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Manfred Lüdicke

Internal Ear Angioarchitectonic of Serpents



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With 21 Figures



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1. Introduction

Serpents lack an external ear, a tympanic membrane, a tympanic cavity, and a Eustachian tube. These negative but very significant characteristics are seen phylogenetically, especially in connection with the reduction of the eye (i.e., Nopsca, 1923; N.B., today *Pachyophis* is grouped together with the *Simoliophidae*, furthermore Mahendra, 1938; Walls, 1940, 1942; Bellairs and Underwood, 1951). Other authors mention these characteristics in connection with characteristics of ingestion (Berman and Regal, 1967). They claim that the formation of a tender tympanic membrane and a tympanic cavity is incompatible with the mobility of the quadratum and its adjacent musculature. The energy of sound can be transmitted either by the bones of the skull or the otic capsule or by the intercalare (medially adjacent to the quadratum) with the stapes and the base of the columella (for the intercalare or rather the extracolumella see De Beer, 1926 and 1937; McDowell, 1967). The vibrations of the apparatus added to the vestibuloquadratum type (Sertakowa, 1950) initiate a movement of the perilymph in the sinus pericapsularis (sinus juxtastapedialis), in the cisterna perilymphatica and in the scala tympani with the helicotrema. This stimulates the sense organs of the papilla basilaris located on the membrana basilaris in the pars limbi of the ductus cochlearis filled with endolymph.

Pituophis, *Thamnophis* and *Natrix* are only moderately sensitive to the lower sounds in the region of 100-700 Hz, whether transmitted by air or by bone conductivity (Wever and Vernon, 1960; see Manning, 1923; Smith, 1946; Jahn and Wulff, 1950; McDonnel, 1950 and Tumarkin, 1949, 1955). Wever and Vernon (1956) observed a similar region of sensitivity in turtles. Miller (1968) gave a quantitative account of the length of the papilla basilaris and the surface ratio between limbus and lagena in the ductus cochlearis in serpents; quantitative measurements of the sense organs of the internal ear were carried out by Weston (1939) for 24 vertebrates.

The function of the macula lagenae in the pars lagenae of the ductus cochlearis is disputed, as is that of the macula neglecta on the base of the utriculus. However, the terminal sense organs of the macula recessus utriculi, of the macula sacculi, and of the three cristae ampullarum is probably functionally equivalent to those in other vertebrates. Trendelenburg and Kuehn (1908) established that in serpents without a labyrinth the head is included in their transversal twisting movement; this does not, however, occur in normal animals (v. Buddenbrock, 1950, 1952).

The anatomy of the reptilian ear has been discussed in reports by Baird (1960 b, 1970). The lizard ear in particular has been studied by Hamilton (1963, 1964), Wever (1965), Miller (1966 a, b; ductus cochlearis), Wever (1967 a, b; membrana tectoria), and Miller et al. (1967; pars limbi of the ductus cochlearis). The inner ear of the *Gekkonidae* has been described by Hamilton (1960) and the ductus cochlearis of *Lanthanotus* and of the very rare *Anelytropsis* by Miller (1966 c). One should note that the Serpentes are derived from lanthanotidelike ancestors. We owe basic research on the morphology of the serpent ear to Hasse (1873), Kuhn (1882), and Retzius (1884). Hoffmann (1890), De Burlet (1934), and Luedicke (1964) often refer to their work.

The ear of digging serpents, especially of the *Typhlopidae*, has been examined by Baird (1960 a, 1961). According to this author the hearing apparatus in *Typhlopidae* can only be derived from very primitive yet definitive structures that are typical of serpents.

Weston (1938 a, b) in comparative anatomic studies points out the relationship between the ganglion cells and the terminal sense organs of the inner ear in vertebrates. For a comparison to the human ear we refer to the *Histology and Microscopic Human Anatomy* by Bargmann (1959). The general blood vessel system in serpents is the topic of papers by Beddard (1904, 1906 a, b), O'Donoghue (1912) and Ray (1934, 1936).

Considering the multitude of studies that discuss the physiologic, phylogenetic and ecologic problems of the serpent ear — we cited some of the most important — it is surprising that there are none that describe the vascularization of the inner ear. The author discovered this lack of information while studying the capillary system in the heads and eyes of serpents (1940) and the eye Luedicke (1977 g.v. for bibliography). Investigations of the capillary blood-supply system of the columella, of the sinus pericapsularis, and the cisterna perilymphatica (Luedicke, 1978) mark the beginning of the endeavour to close this gap. In the following paper the angioarchitectonic structure of the internal ear will be discussed, based on investigations using the "ScribtoI" injection technique.

2. Materials and Methods

For the investigations the species of the following families were used:

Aniliidae: *Cylindrophis rufus* Laurenti, 1768; *Acrochordidae*: *Acrochordus javanicus* Hornstedt, 1787, juv.; *Boidae*: *Eryx johnii* (Russel, 1801); *Eryx conicus* (Schneider, 1801); *Boa constrictor* (Linné, 1758); *Colubridae*: *Natrix natrix* (Linné, 1758); *Coluber viridiflavus* Lacépède, 1789; *Elaphe longissima* (Laurenti, 1768); *Homalopsis buccata* (Hallowell, 1860); *Enhydrys enhydryis* (Schneider, 1799); *Ahaetulla nasuta* Lacépède, 1789; *Malpolon monspessulanus* (Hermann, 1804); *Elapidae*: *Naja naja* (Linné, 1758); *Viperidae*: *Vipera berus* (Linné, 1758); *Vipera aspis* (Linné, 1758); *Cerastes cerastes* (Linné, 1758).

In order to save space only the names of the genus were used in the text, except for the genus *Eryx* and *Vipera*.

The animals were anesthetized with 0,004 ml Nembutal (Na-Pentobarbital from Abbot; concentrated stock solution 50 mg/ml) per 10 g body wt. or with chloroform.

In anesthetizing one has to be careful to avoid heartfailure due to an overdose of chloroform. After opening the skin from the cranial tip of the liver to almost the end of the head, the animals were injected from the a. carotis communis sinistra and if existing also from the a. carotis dextra with undiluted ScribtoI (from Wagner), by means of a mechanical injection device through a short tubing into a needle that has been attached to the vessels. A blackening of the spectacle capillaries generally indicates the success of the injection. In order to prevent the injection compound from getting washed out, the heads of the serpents were first tied together and then cut off and fixed in a 4% formaldehyde solution. The bones of the skull were demineralized in 50 ml formic acid 85%, 40 ml hydrochloric acid (25%), and 400 ml distilled water at 34-35°C under an electric current of 1.5-3.0 A. The membranous labyrinth often shows strong pigmentation. Therefore the melano-phores were bleached in a chlordinoxide-nitric acid solution. After removing the skin and the musculature and after isolating the supratemporale and the quadratum, the skull was cut medially or frontally in half and then dipped in series of alcohol concentrations, then into xylene, and embedded in Caedax. The staining of the histologic preparations was performed with azan or hemalum-eosin.

A method by Kobold (1964) was employed for the special preparation of the arterial system. Its usefulness is based on the fact that the injection compounds of various mixtures of "White Gelatine" (zinc oxide, gelatine, and distilled water) possess different viscosities. Therefore they penetrate into the capillaries in varying degrees, making it possible to distinguish between the arterial and the venous flow. After injection of a physiologic NaCl solution heated to 40°C, a mixture that varies according to the object (i.e., 200 ml distilled water, 26.5 g gelatine and 53.5 g zinc oxide) were injected into the a. carotis communis sinistra at the same temperature. This prevents prema-

ture solidification of the injection compound. Bleaching, using the Spalteholz technique was not necessary; therefore the objects were passed through a series of alcohol concentrations after being prepared and divided medianly, then through xylene, and finally (contrary to the method of Kobold) they were embedded in caedax.

3. Results

3.1 Arteries and Veins of the Membranous Labyrinth

The arterial main root enters into the otic capsule as a branch of the a. auditiva interna with the n. octavus (n. acusticus) (Luedicke, 1964, 1978). The venous main root is situated close to it, in the vicinity of the acoustic nerve. Sometimes, through the blackening effect of the Scribtor injection, it is very hard to distinguish these two vessels, especially if they are surrounding the nerve or if they are lying on top of each other obstructing the view. These difficulties do not occur in differentiating the vessels of the human ear. As Siebenmann (1894), to whom most modern authors refer in their anatomic work, has pointed out that the little trunks and main branches of the arteries are either coiled or corkscrew like. Unfortunately, this is not the case for most of the serpents examined thus far. It was only by lucky coincidence that a primitive serpent like *Eryx conicus*, a boid, was shown to have the same characteristics that are found in the vessels of the human membranous labyrinth. Because the arterial main root in the various families of the Serpentes generally supplies the same areas, there does not seem to be any difficulty later on in distinguishing the veins from the arteries, if they are not twisted. The eye of the observer can be trained to recognize a very weak meandering of the arterial flow as it has been found, for example, in *Natrix* (see also Luedicke, 1978, Fig. 10 a.Z.). One should not be deceived by shrinking processes that can occur after demineralization or after the fading of pigmentation by chlorodioxide in nitric acid. The determination of the type of vessel was confirmed by white-gelatine injection (Kobold, 1964) and by histologic analysis.

The angioarchitectonics of the vessels of the membranous labyrinth in *E. johnii*, the species that was used as an example for reasons mentioned above, demonstrates the strongly winding course of the arterial main root (Fig. 1). It sends out one branch that runs ventrally from the ramus anterior; one can follow it to the capillary net of the crista and ampulla anterior. Distally it is not coiled quite so strongly. One can clearly detect the corkscrewlike course of the sidebranch, which continues to the capillary net of the crista and ampulla externa. The sidebranch is also winding, and rather short. It leads to the recessus utriculi, especially to the macula acustica recessus utriculi, but is omitted in this figure for reasons of clarification.

After further bending of the arterial main root it branches off to the capillary net of the lagena, the periphery of the membrana basilaris of the pars limbi, and to the ventral region of the sacculus. One branch leads to the pars limbi, and supplies parts of the capillary net of the acoustic nerve. Another one supplies the capillary net of the medial section of the ductus perilymphaticus. The role of the capillary net in supplying blood to other parts of the perilymphatic system, as the sinus pericapsularis and the cisterna perilymphatica, was described earlier (Luedicke, 1978). The arterial vessels follow a winding course like the main root itself but less coiled. The same is true for the bough, which ascends dorsocaudally with branches to the capillary net of the sinus utriculi superior, the crista and ampulla posterior (here dorsal of ramus), and the

canales membranacei externus, anterior and posterior. The very thin side artery that supplies only the capillary net in the perilymphatic wall (around the canalis membranaceus externus filled with endolymph) has been omitted in order to render more visible the very important venous drains.

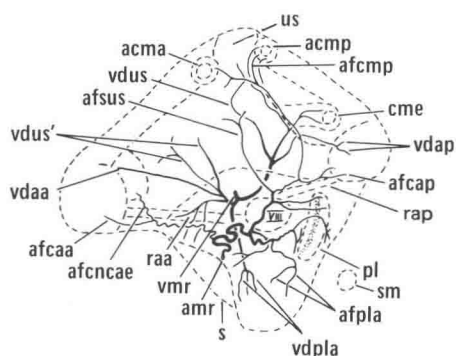


Fig. 1. *E. johnii*. Arterial and venous mainroots with their supply areas in the right membranous labyrinth, after preparation by Scribtor injection, seen medially. Note the twisting course of the proximal arterial sections (x 8.5).

acma apertura canalis membranacei anterioris, *acmp* apertura canalis membranacei posterioris, *afcaa* arterial flow to crista ampullae anterioris, *afcap* arterial flow to crista ampullae posterioris, *afcnp* arterial flow at canalis membranaceus posterior, *afcncae* arterial flow to capillary net of crista ampullae externa, *afpla* arterial flow to pars lagenae, *afsus* arterial flow to sinus utriculi superior, *amr* arterial main root, *cme* canalis membranaceus externus, *pl* pars limbi, *raa* ramus to ampulla anterior, ampulla externa, and macula utriculi, *rap* ramus to ampulla posterior, macula neglecta, papilla basilaris, macula lagenae, and macula sacculi, *s* rostral rim of sacculus, *sm* spatium meningeale, *us* sinus utriculi superior, *vdaa* venous drain from top of ampulla anterior, *vdap* venous drain from top of ampulla posterior, *vdpla* venous drains from pars lagenae, *vdus* venous drains from regions of the sinus utriculi superior, *vdus'* more venous drains lateral of the utriculus, and median of the sacculus, *vmr* venous main root, *VIII* nervus acusticus

The arterial blood is supplied first and mainly to the capillary nets of the three cristae and their ampullas with the canales membranacei. But in this species we also find additional arterial flow towards parts of areas of the capillary nets, or vessels of the nonampullar parts of the three canales membranacei. Furthermore one should note that the branch that continues dorsally to the semicircular ducts is to be found here in the caudal half of the membranous labyrinth. At first it runs laterally from the sinus utriculi posterior, later it runs medially from the canalis membranaceus externus, and finally laterally again from the sinus utriculi superior.

The blood is distributed from the capillary net of the membranous labyrinth to the venous main root. It is located a little further dorsally than the arterial main root but also close to the acoustic nerve. Their major vessels are not coiled. A venous drain leads the blood away from the rostralateral region of the pars lagena of the ductus cochlearis and from parts of the ductus perilymphaticus (Fig. 1). A tree of vessels from the rostralateral region of the membranous labyrinth is located between the sacculus and utriculus. It takes up blood with its branches from the capillary net of the sacculus, of the ampullae anterior and externa with its cristae, and the rostrorodorsal wall regions of the utriculus and the recessus utriculi. Another tree of vessels reaches from the dorsal region to the venous main root. It contains branches from the capillary nets of the

sinus utriculi superior, of the sinus utriculi posterior, of the dorsal entrance around the canalis membranacei anterior and posterior and around the median section of the canalis membranaceus externus, and the top of the ampulla posterior, its crista, and the canalis membranaceus posterior. Finally, this tree of vessels picks up the venous flow from the capillary nets around the pars limbi of the ductus cochlearis. These nets, however, are not shown in Figure 1 for reasons of clarity.

Besides these vessels of the arterial and the venous main root other supply routes are possible. For example, in another specimen of *E. johnii* some capillary nets did receive oxygen rich blood from a second more caudally located arterial root. These were the capillary nets of the right membranous labyrinth around the caudal part of the lagena, around the membrana basilaris, around the ampulla posterior with its crista, around the sinus utriculi posterior and the canalis membranaceus externus, and around the dorsal section of both canales membranacei anterior and posterior. The drainage of the venous blood follows essentially the same pattern as described above.

Aside from osseus arteries ("Knochengefäße"), as Siebenmann (1894) has described them for the human otic capsule, there are a number of drainages in the region around the membranous labyrinth, into the many sinuses of the bones themselves and in part into the large veins of the surrounding areas, as indicated in earlier papers (Luedicke, 1940, 1978). It should be particularly emphasized that *E. johnii* and *Homalopsis bucata* have three long drainages of venous blood that go into the bones of the otic capsule. There exist two other venous parts located ventromedian to the utriculus and to the sinus utriculi posterior and a third one dorsomedian to the sinus utriculi superior that drain this area. All three of them join the more loosely structured bone sinus.

3.2. Capillary Areas of the Sinus Utriculi Superior, the Utriculus With Recessus and Maculae, and the Sinus Utriculi Posterior

These three spaces of the membranous labyrinth viewed medially have the shape of an upside down "y". The utriculus and its recessus utriculi forms one branch and the sinus utriculi posterior forms the other. The sinus utriculi superior, as *Bogengangkommissur* (crus commune) stands dorsally almost upright, joining with the canales membranacei anterior and posterior (Fig. 2). The canalis membranaceus externus enters caudolaterally. If there is strong pigmentation of the membranous labyrinth, the shape of the utricular compartments become distinct and easily recognizable. If pigmentation is too intense the insight into the various sections is impeded; if it is too weak the outer limits are not differentiated enough. The membranous labyrinths of *Coluber viridiflavus* and *Malpolon monspessulanus* were particularly well suited. Differences in the degree of pigmentation will be pointed out later.

The sinus utriculi superior is supplied with oxygen-rich blood by the arterial main root and by a tributary root that branches out like an antler. (Fig. 2, *ar'*) Furthermore, in *V. aspis* from the arterial main root itself caudolaterally two smaller parts lead to the sinus utriculi superior. The connection to the osseus arteria located medially should also be mentioned. It was not shown in Figure 2 because the arteria itself does not belong to the membranous labyrinth and it would have disturbed the clear picture of the central area. In general, the capillary net of the sinus utriculi superior is large meshed and narrow dilated. The latter is especially true for *Cerastes cerastes*.

The oxygen-deficient blood is taken up by the veins, which enter the trunk of the venous main root. Or they may make connections to the sinus in the adjacent bones, in particular to the dorsal of the above-mentioned three long sinuses of the veins in the otica median from the membranous labyrinth, e.g., in *H. buccata*.

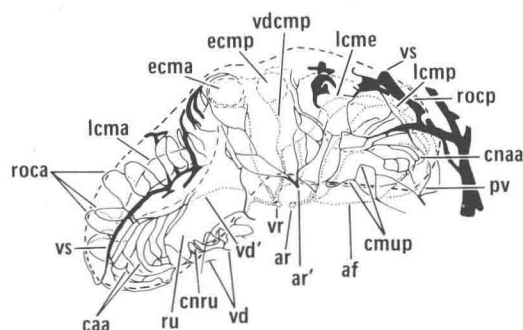


Fig. 2. *V. aspis*. Vessels and capillary nets of the utricle and part of the semicircular ducts of membranous labyrinth of right side and adjacent regions of the osseous labyrinth; after preparation by Scribtor injection (x 12.1).

af arterial flow, ar arterial root, ar' arterial root with branches to sinus utriculi superior, ecma entrance to canalis membranaceus anterior, ecmp entrance to canalis membranaceus posterior, caa capillaries of medio-rostral wall of ampulla anterior, cmup periosteal capillaries medial of sinus utriculi posterior, cnaa capillary net of medial wall of ampulla posterior (adjacent capillary net), cnru basal capillary net of macula utriculi below base of recessus utriculi, lcma longitudinal vessel of canalis membranaceus anterior, lcme longitudinal vessel of canalis membranaceus externus, lcmp longitudinal vessel of canalis membranaceus posterior, pv periosteal vessel, rocp ring vessels of osseus canalis posterior, ru recessus utriculi, vd venous drains, vd' venous drain from recessus utriculi, from ampulla anterior et externa, vdcmp venous drain from canalis membranaceus posterior, vr venous root, vs venous sinus

The membranous labyrinth exhibits differences in the degree of pigmentation. The density of the melanophores increases in the utricle rostrad, toward the recessus utriculi. This is particularly noticeable in nonbleached but more transparent preparations, i.e., those of the membranous labyrinth of *Enhydryis* after treatment with white gelatine (Kobold, 1964). The location of the macula acustica recessus utriculi is easy to find because the stretched field is covered with stateconies and has the shape of a tongue.

The utricle receives arterial blood much as does the sinus utriculi superior (Fig. 1, *afsus*), through a side branch of the arterial main root. This applies particularly to its dorsal part. Its ventral section, especially the capillary net below the macula acustica recessus utriculi, is fed by a short sidebranch of an artery leading to the capillary net of the ampullae anterior and externa. (Fig. 1, *afcaa* and *afcncae*) In *E. johnii* it is very winding, even though it is very short.

The capillary net of the utricle has large meshes and is often narrowly dilated. In *Acrochordus* it is wider meshed than the capillary net of the sinus utriculi posterior or of a partial section of the sinus utriculi superior. In some species one can find a median longitudinal field of the utricle totally free of capillaries, as for example in *V. aspis* (Fig. 2) and *H. buccata*.

The capillary net of "the" utricle or "the" sinus utriculi superior is incorrect terminology because there is not a capillary net of the utricle or sinus utriculi super-