlarging to a diameter of some 150 μ as it forms the main chamber. In three labyrinths this chamber led directly to the internal carotid rete, but in one (Fig. 3) it first divided into two large passages separated by a substantial septum (s) disposed dorso-ventrally.

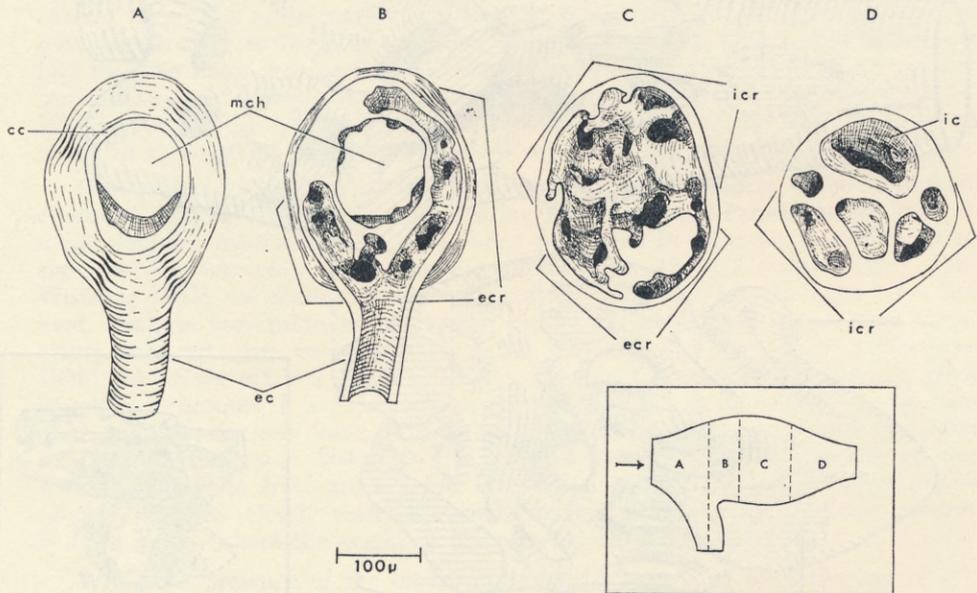


FIG. 4.—A wax-plate reconstruction of another carotid labyrinth in *Breviceps*. The segments indicated in the inset are seen from their proximal aspect. Dorsal is above.

The *internal carotid rete* occupies the entire distal half of the labyrinth and comprises a number of short, wide, intercommunicating passages which arise from the main chamber. The smallest are about 15 μ in diameter but most are wider than this. They communicate freely, and distally they quickly reunite to form the *internal carotid artery*, which has a bore of 80 μ (Fig. 4, D). In one labyrinth (Fig. 3) the ventral part of this plexus ended blindly in the distal pole of the organ as a number of small pockets, although blood from these ventrally-placed channels could easily reach the internal carotid by communications with the dorsal part of the rete.

The *external carotid rete* consists of a system of intercommunicating passages which occupy much of the ventral part of the proximal half of the organ (Figs. 2, 3, 4). The plexus arises by numerous openings from the main chamber, the

larger of these being situated in its ventral, ventrolateral and ventromedial walls (Fig. 3). In addition small channels arise from the dorsal wall of the main chamber; these may communicate with the external carotid rete by sweeping ventrally around the termination of the common carotid artery (Fig. 4, B), or they may rejoin the main chamber almost immediately. The rete lies distal to the commencement of the external carotid so that blood passing to this vessel must follow a recurrent course to a greater or lesser degree (see Figs. 2, 3). The rete is drained by three or four channels which open into the external carotid. These channels are 30–40 μ across and the smallest channels in the rete 15–20 μ .

In the fixed and sectioned specimens the *external carotid artery* has a bore of 70 μ . It commences in the ventral part of the proximal portion of the labyrinth and leaves the organ passing ventrally and slightly anteriorly so that it forms an obtuse angle of about 100–110° with the common carotid. The three or four channels leaving the rete open into its anterodorsal wall so as to form a small *cul-de-sac* extending well into the proximal pole ventral to the common carotid (Fig. 2). In one of the labyrinths, however, the common carotid artery communicated with this *cul-de-sac* by a large *proximal foramen*, 50 μ across, in their common wall (Figs. 2, 3).

The common, internal and external carotid arteries each have a musculo-elastic media: in the common carotid this is 25 μ thick with three layers of muscle cells; in the internal carotid, 15 μ thick with two layers; and in the external carotid, 6 μ thick with a single layer of cells. In each vessel the individual muscle cells are surrounded by numerous elastic fibres and fine collagenous tissue, and the media is bounded internally and externally by elastic laminae which are most prominent in the common carotid and thinnest in the external. The adventitia contains well-developed collagenous tissue with numerous elastic fibres; in the common carotid artery it is relatively thin (5 μ), in the internal carotid it is 10 μ thick and contains occasional solitary muscle cells, and in the external carotid it is 6 μ thick, with fewer elastic fibres. A very thin intimal layer is present in each vessel.

The general structure of the common carotid artery is continued in the walls of the main chamber with, in addition, numerous longitudinally disposed muscle fibres. Where the first openings leave the main chamber the elastic tissue begins to diminish and the internal and external elastic laminae break up and lose their distinctiveness. The external and internal carotid retia have, for the most part, a distinctive structure (Fig. 5): the intercommunicating channels are lined by endothelium and the trabeculae between them comprise numerous cells with irregular, rounded nuclei and very little cytoplasm, lying closely-packed in sparse, delicate collagenous connective tissue; no typical fibrocytes are present and only very occasional elastic fibres. The nuclei of the trabecular cells, although more globular in shape, resemble in their staining properties the elongated, ovoid nuclei of typical smooth muscle cells in the arterial walls. In contrast to the trabeculae the outer walls of the retia, although thin (10 μ), have a strong collagenous adventitia with numbers of intervening fibrocytes and a thin media with a discontinuous single layer of smooth muscle cells and moderate numbers of elastic fibres. In both the outer walls and also in the trabeculae the number of elastic fibres increases towards the commencements of the internal and external carotid arteries. (Throughout the organ generally, elastic tissue in substantial amounts is always associated with the presence of typical elongated smooth muscle cells.) Scattered haphazardly among the cytoplasm-poor cells of the trabeculae are occasional "epithelioid" cells with moderately large nuclei (up to 8 μ diameter) presenting a prominent single nucleolus and abundant pale staining cytoplasm. These cells measured up to 20 μ in length and from 6–8 μ across. The material was inadequately fixed for the demonstration of further cytological detail or for the study of the innervation of the labyrinth.

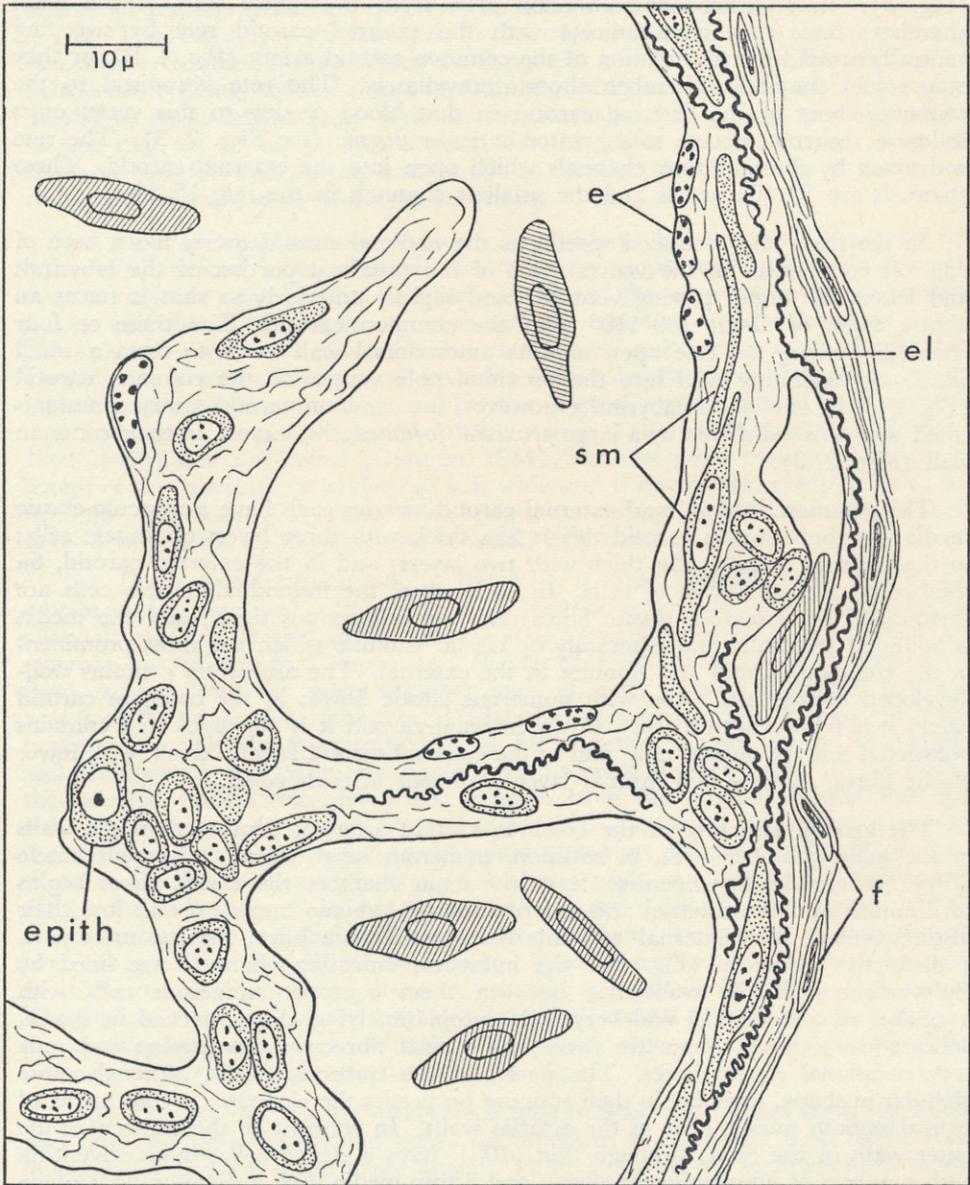


FIG. 5.—A drawing of part of a 10μ histological section of the internal carotid rete in *Breviceps* to show the salient histological features. The peripheral wall is on the right and shows a fibrous "adventia" containing typical fibrocytes (f), and a "media" comprising prominent elastic fibres (el), and an interrupted single layer of smooth muscle cells (sm). The trabecular tissue to the left contains many globular cells—which show similarities to typical smooth muscle cells—lying in very delicate collagenous connective tissue containing occasional elastic fibres. Occasional "epithelioid" cells (epith) are present. The blood spaces, containing erythrocytes (hatched), are lined by endothelium (e).

DISCUSSION

Because of its position at the commencement of the internal carotid artery, the amphibian carotid labyrinth has been of interest not only to those interested in the comparative anatomy of chemo- and pressor-receptors (e.g., Meyer, 1927; Boyd, 1942; Chowdhary, 1951; Adams, 1958; Heymans and Neil, 1958) but also to those interested in the wider field of the cerebral circulation in general (e.g., Ask-Upmark, 1935; de Boissezon, 1939). Although there are now a number of more-or-less detailed accounts of the internal structure of the labyrinth in a variety of anuran and urodelen species (Huschke, 1831; Hyrtl, 1838; Brücke, 1852; Boas, 1882, 1883; Zimmermann, 1887; Pischinger, 1934; Ishida, 1954; Carman, 1955, 1964; Chowdhary, 1958; Wislang, 1964, 1965; Nitecki, 1965) no general consensus of opinion has yet been reached as to the function or functions of the labyrinth (see, for instance, Carman, 1955; Adams, 1958; Nitecki, 1965). Not only do accounts of the histological structure (Pischinger, 1934; Eloff, 1935; Chowdhary, 1958; Rogers, 1963) and innervation (Palme, 1934; Fedele, 1941; Rogers, 1964) of the organ differ considerably, but both the external form and internal structure of the carotid labyrinth show quite remarkable variations from species to species.

It is now clear, however, that the carotid labyrinth comprises three essential components. These are the bulbous termination of the common carotid artery in the proximal part of the labyrinth, the more or less complicated plexus of capillarized channels leading to the internal carotid artery, and a series of channels leading to the external carotid artery. While each of these components has been clearly recognised by those studying the labyrinth, a wide variety of names has been used for them depending on the detailed form of the parts in the particular species being studied. Specific terms were not used by the early workers but in 1887 Zimmermann, describing the labyrinth in *Rana esculenta*, introduced the terms *pars cavernosa* for the proximal part of the labyrinth, comprising the termination of the common carotid artery and the large channels leading to the external carotid, and *pars capillaris* for the rete mirabile leading distally to the internal carotid artery. These terms have proved useful in describing the labyrinth in a number of related anurans (Pischinger, 1934; de Boissezon, 1939; Carman, 1955; 1964) but they have proved less valuable in *Leiopelma* (Carman, 1964), the urodeles (Wislang, 1964), and *Breviceps*, where the channels leading to the external carotid artery are quite complex and as small as those leading to the internal carotid. In these cases the proximal part of the organ is not notably cavernous and there is qualitatively little difference between the channels leading to the external carotid and those leading to the internal carotid. Hence, the terms *pars cavernosa* and *pars capillaris* lose their specificity, and the terms usually used to describe the vessels of origin of the external carotid artery—"roots" or "radicles"—become misleading by suggesting that the vessels passing to the external carotid are significantly different from those in the "pars capillaris" and by failing to indicate the fundamentally plexiform nature of the origin of the external carotid.

In a search for terms which, without being descriptively restrictive, will accurately equate corresponding parts of the carotid labyrinth in various species, I have chosen the term *internal carotid rete* for the vessels leading from the termination of the common carotid artery to the internal carotid (the "pars capillaris" of others) and *external carotid rete* for the channels leading to the external carotid artery. These terms are sufficiently broad to cover the wide variations in the detailed form of these two parts of the labyrinth in various Amphibia, and also highlight the essential feature that both the internal and external carotid arteries arise from the termination of the common carotid by true retia mirabilia.

The dilated termination of the common carotid artery has been termed *Haupt-hohle* (Zimmermann), *Hauptlumen* (Pischinger), central vessel (Ishida), central chamber (Adams; Nitecki) or main chamber (Carman; Wislang). In so far as this cavity is seldom central in the labyrinth I have retained the term *main chamber*.

The carotid labyrinth in *Breviceps mossambicus* obviously differs in form in almost all respects from that described in other Anura and Urodela.

(a) The long axis of the labyrinth in *Breviceps* is directed from caudal to rostral, in contrast to other species where the long axis of the labyrinth lies transversely (Urodeles, Wislang, 1965; *Leiopelma*, Carman, 1955) or runs obliquely from caudo-medial to rostro-lateral (e.g., *Hyla aurea*, Carman, 1955). It is probably owing to this that, in *Breviceps*, the external carotid forms an obtuse angle with the common carotid—and not an acute angle as in other Amphibia—as it passes ventrally and rostrally away from the labyrinth.

(b) In *Breviceps*, the main chamber is quite large but the internal carotid rete is markedly reduced, being relatively short and very simple, with quite wide channels, even having due regard to the much smaller size of the labyrinth in this diminutive species (Fig. 6). This pattern contrasts with the urodeles and the primitive anuran *Leiopelma* in which the main chamber is relatively quite small while the internal carotid rete is very complex, and with the higher Anura where it is usual for the main chamber to be quite large and for the internal carotid rete to be moderately well developed. Thus the internal carotid rete in *Triturus*, *Diemyctylus* (Wislang, 1964; 1965) and *Leiopelma* (Carman, 1964), occupies more than one half of the length of the labyrinth, is as deep as it is wide and is remarkably complex (Fig. 6); in *Bufo* (Carman, 1964) and *Hyla* (Carman, 1955, Fig. 6) it is much more shallow in relation to its width but it is still very plexiform.

(c) The external carotid rete in *Breviceps* is quite different from that in any species so far described, comprising a number of quite long intercommunicating channels confined largely to the ventral aspect of the labyrinth. In contrast, the external carotid rete in *Triturus* and *Diemyctylus* (Wislang, 1964) is truly plexiform, arising from the main chamber and, in part, directly from the proximal aspect of the internal carotid rete (Wislang's "pars plexiformis"), and extending proximally, encircling the termination of the common carotid artery; structurally and histologically it is indistinguishable from the internal carotid rete. In *Leiopelma* the external carotid rete also arises, in part, from the internal carotid rete and although it is well formed right around the termination of the common carotid it is less plexiform than in the urodeles and comprises channels rather larger than those in the internal carotid rete. In higher Anura—e.g., *Rana* (Zimmermann, 1887); *Bufo* (Pischinger, 1934); *Hyla aurea* (Carman, 1955)—the external carotid rete is further reduced and comprises a series of four or six roots leading directly from the main chamber. While in *Rana* and *Bufo* the communications between these roots completely encircle the common carotid, this feature is lost in *Hyla aurea*. The finding, therefore, of a remarkably complex external carotid rete in *Breviceps*, a very advanced anuran, is of particular interest, especially as it is found in the presence of a very simple internal carotid rete.

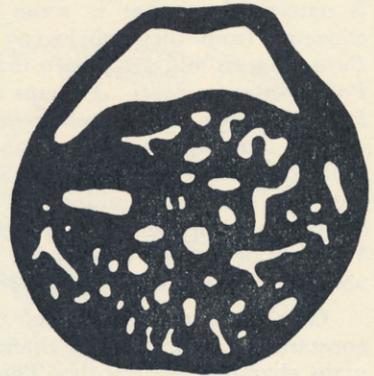
(d) The external carotid artery in *Breviceps*, once it is formed from the recurrent rete, angulates sharply and leaves the labyrinth at an obtuse angle to the common carotid and not at an acute angle. Thus, although the external form of the labyrinth gives the impression that the external carotid arises in a normal and not a recurrent fashion, it does have a recurrent origin. Study of the external form of the labyrinth may therefore be very misleading because the pattern of the external carotid rete is very poorly revealed externally, and further, even from a study of serial sections it is extremely difficult to arrive at a correct interpretation unless careful reconstruction is carried out.

(e) *Breviceps* is the first species to be described where a large communication occurs—but only in one labyrinth—between the common and external carotids, completely short circuiting the external carotid rete. This proximal communication has the same position as a quite small channel in one specimen of *Triturus* described

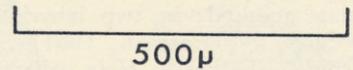
by Wislang (1964), where the origin of the external carotid artery proper from the rete was at right angles to the common carotid and not parallel to it as is usual in *Triturus*. What significance attaches to these direct communications I do not know, unless that in *Breviceps* is merely a secondary break-down in the wall between the two vessels.



BUFO



HYLA



LEIOPELMA



BREVICEPS

FIG. 6.—Cross-sections of the internal carotid rete in a series of Anura, illustrating the simplicity of the rete and the relatively large size of its channels in *Breviceps*.

Although the carotid labyrinth in *Breviceps* differs so strikingly from that in other Anura, these differences can in no way be correlated, at this stage, with the non-aquatic mode of development in *Breviceps*. Although a number of Anura—*Leiopelma* (Archev, 1922), *Breviceps* (de Villiers, 1929), *Eleutherodactylus* and others (Lynn, 1942)—have a similar type of life history, the carotid labyrinths of two of them at least, *Leiopelma* (Carman, 1955) and *Breviceps*, have significantly different forms. These species are, however, widely separated phylogenetically (Noble, 1931) and it seems probable that phylogenetic relationships are of considerably greater significance in determining the form of the carotid labyrinth than is the life history. The labyrinths of *Rana nigromaculata*, *Rana rugosa* and *Polypedates buergeri* (Ishida, 1954) are very similar and these species are closely related phylogenetically (Noble, 1931). Moreover, the labyrinth of *Hyla arborea* is remarkably similar in some respects to that in *Hyla aurea* and, as would be expected from their phylogeny (Noble), both are more closely akin to that in *Bufo vulgaris* and *Bufo bufo* than to those of *Rana nigromaculata*, *Rana rugosa* or *Polypedates buergeri*. Perhaps the most striking demonstration of this phylogenetic factor is shown by *Leiopelma* (Carman, 1955) and *Triturus* (Wislang, 1964) whose carotid labyrinths are remarkably similar in their external and internal form and quite different from those in the other Anura mentioned, which accords with the fact that the Leiopelmidae and Salamandridae show striking similarities in a number of other, phylogenetically significant, morphological features (Stephenson, 1951). Whether or not the type of life history modifies the form of the labyrinth over and above its apparent phylogenetic variations cannot be determined at this stage.

One particular feature of the labyrinth, however, appears to be remarkably constant: that is, that the channels leading to the external carotid artery leave the main chamber recurrently. This has been confirmed in all cases (including *Breviceps*) where wax-plate reconstruction (Pischinger, 1934; Carman, 1955, 1964; Wislang, 1965) or shellac injection (Zimmermann, 1887) techniques have been used. Only in two instances has it been specifically stated that the external carotid artery does not arise recurrently from the labyrinth: in *Bufo bufo* (Chowdhary, 1958) and *Hyla arborea* (Ishida, 1954). Because Chowdhary did not use reconstruction techniques I have reconstructed the labyrinth in *Bufo bufo* by the wax-plate method; in two labyrinths so far studied the external carotid has arisen recurrently (Carman, 1964). It has not yet been possible to confirm or deny Ishida's finding in *Hyla arborea* but the section of the labyrinth of *Hyla arborea* (Fig. 17, p. 98) closely resembles corresponding sections which I have observed in *Hyla aurea*, where the origin of the external carotid is recurrent.

While the presence of the labyrinth is usually associated with the loss of gills, Baker (1949) remarks that it is *not* present in those urodeles which have lost gills but in which the ductus caroticus persists (*Amphiuma* and *Cryptobranchus*). It is of particular interest too, that Nitecki (1965) has recently confirmed McCourt's finding (1954) that (as in *Gymnophiona*, Boas, 1883) the carotid labyrinth is absent in the urodele *Plethodon* where the carotid bifurcation has the normal pattern (i.e., with the external carotid forming an acute angle with the internal and not with the common carotid), while in the closely related genus *Eurycea* the origin of the external carotid is recurrent and the labyrinth is present. Thus the labyrinth does not seem to be unique to any one type of amphibian; it is present in terrestrial, aquatic and amphibious forms, in those with lungs and those without, in those with tadpoles and those which metamorphose in the egg, and it may be present in one genus and absent in a closely related one. One thing only seems to be constant: when the labyrinth is present, the external carotid artery arises recurrently.

The histological findings in *Breviceps* confirm previous findings (Chowdhary, 1958; Wislang, 1964; Rogers, 1966) that the trabecular tissue of the retia contains

collagenous connective tissue with occasional elastic fibres, few typical smooth muscle cells, but many closely packed globular cells whose nuclei, apart from their rounded shape, are morphologically and tinctorially similar to smooth muscle nuclei and which, although they have very little cytoplasm, may well be modified smooth muscle cells (as Chowdhary, Wislang and Rogers have concluded), and not fibrocytes, as I believed was the case in *Hyla aurea* (Carman, 1955). The peripheral walls of the retia are similar to those in other species with a thin, outer layer of dense collagenous tissue ("adventitia") and an inner layer resembling the media of the main arteries, though much thinner, with strong elastic fibres and a discontinuous single layer of transversely arranged smooth muscle. In all cases, the carotid arteries are typical small musculo-elastic vessels, and the wall of the main chamber shows a gradual reduction in muscularity as it passes distally into the organ.

The "epithelioid" cells in *Breviceps* are apparently similar in some respects, particularly their stellate appearance in fixed material, to the α -cells described by Rogers (1966) in *Bufo*, *Hyla* and *Neobatrachus*. Using numerous histological and histochemical tests Rogers concludes that these α -cells resemble mammalian carotid body glomus cells in many ways and that "the carotid labyrinth is histologically adapted to carry out similar functions" to the carotid sinus and carotid body. Wislang (1965) also noted the similarities between "epithelioid" cells in the urodelan labyrinth and mammalian carotid body cells, although it must be noted that the labyrinth in *Triturus* and *Diemyctylus* receives its nerve supply from the sympathetic nervous system, along the internal carotid artery, and not from the glossopharyngeal nerve as in *Anura*. Whether or not the labyrinth in fact subserves chemo- and/or pressor-receptor functions remains to be determined.

Even if the labyrinth does subserve these functions it remains to be decided whether they are the principal functions of the organ, or whether they are more properly to be considered as functions of the carotid arch system in general and that the prime function of the labyrinth is related to the recurrent origin of the external carotid artery.

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