XI. THE MIDDLE EAR OF INDIAN FROGS.

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(With Plate IX.)

On each side of the head of the common frog the skin in the middle of the temporal patch is distinguished as the tympanic membrane or tympanum. The description of this structure in Rana temporaria may be given in the words of Marshall (13): "Behind the eye on either side is an obliquely placed elongated patch of a dark colour, in the middle of which is a circular area—the tympanic membrane—supported by a marginal ring." Other text books of Zoology in their accounts of R. temporaria describe the condition in the same way as Marshall, while some say that the tympanic membrane is close to the surface and only covered over with skin.

Claus-Sedgwick (5) in the general account of the amphibia try to get over the difficulty in the following way: "In the Batrachians alone there is a tympanic cavity which is closed externally by a tympanic membrane, which is sometimes freely exposed on the surface and sometimes covered by the skin." Boulenger (2-4) in his systematic works describes the tympanum as distinct, indistinct or hidden under the skin, according as the area of skin is marked off from the surrounding skin or otherwise. Hoffman (12) is not definite as to whether the tympanum is a structure distinct from the skin covering it. Cope (6) states that there is a dermal membrana tympani connected with the stapes through a chain of ossicula auditis; evidently he considers the tympanum to be a distinct structure from the skin covering it, though he does not definitely say so. (7) deals with the function and tension of the membrana tympani of the mammals only. Fox (8) in his paper on the development of the tympano-eustachian passage of the common American toad deals with the development of the tympanic cavity, the eustachian tubes and the ossicula auditis, but says nothing about the tympanum. Villy's admirable paper (16) on the development of the ear of the European frog does not contain any reference as to the development of this structure or its relations with the skin. Hasse in his two papers (10, 11) deals with the structure of the internal ear of the frog only. Norris (14) does not try to clear the problem. Retzius (15) is the only author who has definitely stated that there is a distinct tympanic membrane underlying the skin. Haslam in his translation of Ecker's "Anatomy of the Frog" (9) has rewritten the whole section on the ear from Retzius' paper cited above.

From the review of literature on the subject it will be clear that great deal of confusion exists regarding the tympanum being a str distinct from the skin or otherwise. It was with a view to do so

towards the solution of this problem that the present work was undertaken.

MATERIAL AND METHODS.

I have investigated in detail the structure of the middle ear of the large Indian frog Rana tigrina, Daud.¹ There are several forms closely allied to this frog in India, but the form common in Lahore where the work was done is the typical one, as was ascertained by sending some specimens to Dr. Boulenger in London. Besides a large number of dissections of this frog I cut sections of decalcified specimens of both young and adult frogs; these sections were found to be very useful in clearing up the doubtful points and indicating the exact relationships of the various parts.

Through the kindness of Dr. N. Annandale, Director of the Zoological Survey of India, Calcutta, I was able to examine the large collections of frogs in the Indian Museum, Calcutta, and so am able to add an account of the structure as it occurs in a large number of other Indian frogs. I am also deeply indebted to Lt.-Col. J. Stephenson, D. Sc.. I.M.S., Professor of Zoology and Principal, Government College, Lahore, for kindly giving me leave to go to Calcutta to work in the Indian Museum, and for sanctioning a special grant towards the expenses.

Rana tigrina.

The structure of the middle ear in this frog will be described in the following order:—

(1) The tympanic area.

(2) The tympanic membrane.

(3) The tympanic cavity and associated skeletal structures.

The Tympanic area (fig. 1).—I have reluctantly changed the widely accepted nomenclature in order to remove the existing confusion, and have given the name of tympanic area (T a.) to the area of skin situated in the temporal patch on the side of the head. This area is continuous with the skin, but is tightly stretched over the marginal ring of the annulus tympanicus, and is slightly more depressed than the skin all round it. It is nearly circular in outline and is a little smaller than the eye. About the middle of this structure the attachment of the columella auris can be seen as a nodular protrusion.

The histological structure of this portion of the skin is quite similar to that of other parts of the skin, except that the number of cutaneous glands is much smaller; about the middle no cutaneous glands are to

be seen (text fig. 1).

The Tympanic membrane (figs. 2, 3, and 4).—This is quite a distinct structure lying immediately underneath the so-called tympanic membrane of authors. It can be easily separated from the skin covering it. On the skin being reflexed by a cut, the tympanic membrane (T m.) is seen to be of a rounded-oval form slightly notched at the upper side, and produced into a little projection on its lower.

rave satisfied myself by examination of specimens of R. esculenta and R. temnat the structure in these frogs is also essentially similar to that of R. tigrina,

It is attached all along the circumference to the slightly up and inturned edges of the annulus tympanicus. The tympanic membrane is thin along the margin but is specially thickened in the middle on its inner side for the attachment of the distal end of the columella auris.

The membrane is formed of connective tissue fibres which radiate from the central point of attachment of the columella to the periphery. A few blood vessels, nerve cells and a large number of pigment corpuscles are also found scattered in the connective tissue. Along the margin some unstriated muscle fibres are also to be seen. Internally the tympanic membrane is lined by columnar epithelium (text fig. 2) which is continuous lower down with the mucous membrane lining of the tympanic cavity.

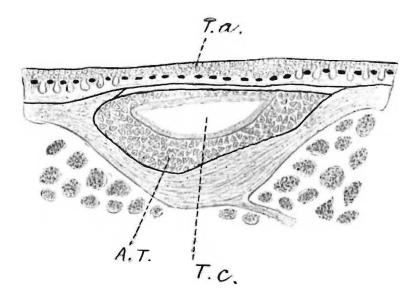


Fig. 1.—Transverse section of the ear of R. tigrina.

The Tympanic cavity and associated skeletal structures.—After the removal of the tympanic membrane the tympanic cavity is seen to be a funnel-shaped structure. The upper margin of the funnel is slightly turned inwards for the attachment of the tympanic membrane as seen in a transverse section (text fig. 1). The funnel-shaped tympanic cavity has its longer axis directed downwards and backwards from the anterior and upper side. This upper or outer portion of the tympanic cavity is formed by the annulus tympanicus (A. T.); from the lower end of the annulus tympanicus the tympanic cavity becomes very much reduced and continues as a slightly depressed tubular structure, the cross section of it hence is not circular but slightly elongated. The beginning of this second or inner portion of the tympanic cavity may be termed the tympanic recess (T r.), while the opening by which it communicates with the internal ear is known as the fenestra ovalis (fig. 4, f. o.). From the ventral surface of this deeper portion of the tympanic cavity a short wide eustachian tube puts the tympanic cavity of each side into communication with the pharyngo-oral cavity. deeper portion of the tympanic cavity is bounded by the squamosal and prootic bones anteriorly, by the prootic dorsally, by the cartilaginous portion between the prootics and exoccipitals internally and by muscles posteriorly.

The tympanic cavity is lined all along by mucous membrane which

is very vascular and pigmented.

The annulus tympanicus (figs. 4, 5, A. T.) is a cartilaginous framework of the shape of a short truncated cone, broad outwards and narrowing towards the inner side. The frame is not a complete structure, but is interrupted on the dorsal surface, the space between the two parts being occupied by a cartilaginous process (a', Parker's suprastapedial) of the extrastapedial cartilage of the columella auris. The annulus tympanicus is supported on the anterior, dorsal and ventral surfaces by the squamosal bone, while posteriorly by muscles. The columella auris (fig. 6) has the oval outer surface of the extrastapedial cartilaginous portion (a) embedded in the tympanic membrane (text fig. 2), whilst the suprastapedial processes (a') from its posterior surface

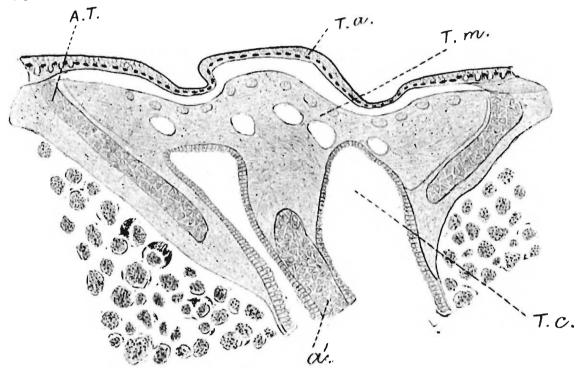


Fig. 2.—Transverse section of the ear of R. tigrina through the region of the columella.

goes to complete the annulus tympanicus as has been described above. The middle bony portion or the mediostapedial (b) after passing through the tympanic recess continues through the deeper portion of the tympanic cavity, to end in the cartilaginous interstapedial (c), which fits into the fenestra ovalis (fig. 4, f. o.).

Having described in detail the structure in R. tigrina, I will now describe the condition of the tympanic area of some other Indian frogs.

FIRMISTERNIA.

Family RANIDAE.

Oxyglossus.—According to Boulenger (3) the tympanum ¹ is indistinct in this genus. In specimens of O. lima and O. lævis the tympanic area is not distinctly marked off, but the attachment of the colu-

¹ The word tympanum used here and further on is used in the sense in which it is used by Boulenger and is equal to tympanic area of the suggested nomenclature.

mella is visible as a distinct nodule raising up the skin. The tympanic membrane is quite a distinct structure underneath the skin.

Rana.—The tympanum in most species is distinct, but in a few may be hidden. The condition in R. tigrina has been described in detail. In R. $liebigii^1$ the tympanic area is not distinct, but the tympanic membrane is seen to be quite a distinct structure lying under the skin.

Micrixalus.—The tympanum may be indistinct or hidden. In a large series of specimens of *M. silvaticus* of different ages it was seen, that the tympanic area is quite distinct in the young, becoming indistinct in older specimens, and in the fully adult it is not to be distinguished. The tympanic membrane is quite a distinct structure.

Nyctibatrachus.—The tympanum in this genus is described as hidden. In some well preserved specimens of *N. major* the tympanic area was distinctly marked off as a light-brown patch of skin; in the other poorly preserved specimens however it was not distinct.

Nannobatrachus.—The tympanum for this genus also is described as hidden. The condition in specimens of N. beddomii examined was the same as described for Nyctibatrachus major; and the distinctness of the tympanic area depended largely on the condition of preservation.

Rhacophorus.—The tympanum is usually distinct. In R. maximus it is distinctly depressed and is overhung on the upper side by a fold of skin, which makes the structure very prominent.

Ixalus.—The tympanum may be distinct or hidden. In the two species *I. glandulosus* and *I. leucorhinus*, examined by me it was quite distinct.

Family Engystomatidae.—This family is peculiar in having the tympanic area shifted to a much more forward position than in the Ranidae; it lies quite close to and at a much lower level than the eyes, in some it lies just below the eyes.

Calophrynus.—The tympanum is distinct. In *C. pleurostigma* tympanic area was found to be definitely marked off, and covering over the tympanic membrane lying under it.

Microhyla.—The tympanum is described as hidden. In specimens of *M. rubra* examined by me the condition (fig. 10) was the same as in *Calophrynus* described above.

Kaloula.—The tympanum according to Boulenger is hidden. In three specimens of K. obscura, the tympanic area was not a distinctly marked off portion, but in two better preserved specimens it was quite distinct. In K. pulchra (fig. 9) the tympanic area was slightly depressed and so better marked.

Cacopus.—The tympanic area in specimens of *C. systoma* is quite indistinguishable externally (fig. 7) but on removal of the skin (fig. 8) the tympanic membrane is seen to lie under the skin quite close to the eye.

Glyphoglossus.—The tympanum is described as hidden. In two well preserved specimens of G. molosus the tympanic area was seen as a slightly depressed circular area with raised edges, and lying just

¹ Dr. Annandale informs me that there is a very great confusion about this species, several species being confused under the name, but the form referred to is the true R. liebigii, Gthr.

below the eyes. The colour was the same as that of the skin covering the rest of the body.

ARCIFERA.

Family Bufonidae.—The conditions are essentially similar to those in the Ranidae.

Bufo.—The tympanum is distinct or hidden, seldom absent. In B. himalyanum (fig. 11) the tympanic area is a comparatively small structure, in some specimens it was partially covered over by the well developed parotid gland arching over it.

Cophophryne.—In C. sikkimensis no tympanic area is marked off externally, but on removal of the skin the tympanic membrane is seen to be quite distinct.

Family HYLIDAE.—

Hyla.—In *H. annectens* (fig. 12) there is a distinct tympanic area, but in some other species it is absent.

Family Pelobatidae.—Boulenger described the condition of the tympanum for the only Indian genus Leptobrachium (now united with Megalophrys) in his original account (3) as indistinct or hidden; in a later paper (4) for Megalophrys he says "distinct or hidden under the skin." In M. carinense (fig. 13) the tympanic area was seen to be quite distinct, lying very far back. The tympanic membrane was found to lie underneath it, and the annulus tympanicus was found to have shifted to a much lower position, being now supported by the vertical limb of the T shaped squamosal. This position is due to the greatly depressed condition of the head, and with it the great forward inclination of the squamosal bone.

SUMMARY.

The structure of the middle ear of *R. tigrina* is described in detail. A change of the usually accepted names is proposed in view of the present work. The name of the so-called "tympanic membrane" has been changed to "tympanic area," because the "tympanic membrane" is a distinct structure lying underneath the tympanic area stretched over the annulus tympanicus. An account of the tympanic area as seen in a large number of Indian frogs of the various families is also given.

The condition of preservation of the specimens was often found to be responsible for the distinctness with which the tympanic area was marked off from the rest of the skin; whereas it was quite well seen in well preserved specimens, it could hardly be distinguished in poorly preserved ones.

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