

A note on the development of the tubotympanic recess in the human embryo

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INTRODUCTION

The tubotympanic recess is the name given to the anlage which subsequently develops into the tympanum and pharyngotympanic tube. There are conflicting views on the composition of the tubotympanic recess, particularly with reference to that portion of the recess which gives origin to the tympanum. According to Hammar (1902), whose views are widely quoted by most embryologists including Mall (1912), Patten (1949) and Arey (1965), the portion of the recess which is destined to form the tympanum is derived solely from the first dorsal pharyngeal pouch, whereas Frazer (1910, 1914, 1922, 1931) has contradicted Hammar's views and has observed that the tympanum not only receives contributions from the first dorsal pouch but also from the second arch entoderm as well as from the second dorsal pouch. Frazer's views have since then been accepted by Davies & Davies (1962) and Hamilton, Boyd & Mossman (1962). The present investigation is to ascertain the cause for this discrepancy in the views regarding the development of the tympanum and to present additional facts which appear to support the origin of the tympanum from the first dorsal pouch.

MATERIALS AND METHODS

Sixteen human embryos ranging from 6 mm crown-rump (C.R.) length to 37 mm C.R. length, which have been serially sectioned, have been included in the present investigation. The C.R. lengths of specimens examined were as follows: 6 mm, 8.5 mm, 10 mm, 11 mm, 13 mm, 14.5 mm, 16 mm, 17 mm, 20 mm, 23 mm, 24 mm, 26 mm, 27 mm, 29 mm, 35 mm, and 37 mm. Moreover the tubotympanic recess (cavity) was plastically reconstructed in the 10 mm, 11 mm, 13 mm, 14.5 mm, 16 mm, 20 mm, 29 mm, and 37 mm. C.R. length embryos. Wherever necessary the ninth nerve and Reichert's bar were also included in the reconstructions. These were subsequently photographed and reduced to the same magnification so that a direct comparison could be made of the size of the recesses in the various embryos. All drawings of the recesses presented in this paper are based on photographs of the reconstructions. Furthermore, the method of obtaining the direction of the recess in relation to the pharynx is shown in Fig. 1.

OBSERVATIONS

Only some of the embryos in the series have been described in detail: a passing reference is made to a few others either in the text or in the figures.

Embryo length: 11 mm C.R. (Fig. 2). The roof and floor of the pharynx in relation to the first two pouches are separated from each other by a narrow interval which

forms the anterior part of the cavity of the primitive pharynx. The second pouch is much smaller than the first and does not extend as far laterally as the first pouch. The dorsal and ventral components of the second pouch are continuous with one another and pass medially and downwards. Behind the second pouch the cavity of the pharynx curves gently inwards till the narrower part of the pharynx is reached towards the caudal part of the third arch.

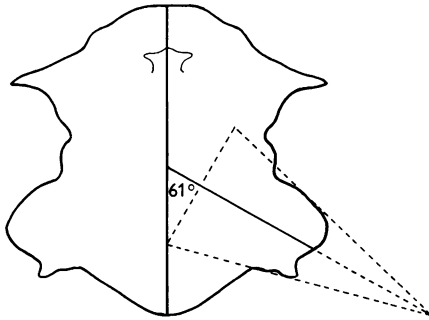


Fig. 1

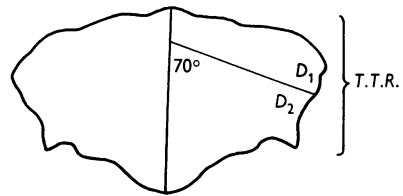


Fig. 2

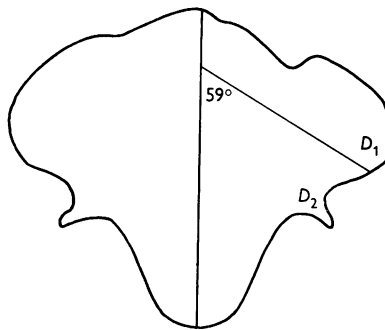


Fig. 3

Fig. 1. Dorsal view of a reconstruction of the tubotympanic recess of a 10 mm C.R. length embryo showing the method of determining the slope of the recess in relation to the pharynx. Note also that the shape of the recess in this embryo resembles the 14.5 mm stage, and consequently the 10 mm embryo is probably older than its C.R. length indicates. $\times 33$.

Fig. 2. Dorsal view of a reconstruction of the tubotympanic recess (T.T.R.) in a 11 mm C.R. length embryo. D_1 and D_2 indicate the first and second dorsal pouches. $\times 33$.

Fig. 3. Dorsal view of a reconstruction of the recess in a 13 mm embryo. Note that the second dorsal pouch (D_2) lies postero-medial to the first dorsal pouch. $\times 33$.

The antero-lateral end of the first pouch is still in contact with the surface ectoderm of the first ectodermal groove while the second pouch has contact with the ectoderm of the cervical sinus. The ninth nerve lies behind and medial to the second pouch and passes directly medially to reach the third arch tissues forming the posterior part of the anlage of the tongue. Reichert's bar does not show any chondrification at this stage.

Embryo length: 13 mm C.R. (Fig. 3). In this embryo, unlike in the 11 mm specimen,

the first dorsal pouch has lost contact with the surface ectoderm while the second pouch retains its connexions with the cervical sinus. The cavities of the first and second dorsal pouches still communicate freely with one another. While the first pouch is broad and has an extremely wide communication with the pharynx, the second pouch is much smaller and its aditus into the pharynx is also much narrower. The dorsal part of the second pouch lies behind the anlage of Reichert's cartilage and its tapering posterior extremity is found to lie between Reichert's bar and the

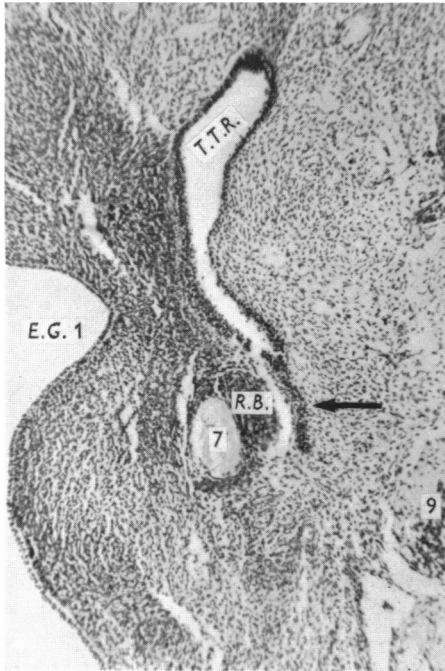


Fig. 4

Fig. 4. Transverse section through the region of the tubotympanic recess in a 14.5 mm C.R. length embryo. Note the fusion of the walls of recess (arrow) in relation to Reichert's bar (*RB*) and seventh cranial nerve (7). $\times 90$.

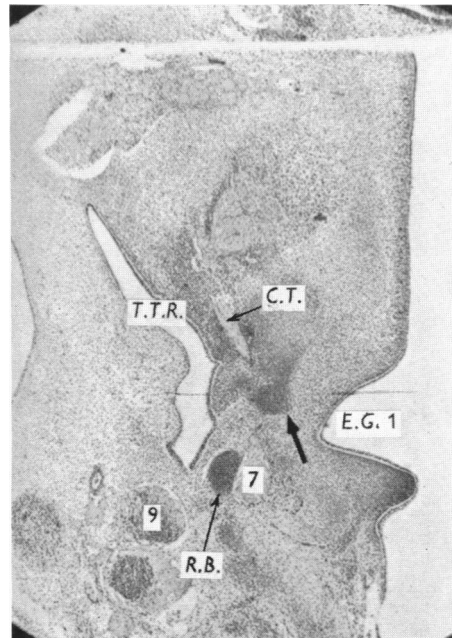


Fig. 5

Fig. 5. Transverse section through the tubotympanic recess of a 16 mm C.R. length embryo showing the manubrial extension (arrow). Note Reichert's bar (*RB*) lying behind the deepest part of the first ectodermal groove (*E.G. 1*). $\times 36$.

| | | | |
|----------------------|------------------------|---------------|---------------------|
| <i>C.T.</i> | Chorda tympani nerve | <i>M.N.</i> | Manubrial notch |
| <i>D₁</i> | 1st dorsal pouch | <i>M.P.</i> | Meatal plate |
| <i>D₂</i> | 2nd dorsal pouch | <i>R.B.</i> | Reichert's bar |
| <i>E.G. 1</i> | 1st ectodermal groove | <i>T.O.</i> | Tubal orifice |
| <i>H.M.</i> | Handle of malleus | <i>T.T.R.</i> | Tubotympanic recess |
| <i>L.P.</i> | Levator palati muscle | 7 | 7th cranial nerve |
| <i>M.C.</i> | Manubrial condensation | 9 | 9th cranial nerve |

ninth nerve. The ventral portion of the second pouch is much larger than its dorsal counterpart. The third arch, in comparison to its size in the preceding embryo, has undergone enlargement as indicated by the area supplied by the ninth nerve whereas

the second arch is very much reduced in size, especially in that portion lying on either side of the midline. The ninth nerve still lies posterior and medial to the second pouch as it was in the preceding 11 mm embryo except that the nerve now passes below the medial end of the ventral portion of the second pouch and lies superficial

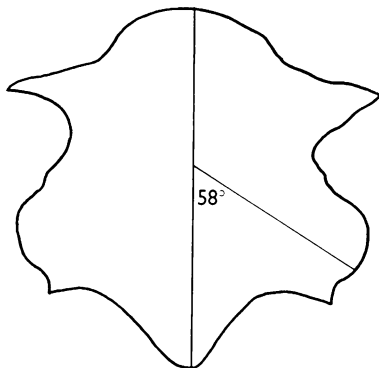


Fig. 6

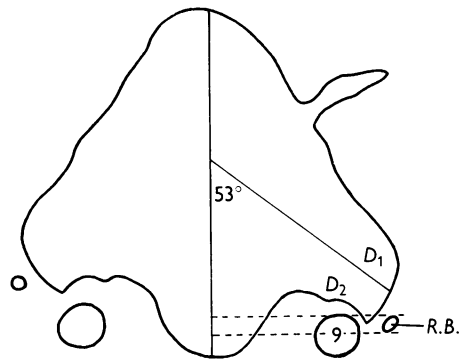


Fig. 7

Fig. 6. Dorsal view of a reconstruction of the tubotympanic recess in a 14.5 mm c.r. length embryo. $\times 33$.

Fig. 7. Dorsal view of a reconstruction of the tubotympanic recess in a 16 mm c.r. length embryo. Note that the second pouch has now moved medially. $\times 33$.

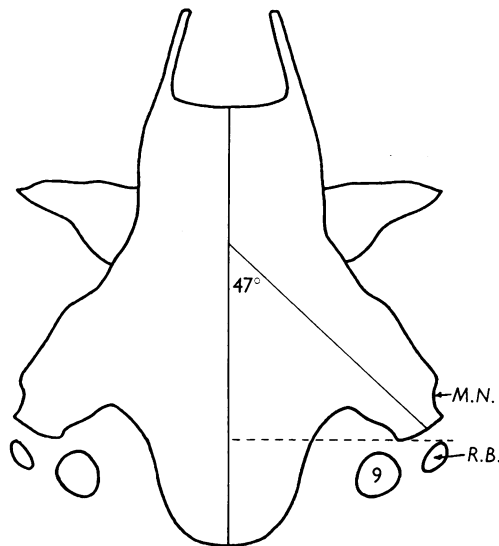


Fig. 8. Dorsal view of a reconstruction of the tubotympanic recess in a 20 mm c.r. length embryo. The recess lies entirely in front of Reichert's bar. $\times 33$.

to Reichert's bar before supplying the posterior part of the anlage of the tongue. Epithelial fusion of the walls of the posterior part of the recess in relation to the hyoid bar is well seen in the 14.5 mm embryo and is more marked in the succeeding

16 mm embryo (Fig. 4). Moreover the recess in this embryo (Fig. 6) is intermediate in development between the 13 mm and 16 mm embryos.

Embryo length: 16 mm C.R. (Fig. 7). This embryo is remarkable in that there is a considerable change in the shape of the recess. The anterior margin of the recess, instead of sloping backwards gently as it did in the 13 mm embryo now shows a marked obliquity directed backwards and outwards. The posterior margin likewise shows a change in that it now slopes forwards and medially without showing much of the prominence due to the backward projection of the second pouch which was much in evidence in the 13 mm embryo. Moreover, there is practically no change in the antero-posterior width of the recess at the site of its communication with the pharynx although the recess now appears to be more clearly demarcated off from the pharynx than in the preceding 13 mm embryo. Another remarkable feature of the 16 mm embryo is the fact that no part of the recess passes dorsal to the line connecting the posterior margins of the lateral ends of the anlagen of Reichert's cartilages of the two sides. The portion of the recess belonging to the first pouch can be seen to be separated off from the remaining part of the recess by a groove situated on the dorsal aspect of the recess. Behind the first pouch area is the portion of the recess which overlies the anlage of Reichert's cartilage and this part of the cavity is filled with epithelial cells. The second pouch has become much less prominent and is now situated very close to the side wall of the pharynx. The cranial portion of this pouch has a narrow lumen and in transverse sections appears as a deep groove in the dorso-lateral wall of the pharynx. More caudally, the pouch becomes slightly wider. The ninth nerve, which was occupying a position medial to the second pouch in the 13 mm embryo, now comes to lie postero-lateral to the caudal portions of the (second) pouch. The anlage of the outer end of Reichert's cartilage lies behind the plane of the first ectodermal groove (Fig. 5) and is much thinner than that of the 13 mm embryo.

There is a condensation of mesoderm which extends backwards from the anlage of Meckel's cartilage (manubrial extension) and lies on the lateral side of the first pouch (Fig. 5). Behind this extension lies the extreme lateral end of the first dorsal pouch and this area of the pouch is situated directly opposite the deepest part of the broad first ectodermal groove (Fig. 5). The first arch tissues, including the condensation representing the anlage of Meckel's cartilage and its manubrial extension, are larger and better defined than they were in the 13 mm embryo. In this 16 mm embryo the first and third arch tissues appear to be in contact with one another so that there seems to be no second arch tissue in the floor of the pharynx where the developing tongue is situated.

Embryo length: 20 mm C.R. (Fig. 8). The tubotympanic recess in this embryo is of interest in that no part of the recess extends backwards even as far as a line joining the anterior margins of Reichert's cartilages at their cranial (lateral) ends. The recess is more elongated than in the preceding 16 mm embryo but the antero-posterior width of the opening of the recess into the pharynx remains the same as it was in the 16 mm embryo. The medial margin of the recess is now more indrawn than in the preceding state. The manubrial extension is more clearly defined and is situated opposite a well-marked concavity on the lateral part of the recess. Reichert's bar at its upper and lateral end still lies behind the deepest part of the first ectodermal groove.

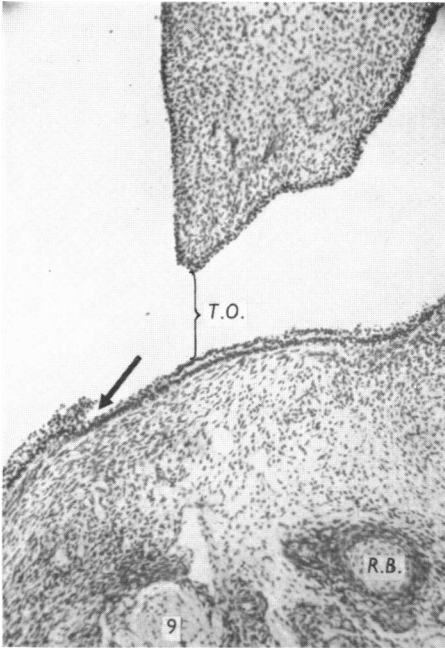


Fig. 9

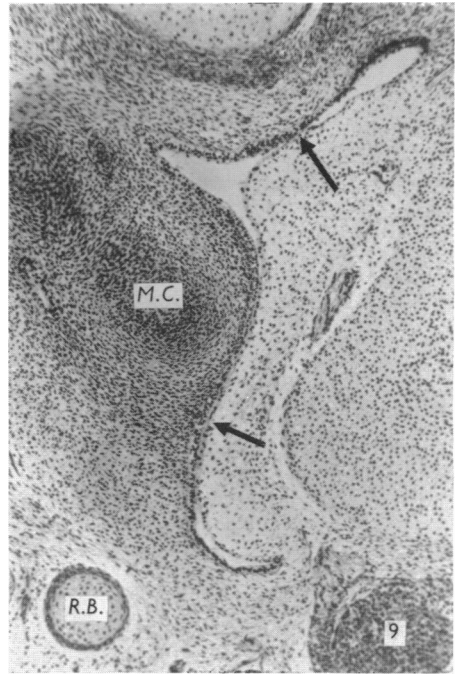


Fig. 10

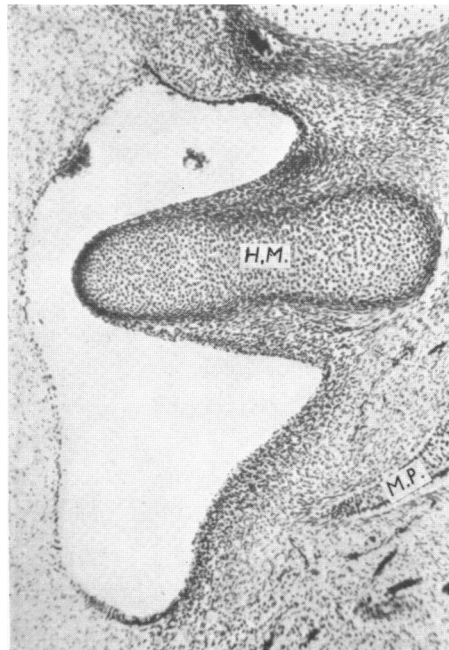


Fig. 11

A groove, wedge-shaped in section, is situated on the lateral wall of the pharynx immediately behind and below the opening of the recess (Fig. 9). This groove extends downwards for about $56\ \mu\text{m}$ before it becomes continuous with the ventral part of the second pouch. There is another groove extending for only some $24\ \mu\text{m}$ and is directly related to the caudal end of the tube along its posterior margin. The two grooves are discontinuous over a length of $66\ \mu\text{m}$ although traces of the groove are occasionally seen along the lateral wall of the pharynx in the intervening area separating the two grooves. The ninth nerve is seen to pass lateral to the caudal part of the second ventral pouch.

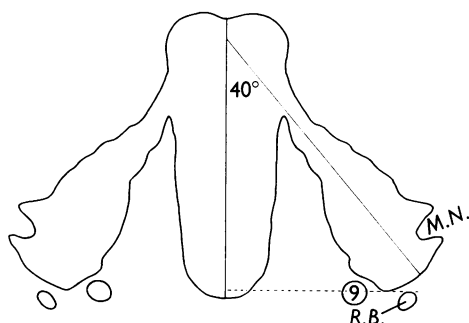


Fig. 12

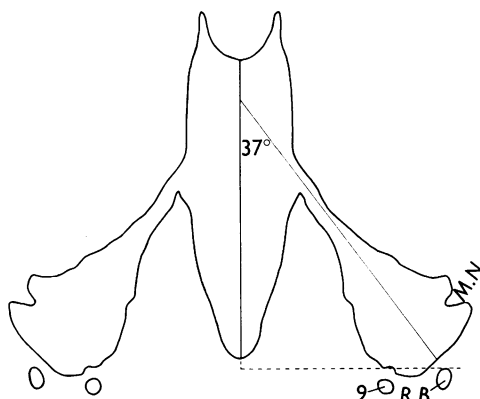


Fig. 13

Fig. 12. Dorsal view of a reconstruction of the recess in a 29 mm C.R. length embryo. Note that the tubal and tympanic parts of the cavity are distinguishable. $\times 33$.

Fig. 13. Dorsal view of a reconstruction of the recess in a 37 mm C.R. length embryo. Note the elongation of the tubal segment in comparison to the 29 mm stage. $\times 33$.

In the 27 mm embryo the walls of the recess in relation to the handle of the malleus are in apposition (Fig. 10) while pouch-like cavities are seen in a corresponding situation in a 35 mm embryo (Fig. 11).

Embryo length: 29 mm C.R. (Fig. 12). In this embryo, the length of the tubotympanic recess is increased to double that seen in the 20 mm embryo. The tubal portion which has commenced its formation in the 26 mm embryo is now easily distinguished from the tympanic part by the marked degree of constriction that characterizes the tubal segment. Thus the width of the recess at its entry into the pharynx is now about a third of what was observed in the 20 mm embryo. The postero-medial margin of the recess slopes even more acutely than in the 20 mm

Fig. 9. Transverse section through the region of the opening of the recess into the pharynx in a 20 mm C.R. length embryo. Arrow indicates the site of the remnant of the second groove in the pharynx behind the tubal opening (T.O.). $\times 90$.

Fig. 10. Transverse section through the outer part of the tympanic cavity in a 27 mm C.R. length embryo showing an apposition of the walls of the tympanic cavity in relation to the manubrial condensation (M.C.). $\times 90$.

Fig. 11. Transverse section through the outer part of the tympanic cavity in 35 mm. C.R. length embryo showing pouch-like dilatations in front of and behind the handle of malleus (H.M.). $\times 90$.

embryo. It is noteworthy that no portion of the recess reaches a line joining the anterior margins of the right and left Reichert's cartilages, thus simulating the condition observed in the 20 mm embryo. The deep groove on the lateral side of the recess is in relation to the handle of the malleus while another groove placed anterior to this is related to Meckel's cartilage. Although a second ventral pouch had been observed in the 23 mm, 26 mm and 27 mm embryos examined, there is in

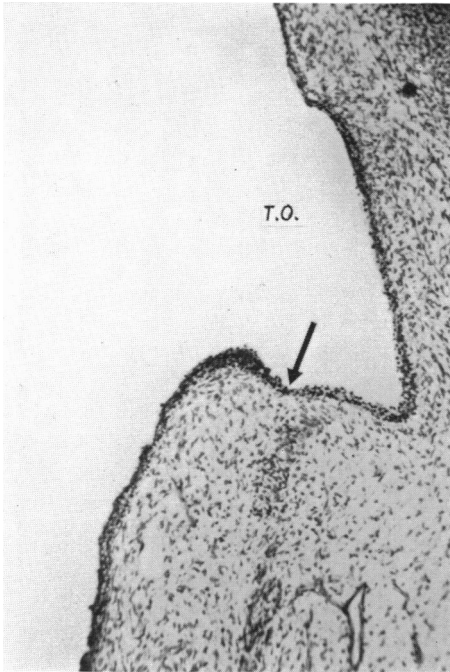


Fig. 14

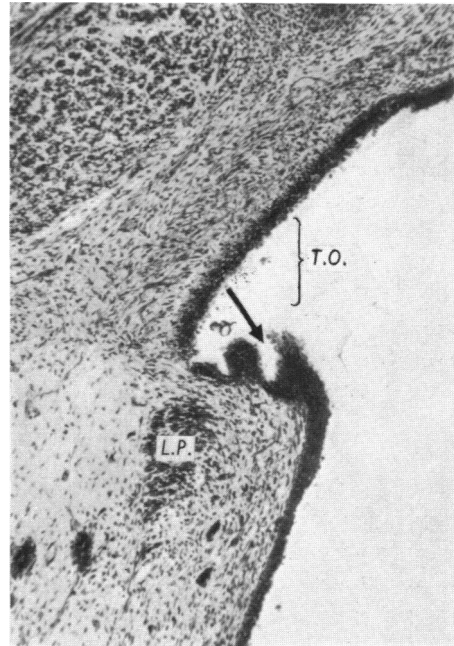


Fig. 15

Fig. 14. Transverse section through the tubal orifice of a 29 mm C.R. length embryo to show the remnant of the cranial part of the second pouch (arrow). $\times 90$.

Fig. 15. Transverse section through the tubal orifice of a 37 mm C.R. length embryo showing the remnant of the second pouch (arrow). Note that the levator palati muscle (*L.P.*) lies on the lateral side of the second groove.

the 29 mm embryo only an outpocketing of the pharyngeal endodermal wall medial to the ninth nerve just prior to the entry of this nerve into the posterior part of the tongue. A groove is also observed along the lower margin of the tubal portion of the recess and is situated close to the opening of the tube into the pharynx (Fig. 14). This groove extends upwards into the tube for a distance of about $70 \mu\text{m}$ and lies medial to and above the levator palati muscle.

Embryo length: 37 mm C.R. (Fig. 13). In this embryo the recess shows little change in its tympanic portion while its tubal segment is more elongated than in the 29 mm embryo. Moreover, the angle between the recess and the pharynx has become slightly more acute than in the preceding stage. Only a very minute segment of the recess in

its extreme postero-lateral part lies behind the line joining the anterior margins of the two Reichert's cartilages. The groove seen along the lower margin of the tubal segment of the recess in the 29 mm embryo is now about 180 μm and lies medial to the levator palati muscle (Fig. 15) before the latter enters the palate. This groove opens caudally into the pharynx immediately above the level of the palate, whose folds have now fused completely along the mid-line. Below the palate the groove cannot be identified until one again meets with the remnants of the second ventral pouch in close relation to the ninth nerve just above the entry of the nerve into the posterior part of the tongue.

DISCUSSION AND CONCLUSIONS

Period of formation of the primary tympanic cavity. During this period, which extends up to the 20 mm stage, the contributions from the second pouch and arch to the posterior part of the tubotympanic recess is being gradually eliminated from the remaining part of the recess formed by the first dorsal pouch. Moreover, there is also a backward extension of the first arch tissues into the area occupied by the first pouch. It is this backward extension which appears to have been erroneously interpreted by both Hammar (1902) and Frazer (1910, 1914, 1922, 1931). They both agree that the 'manubrial extension' from the first arch lies within the anterior part of the second arch. However, that the manubrial extension does, in fact, lie in relation to the antero-lateral part of the first pouch is substantiated by the observation that it lies well in front of the deepest part of the first ectodermal groove in the 16 mm embryo. Moreover, it is also noteworthy that the extreme lateral end of the first pouch lies opposite the deepest part of the first ectodermal groove in this embryo as in earlier embryos but behind the manubrial extension. The increasing obliquity of the anterior margin of the tubotympanic recess is also in support of a backward extension of the lateral portion of the first arch tissues. Thus by the 16 mm stage most if not the entire tubotympanic recess is formed by the first dorsal pouch, although the tympanic or lateral part of the recess still retains some second arch tissues in its floor. However, by the 20 mm stage, even this little contribution from the second arch appears to have disappeared, since the lateral part of the recess now lies entirely in front of Reichert's bar. This disappearance of the second arch contribution from the floor of the lateral end of the recess is preceded by an epithelial fusion which obliterates this part of the cavity as has been observed in the 14.5 mm and 16 mm embryos. Moreover, the changes described above are compatible with the alterations in the size and shape of the recess in the 16 mm and 20 mm embryos.

The changes observed in the postero-medial part of the recess during this period consist of a gradual reduction and medial displacement of the entire second pouch, so that by the 16 mm stage the pouch appears as a small projection attached to the postero-medial part of the recess. In the 20 mm embryo there is a further reduction in the size of the pouch in its cranial (upper) part with the result that this part of the pouch is now reduced to a mere groove at the postero-medial end of the recess close to the opening of the tube into the pharynx.

This inward displacement of the entire second pouch and its gradual but drastic

reduction in its cranial part is in agreement with the findings of Hammar but run counter to the views expressed by Frazer, who seems to think that the second pouch is split into two parts, a cranial lateral portion remaining in the tympanum while the medial caudal part forms the ventral part of the second pouch. According to him, this is the result of a forward growth of the third arch tissues. This interpretation is not only unsupported by any actual facts but would also introduce a difficulty in correlating the nerve supply to the tympanum. Moreover, if Frazer's views are to be entertained, the progressive reduction and inward displacement of the second pouch from the 6 mm to the 16 mm stages would become meaningless as Frazer's ideas imply a sudden lateral displacement of the upper, lateral portion of the second pouch at the 16 mm stage. Furthermore, the reduction and medial displacement of the second pouch would enable the third arch tissues to pass lateral to the second pouch and meet the structures developed from the first arch not only in the region of the developing palatal folds but also all along the entire length of the tubal and tympanic portions of the recess. That such a change occurs is indicated by the course of the ninth nerve between the 14.5 mm and 20 mm stages. Consequently, there is no difficulty in explaining the position of the ninth nerve to the pouch. It must, however, be realized that this change occurs only after the second ventral pouch has become disconnected from the insignificant cranial dorsal part, which in the 20 mm embryo is only a microscopic appendage attached to the caudal and posterior margin of the tubal orifice. Once these changes are appreciated there would hardly be any difficulty in accounting for the nerve supply of the tube and tympanum from the fifth and ninth cranial nerves. Moreover, the absence of any nerve supply from the seventh cranial nerve also becomes understandable.

Period of the tubotympanic canal and the transformation period. The separation of the tubal segment from the tympanum begins in the 26 mm embryo and is clearly seen in the 29 mm stage. That this change is brought about by the forward migration of the third arch tissues is strongly suggested by the change in shape which can be seen in the models of the 29 mm and 37 mm embryos. The extension of the tympanic portion of the recess into the area overlying the antero-lateral end of Reichert's cartilage in the 37 mm embryo has to be interpreted as a secondary expansion similar to the recesses formed in front of and behind the handle (manubrial mesoderm) of the malleus. It is therefore concluded that the whole of the tympanum is developed from the first pouch and Frazer's interpretation that the first pouch occupies only that area in front of the handle of the malleus seems to be unwarranted.

SUMMARY

1. The development of the human tubotympanic recess has been investigated in sixteen embryos ranging from 6 mm to 37 mm C.R. length.
2. Migration of the first arch tissues into the area of the first pouch occurs from the 10 mm to 20 mm stages so that the manubrial extension lies in relation to the first pouch and not within the region of the second arch.
3. Between the 10 mm and 20 mm stages there is a gradual reduction in the contributions from the second arch and second pouch to the tubotympanic recess so that the tympanum and tube are formed solely from the first pouch.

4. The differentiation of the tubal and tympanic segments of the recess is first seen in the 26 mm embryo.

5. Changes occurring from the 16 mm to the 37 mm stages are compatible with the forward migration of the third arch tissues with the result that the first and third arches meet all along the length of the tubal and tympanic segments of the recess thus accounting for the adult pattern of nerve supply to these regions.

It is a pleasure to thank Professor J. D. Boyd of the University of Cambridge not only for the loan of the material but also for his constant encouragement during the progress of this investigation. I also wish to express my sincere thanks to Mr J. F. Crane, Department of Anatomy, University of Cambridge, for the photomicrographs and Mr Baharuddin bin Haji Osman of the Department of Anatomy, University of Singapore, for the line-drawings.

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