

The Middle Ear and Columella of Birds.

By

Geoffrey Smith, B.A.,

New College, Oxford.

It may seem a supererogatory task to add to the pile of literature which deals with the ear-bone homologies a straightforward account of those anatomical and embryological facts which may be ascertained by the examination of such familiar types as the fowl and pigeon; but after a painstaking research into the literature of the Sauropsidan middle ear I have unwillingly concluded that such a course was desirable. Although this literature is voluminous there is no single description of any Sauropsidan type which from a modern standpoint can be considered at all complete; that is to say, there is no account which describes in any one type—

1. The development and transformation of the auditory ossicles from the earliest procartilage stage upwards;
2. The relations of the seventh nerve and chorda tympani to the ossicles at different stages of development.

The words in italics are emphasised because a large part of the work on this subject fails to be conclusive owing to the lack of sufficiently early stages of development, and this most unfortunately is the case in the recent descriptions of *Sphenodon* by Howes (14) and Schauinsland (12). Kingsley (13) gives one isolated procartilage stage in a Lacertilian;

which serves to prove, at any rate, that these early stages are absolutely necessary for the interpretation of the later.

The following essay will be divided into three parts:—(1) anatomical, in which certain new details are described, and an adequate account of the disposition of the chorda tympani is given for the first time; (2) embryological, in which special attention is paid to the derivation and homology of the stapes or proximal portion of the columella (an homology which constitutes the crux of the Sauropsidan middle ear); and finally (3) a summary with some general conclusions.

I am much indebted to Mr. Jenkinson, Lecturer in Embryology in the University Museum, for his advice and a great deal of material.

1. ANATOMY.

The Columella (Fig. 1)—Anatomically the columella of birds is composed of two pieces, an inner ossified piece, the stapes, apposed to the fenestra ovalis, and an outer cartilaginous piece, the extra-columella, united to the stapes proximally, and attached distally to the tympanic membrane. There is no real joint between the stapes and extra-columella, but great flexibility exists between the two, owing to the pliability of the cartilaginous neck which unites them. The extra-columella may be described as consisting of three pieces, supra-, extra-, and infra-stapedial, all perfectly continuous. The disposition of these parts is shown in fig. 1, which represents the left columella of Gallus, viewed from within the tympanum.

The columella is supplied with a single muscle, the tensor tympani, which is attached to the infra-stapedial, and to the edge of the tympanic membrane, between the infra- and extra-stapedial cartilages. The muscle passes out of the ear by a large foramen close to the stylo-mastoid foramen, curls round on to the back of the skull, and is broadly attached to the basi-occipital bone in a shallow groove which slopes nearly to the occipital condyle.

The extra-columella is supplied with one ligament in all birds, Platner's ligament, which stretches across the cavity of the middle ear to the posterior face of the quadrate bone (*Plat.*, Figs. 1 and 3). In *Gallus* there are present two other ligaments attached to the extra- and infra-stapedials which are in part concentrations of the fibrous constituents of the tympanic membrane; I can only find these erroneously described by Parker (3) as being attached to the quadrate. In reality they pass beneath the quadrate, are continued beyond the region of the tympanic membrane into the lining of the Eustachian tube, and are finally attached to the walls of the bony Eustachian groove near the point where it debouches into the mouth (Fig. 2). This is a peculiar disposition, not found in other birds that I have examined.

The Seventh Nerve.—This nerve has three branches, which are, counting in order from the root of the nerve outwards, the sphenopalatine, the chorda tympani, and the main branch of the seventh. In *Gallus* the sphenopalatine and the chorda tympani come off together from the geniculate ganglion and do not take up any intimate relation to the middle ear. The chorda tympani, after its origin from the seventh nerve, runs a little way with it in the Fallopian tube, then enters a bony canal of its own and so gains the posterior face of the quadrate. The cross in Fig. 3 shows the approximate point at which the chorda tympani comes off the seventh nerve in the fowl. After giving off the chorda the main branch of the seventh crosses the stapes externally and dorsally to it in the cancellated bone, and then leaves the skull by the stylo-mastoid foramen.

In other birds, e. g. *Columba*, the chorda has a quite different disposition (Fig. 3). It leaves the seventh nerve by a special foramen in the Fallopian tube just before the seventh nerve makes its exit from the skull by the stylo-mastoid foramen; it then traverses a small piece of cancellated bone and enters the cavity of the middle ear quite superficially, viz. between the extra-columella and the tympanic membrane. It now crosses the extra-columella, keeping this same relation

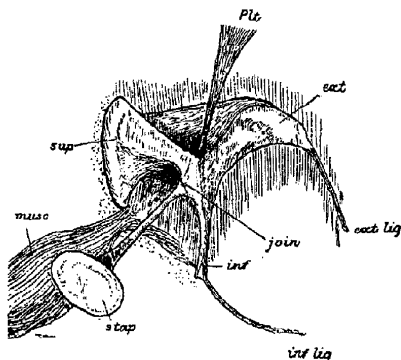


FIG. 1.—Left columella of Gallus from inside tympanic cavity. *plt.* Platner's ligament. *ext.* Extra-stapedial. *ext. lig.* Extra-stapedial ligament. *inf.* Infra-stapedial. *inf. lig.* Infra-stapedial ligament. *sup.* Supra-stapedial. *stap.* Stapes. *musc.* Tensor tympani.

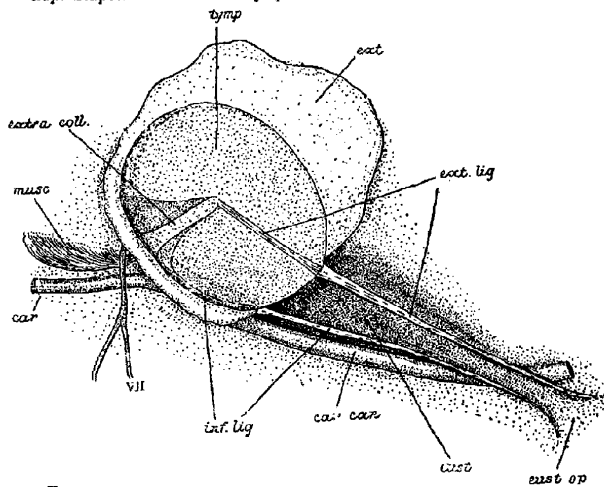


FIG. 2.—Right ear of Gallus. External ear is cut away, and the quadrate and bony roof of the lower tympanic recess are removed. *tymp.* Tympanum. *ext.* External ear lining. *extra coll.* Extra-columellar. *ext. lig.* Extra-stapedial ligament. *inf. lig.* Infra-stapedial ligament. *musc.* Tensor tympani. *car.* Carotid. *car. can.* Bony carotid canal. *vii.* Seventh nerve. *eust.* Bony Eustachian groove. *eust. op.* Opening of groove into mouth.

to the tympanic membrane, namely lying just internal to it and external to the extra-columella, save that at the point where it crosses the neck which unites the supra- and extra-stapedials it pierces the cartilage superficially.

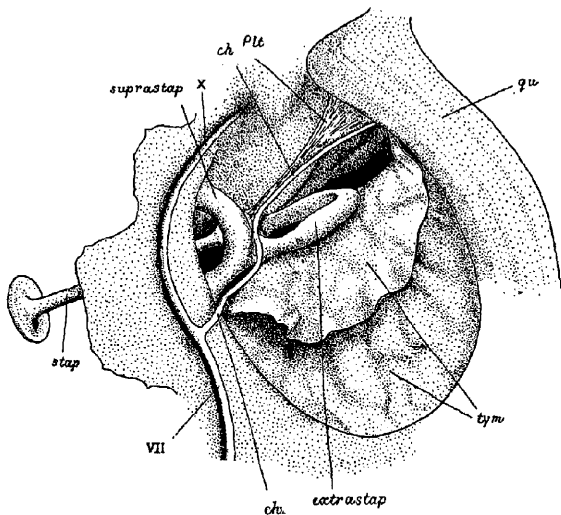
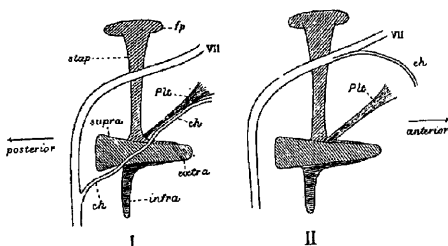


FIG. 3.—Right ear of *Columba*. Upper half of tympanic membrane deflected to show the structures upon its other side. *stap.* Stapes. *suprastap.* Supra-stapedial. *extrastap.* Extra-stapedial. *plt.* Platner's ligament. *VII.* Seventh nerve. *ch.* Chorda tympani. *X* Point at which chorda tympani comes off in *Gallus*. *tym.* Tympanum. *qu.* Quadratum. For this drawing I am much indebted to Mr. Darbishire.

Having traversed the extra-columella, the chorda joins Platner's ligament and crosses the tympanic cavity in company with it, so gaining the posterior face of the quadratum. This course of the chorda tympani has been confirmed by means of serial sections in a late embryo of the starling.

The essential difference between the relations of the chorda

tympani in *Gallus* and in *Columba* may be seen in the following diagram.



I. Columella of *Columba*; II, of *Gallus*, from without. *fp.* Foot plug. *stap.* Stapes. *Plt.* Platner's ligament. *vii.* Seventh nerve. *ch.* Chorda tympani. *supra*, *extra*, and *infra.* Stapedial cartilages.

In these two relations of the chorda tympani to the columella we see a striking convergence towards the two conditions in *Lacertilia* described by Versluys (10). In *Lacertilia* the chorda tympani may come off the seventh nerve behind the columella, and then run forwards, across, and external or dorsal to the extra-columella, or else it may come off anteriorly to the columella altogether (e.g. *Gecko* and those forms which have no processus internus to the extra-columella). There can be little doubt that the backward origin is primitive, since *Sphenodon* shows it, and that the forward origin in the fowl is secondary, as first suggested by Hasse (2), who supposed that its forward origin had to do with the peculiar development of the quadrate articulation in that bird.

2. EMBRYOLOGY.

The middle ear cavity is formed from the first gill slit (5). The earliest stage which is instructive for the purpose in hand is the five-day-old chick. As yet no chondrification has taken place, but the hyoid arch and the auditory capsule are recognisably shown by the thicker aggregation of connective-

tissue corpuscles in those regions (Fig. 4). The proliferation of tissue to form the hyoid arch takes place from below upwards; this is shown in the figures where the more ventral portion of the arch (*hy.*) is thicker than the more dorsal (*stap.*), the two portions passing into one another more or

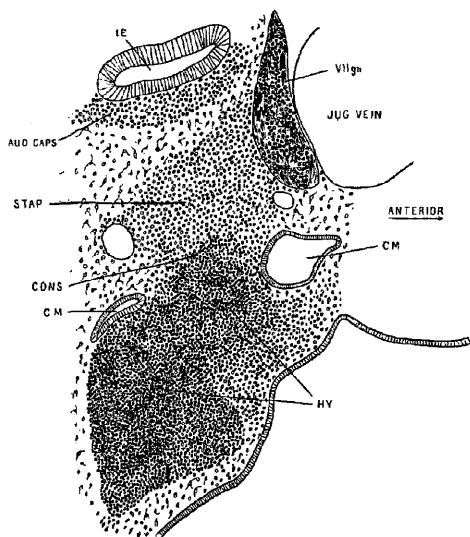


FIG. 4.—Longitudinal (slightly horizontal) section through hyoid region of five-day chick.

less suddenly at the constriction, marked *cons.*, fig. 4. The seventh nerve crosses the hyoid arch just dorsal to the constriction. The hyoid and auditory capsule proliferations are completely separate, being divided by a space where the connective-tissue corpuscles are much more thinly scattered. It is seen in fig. 4 that the dorsal or proximal portion of the

hyoid (*stap.*) has approached quite near to the auditory capsule, while the latter shows no sign of sending an out-growth to meet it.

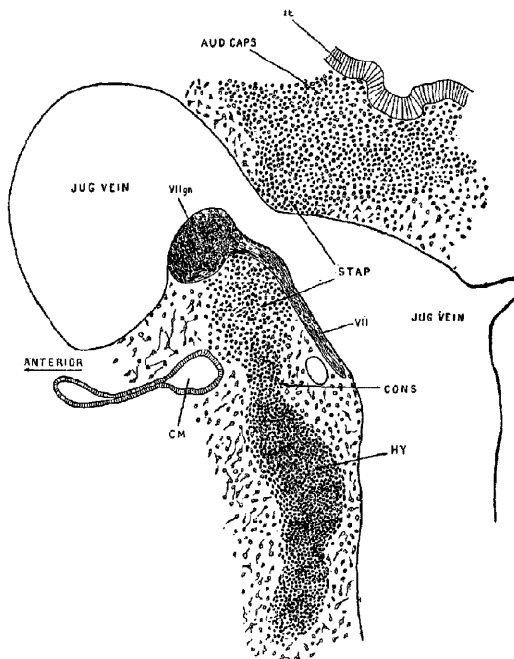


FIG. 5.—Longitudinal section through six-day chick.

In the six-day-chick the top of the hyoid has fused with the auditory capsule, both being still in the pro-cartilaginous condition. This is shown in Figs. 5 and 6. Fig. 5 shows the seventh nerve crossing the hyoid above the constriction in

sensibly the same position as in the five-day-chick. It is quite clear from Figures 4 and 5 that no considerable outgrowth from the auditory capsule can have taken place to complete the continuity of hyoid and auditory capsule. There is no evidence of such an outgrowth, and even if it occurs between the stages Figs. 4 and 5, the outgrowth can only

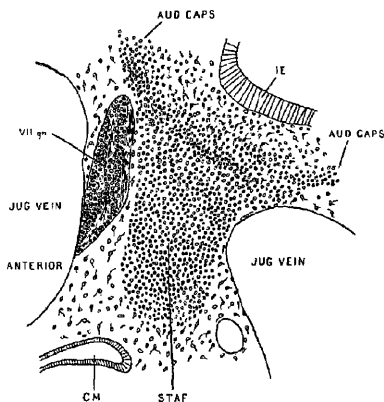


FIG. 6.—Ditto; a more median section to show continuity of stapes with auditory capsule.

Letters used in Figs. 4, 5, and 6:

I. E. Internal ear. AUD. CAPS. Auditory capsule. STAF. Stapes. CONS. Constriction in hyoid arch. HY. Hyoid arch. CM. Cavity of middle ear. JUG. VEIN. Jugular vein. VII gn. Geniculate ganglion. VII. Seventh nerve.

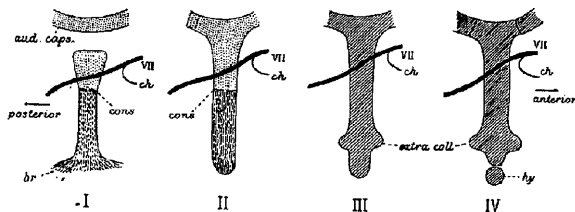
Figs. 4, 5, and 6 drawn with camera under Zeiss 4, AA.

occupy a very small part of the space subsequently occupied by the stapes, unless we imagine it bodily thrusting the hyoid arch before it, a process which is not easy to imagine in ill-defined pro-cartilaginous structures, and for which there is not the least shadow of evidence.

During the sixth and seventh days of incubation chondrification sets in. In the seven-day chick auditory capsule and hyoid are both perfectly chondrified and perfectly continuous

with one another, the constriction observable in the five- and six-day chicks having, moreover, disappeared.

In the eight-day chick the stapes is divided off from the auditory capsule, and the extra-columella is severed from the extreme distal end of the hyoid arch. This extreme end of the hyoid arch, which takes no part in the formation of the extra-columella is excessively small, only running through a few sections. My series of sections at this stage show the continuity and homogeneity of the stapes and all parts of the columella, the ossification of the stapes not occurring until a later period.



I. Five-day chick. II. Six-day. III. Seven-day. IV. Eight-day. All viewed from without. *aud. caps.* Auditory capsule. *vii. ch.* Seventh nerve. *ch.* Chorda tympani. *cons.* Constriction. *br.* Branchial blastema. *extra coll.* Extra-columella. *hy.* Hyoid.

It should be plain from this account that the chondrified stages in the seven- and eight-day chicks, with the description of which previous authors have been content, really tell us little by themselves; but the previous history of the hyoid arch in the pro-cartilage condition shows (1) that the whole of the extra-columella and part, at least, of the stapes are formed from it; (2) that the derivation of the foot-plug of the stapes, and perhaps the extreme distal part of the stapedal rod may be either from hyoid or from auditory capsule, but from which of the two it is impossible to assert, since the two elements are already inextricably fused before chondrification occurs; without leaving any visible boundary between them. It would be safe to say that certain cells in

the foot-plug are derived from the hyoid arch and certain cells from the auditory capsule. The important fact, however, clearly expressed in Figs. 4 and 5 is that the dorsal part of the hyoid arch, i. e. the part lying between the seventh nerve and the auditory capsule (*stap.* in Figs. 4, 5, and 6), gives rise to part, at least, of the stapes. The meaning of the constriction in the five- and six-day chicks must remain doubtful; it corresponds in position to a division between hyomandibular and keratohyal, and to the later division between stapes and extra-columella.

The following diagrammatic reconstructions will make the foregoing observations clear.

3. CONCLUSION.

The value of the embryological evidence here presented is partly positive, partly negative.

Positively, it may be stated that in the chick the contribution of the auditory capsule to the columella is exceedingly small, probably confined to the foot-plug of the stapes; at any rate the main part of the stapes and the whole of the columella is formed from the hyoid arch. Negatively, it proves the futility of basing arguments upon this question on isolated stages, or on cartilaginous stages which have not been traced back to their earliest procartilaginous forerunners. Taking this into consideration the supposed derivation of the stapes of Sauropsida from the auditory capsule (9), and the possible interpretation of *Sphenodon* in this manner (12 and 14) becomes exceeding doubtful; in birds, at any rate, as we have seen, the condition confirms the opinion arrived at on theoretical grounds by Gaupp (11), that the stapes of Sauropsida corresponds to the stapes of Mammalia, and to the hyomandibular of fishes. Mammalia and Sauropsida have this much in common, that they have both converted the hyomandibular or dorsal portion of the hyoid arch into the stapes; but subsequently they have gone on different lines in evolution, the Sauropsida making use of the more ventral part of

the hyoid to complete their chain of ossicles (extra-columella), while the Mammalia have pressed into this service the constituents of the arch in front—namely, the quadrate and articular (incus and malleus).

(Since this article was in type Versluys (15) has published a most thorough account of the development of the Lacertilian columella. I am happy to see that his results are in complete accord with my own).

LITERATURE.

1. PLATNER, F.—'Bemerkungen über das Quadrat-bein und die Paukenhöhle der Vögel,' 1839.
2. HASSE, C.—'Zur Morphologie des Labyrinths der Vogel,' 'Anatom. Studien,' Bd. i, 1873.
3. PARKER, W. K.—'On the Structure and Development of the Skull of the Common Fowl,' 'Phil. Trans. Roy. Soc. Lond.,' vol. clix, pt. ii, 1869.
4. HUXLEY, T. H.—'On the Representatives of the Malleus and Incus of the Mammalia in the other Vertebrata,' 'Proc. Zool. Soc. Lond.,' 1869.
5. MOLDENHAUER, W.—'Die Entwicklung des mittleren und des äusseren Ohrs,' 'Morph. Jahrb.,' Bd. iii, 1877.
6. MAGNIEN, L.—'Recherches sur l'anatomie comparée de la corde du tympan des oiseaux,' 'Comptes Rendus de l'Académie des Sciences,' t. ci, 1885.
7. GADOW, H.—'Phil. Trans.,' 1888, vol. clxxix.
8. GADOW und SELENKA.—'Vögel,' 'Bronn's Klassen und Ordnungen,' Bd. vi, Abt. 4, 1891.
9. HOFFMANN, C. K.—'Reptilien,' 'Bronn's Klassen und Ordnungen,' Bd. vi, Abt. 3, 1891.
10. VERSLUYS.—'Die mittlere und äussere Ohrsphäre der Laccartilia und Rhynchocephalia,' 'Zool. Jahrb.,' Bd. xii, Heft. 2.
11. GAUFF, E.—'Ontogenese und Phylogense des schalleitenden Apparates bei den Wirbelthieren,' 'Anät. Hefte,' 2te Abt., 1898.
(See this paper for discussion of whole question and complete list of literature.)
12. SCHAUMSLAND, H.—'Weitere Beiträge zur Entwicklungsgeschichte der Hattaria,' 'Arch. Mikr. Anat.,' lvi, 1900.
13. KINGSLEY.—'The Ossicula Auditus of Vertebrates,' 'Tuft's College Reports,' 1900.
14. HOWES, G. B., and SWINBERTON, H. H.—'Development of the Skeleton of the Tuatara,' 'Trans. Zool. Soc. Lond.,' vol. xvi, pt. i, 1901.
15. VERSLUYS, J.—'Entwicklung der Columella auris bei den Lacertilien,' 'Zool. Jahrb.,' Bd. xix, Heft 1.