

ON THE DEVELOPMENT OF THE TASTE-ORGANS
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WHILE it will not be denied that something has been accomplished of late years towards a better understanding of the nature and distribution of the mammalian taste-organs, as well as a clearer recognition of their behaviour when exposed to different and often widely varying conditions, yet it must be conceded that, so far as their mode of development is concerned, our knowledge is still very limited. The valuable researches of Drasch¹ and of Hermann² on the more intimate structure of the gustatory papillæ and taste-bulbs (notwithstanding a failure on the part of these observers to agree in many of their conclusions), not only throw light upon several important questions which had hitherto been veiled in almost complete obscurity, but they also reveal new fields of inquiry for the conscientious investigator. To the labours of these histologists should be added those of Griffini.³ This observer approached the subject mainly from the experimental side, and studied the taste-organs with a view to learning, if possible, something of the phenomena of reproduction and regeneration. Of the important results obtained by him I shall have occasion to speak a little later in the course of this paper.

HISTORICAL REVIEW.

Hans v. Wyss⁴ is the earliest writer on the taste-organs who, so far as I am aware, makes any allusion to their appearance at different

¹ "Histologische und Physiologische Studien über das Geschmacksorgan," *Sitzb. d. k. Akad. d. Wiss. Wien*, Bd. lxxxviii. Abth. iii. p. 516, 1883; "Untersuchungen über die Papillæ foliatæ et circumvallatæ des Kaninchen und Feldhasen," *Abhandl. d. k. s. Gesellsch. d. Wiss. Leipzig*, Bd. xxiv. p. 231, 1887.

² "Studien über den feineren Bau des Geschmacksorganes," *Sitzb. d. math.-phys. Classe d. k. b. Akad. d. Wiss. München*, p. 277, 1888.

³ "Sulla riproduzione degli Organi Gustatorii," *Rendiconti Reale Istituto Lombardo*, ser. ii. vol. xx. p. 667, 1887.

⁴ "Die becherförmigen Organe der Zunge," *Arch. f. mikr. Anat.*, Bd. vi. p. 237, 1870.

stages of growth. He examined the papilla foliata of new-born and partly-grown rabbits. In the new-born rabbit he found the foliate organ quite perfectly formed, and experienced no difficulty in identifying taste-bulbs. The bulbs of this period, however, differed from those of the full-grown animal in having a more rounded shape, and in being less than one-half as large. Within three weeks this difference ceased to be longer noticeable.

J. Hönigschmied,¹ in a communication on the microscopic anatomy of the taste-organs, merely states that he failed to detect in the circumvallate papillæ of the new-born child any regular arrangement of the taste-bulbs.

Hönigschmied was followed a little later by Hoffmann,² who investigated the human embryo and new-born child for the purpose of studying the distribution of the taste-organs in man. The earliest organs examined by him came from an embryo three and one-half months' old, and the oldest from a woman about sixty years of age. In a fungiform papilla of a four and one-half months' foetus, and also in the papillæ of one at the sixth month, taste-bulbs were present. In the six months' foetus the peripheral ends of the supporting cells of the bulbs were prolonged to an unusual extent, giving the bulbs somewhat the form of a matrass. Hoffmann concludes that taste-bulbs are more frequent in embryos and the newly-born than in older individuals; that in embryos and new-born children they occur more frequently and in greater number on the free surface of the papillæ than in the adult, and that in old persons they are but rarely met with in this region.

In 1884, both Hermann³ and Lustig⁴ published papers on the development of the taste-organs in mammals. The former investigator confined himself wholly to an examination of the circumvallate and foliate papillæ of the foetal and new-born rabbit, whilst the latter studied these organs in both the rabbit and man. Hermann and Lustig were the first histologists to make a special study of the evolution of the taste-organs of the rabbit, whilst to Lustig is due the merit of first investigating, in detail, the development of the taste-organs of man.

According to Hermann, the development of the gustatory papillæ takes place during the latter period of intrauterine life and in the first few days following birth. In a rabbit embryo, 54 mm. long, he was able to distinguish, with the unaided eye, the circumvallate and foliate papillæ, but the trenches of the former and furrows of the latter were wanting. With reference to the development of these

¹ "Ein Beitrag zur mikroskopischen Anatomie der Geschmacksorgane," *Zeitsch. f. Wiss. Zool.*, Bd. xxiii. p. 414, 1873.

² "Ueber die Verbreitung der Geschmacksknospen beim Menschen," *Virchow's Archiv*, Bd. lxii. p. 516, 1875.

³ "Beitrag zur Entwicklungsgeschichte des Geschmacksorgans beim Kaninchen," *Arch. f. mikr. Anat.*, Bd. xxiv. p. 216, 1884.

⁴ "Beiträge zur Kenntniss der Entwicklung der Geschmacksknospen," *Sitzb. d. k. Akad. d. Wiss. Wien*, Bd. lxxxix. Abth. iii. p. 308, 1884.

papillæ, Hermann (*loc. cit.*, p. 227) makes the following statement:—“Fasst man nun die Resultate vorliegender Untersuchung zusammen, so ergibt sich für's erste, das die Papilla foliata und vallata aus einfachen Epitheleinstülpungen sich entwickeln, welche dadurch, dass sie seitliche Fortsätze—secundäre Epitheleinstülpungen—treiben, bei ersterer zur Bildung der secundären Blätter, bei der Papilla vallata des Walles Anlass gaben. Die primären Epitheleinstülpungen sind bei Kaninchenföten von 50 mm Länge, also vom 23. Tage, schon vorhanden, die Bildung der secundären Blätter, resp. des Walles, beginnt jedoch erst bei föten von 70 mm Länge, nach dem 24. Tage des intrauterinen Lebens und ist bei Neugeborenen noch nicht zum Abschluss gekommen.” The complete differentiation of the circumvallate papillæ and of the folds of the foliate organs ensues only after birth. Respecting the mode of formation of the serous glands, Hermann says:—“Ausser zur Bildung der Papillen stehen die primären Epitheleinstülpungen noch in Beziehung zur Genese der an die Geschmacksorgane eng gebundenen Ebner'schen acinösen Drüsen, indem sie als anfangs solide Zellstränge in das Muskelgewebe hineinwuchern, durch Atrophie der central gelegenen Zellen sich zu blind und kolbig endenden Gängen aushöhlen, von denen sich seitliche Ausbuchtungen—die Acini—abzweigen. Dieser letztere Process findet ebenfalls erst beim neugeborenen Kaninchen statt.”

In a rabbit's embryo, some 50 mm. in length, Hermann found taste-bulbs, in the first stages of formation, on the free surface of the circumvallate papillæ. In an embryo rabbit, 70 mm. long, the bulbs of this area were perfectly developed and numerous. In the secondary lamellæ of the foliate organ and lateral wall of the circumvallate papillæ of an embryo, 95 mm. long, were seen the forerunners of the definite taste-bulbs, in the form of modified basal cells of the epithelium. In embryos of a later period these fusiform cells traverse the entire thickness of the epithelial investment of the papilla. At birth a few of these bulbs had matured, and by the sixth day of life their development was completed. With the appearance of the definite bulbs those of the free surface (having attained their completion during intrauterine life) undergo degeneration, and by the third day there is scarcely a vestige of them remaining.

Lustig failed to discover taste-bulbs in rabbit embryos; even in those 10 cm. in length the papillæ were destitute of them. He therefore inferred that taste-bulbs are utterly lacking in the embryonic circumvallate and foliate papillæ. The smallest rabbit embryos investigated by him were from 6 to 7½ cm. in length. In these the circumvallate papillæ were sufficiently advanced to be recognised with the naked eye; the foliate organs, however, required the microscope to reveal their presence. In a rabbit 12 cm. long, and which had lived thirty-six hours, the circumvallate and foliate papillæ bore taste-bulbs in various stages of development. Those in the incipient stages of growth consisted of three to six strongly refractive taste-cells, the peripheral extremities of which protruded through the taste-pore. Lying between these cells were broad, swollen, nucleated, spindle-shaped ones, which Lustig considered the future supporting

cells. The development of the bulbs of both gustatory areas was not fully completed until the beginning of the third week following birth.

The youngest human tongue investigated by Lustig came from a fœtus of the fifth month of intrauterine life. Seated near the base of this tongue were five circumvallate papillæ. The foliate organs also were visible. No taste-bulbs were detected in either taste-area or elsewhere on the tongue. The next tongue examined came from a fœtus of the seventh month, and possessed seven circumvallate papillæ. These papillæ differed from those just mentioned in having their lateral area entirely protected by the enclosing wall; in the former, the outer wall only protecting the papillæ in their lower third. Some of these papillæ bore on their free surface facing the buccal cavity small, but sharply-defined, and, in some cases, well-developed taste-bulbs. The bulbs of the foliate papillæ were less numerous, and only present on the exposed surface of the folds, the furrows being filled for more than half their depth with epithelium. In the circumvallate papillæ of a child born at the beginning of the eighth lunar month, the bulbs still exhibited the embryonic characters. The foliate areas of this child were well formed, and possessed bulbs on both the free surface and upon the sides of the folds. In a mature still-born child, all of the circumvallate papillæ bore bulbs, yet not in all cases on their lateral wall. On one of these papillæ was superposed a papilla of the fungiform type, bearing bulbs on both its lateral slopes. In a normally developed child, which died twelve hours after delivery, all of the circumvallate papillæ contained bulbs, but they differed in size, form, and arrangement from those of the adult.

Griffini's¹ recent researches on the reproduction of the gustatory papillæ and regeneration of the taste-bulbs in the rabbit and dog are of signal value. From his experiments it appears that after excision of a foliate papilla of the rabbit, the area corresponding to the part removed is shortly re-vested with pavement epithelium. Later, from the sixteenth to the twentieth day a few small hemispherical elevations make their appearance, and these subsequently increase in size and number. During this period also many of the injured gland-ducts undergo repair, and communicate with the free surface of the epithelium. Within the secondary papillary processes of the elevations above referred to, taste-bulbs, lying partly in the mucosa (and in process of formation), first make their appearance. Thirty days after the complete removal of the circumvallate papilla of the dog a newly-formed papilla makes its appearance, having, however, the characters of the fungiform type. At the fortieth day (in a single instance only) a few taste-bulbs, situated at the lateral margin of the new papilla, were seen. Following section of the glosso-pharyngeals, the papillæ are changed but slightly, but the taste-bulbs begin to degenerate within twenty-three hours. The taste-cells are first destroyed, disappearing completely by the fifth day; the supporting cells soon after undergo

¹ *Op. cit.*

atrophy, and by the twenty-eighth day no bulbs are visible. At the seventy-sixth day after the division of the nerves, bulbs in various stages of formation were seen; but by the 209th day their development was still incomplete. According to Griffini, reproduction of the taste-bulbs, following the removal of a papilla or after section of the glosso-pharyngeal nerve, is effected in the following way:—The axis cylinders of the divided nucleated nerve-fibres are regenerated and penetrate the epithelium; active proliferation of the adjacent epithelial cells then occurs, the latter placing themselves around the intra-epithelial nerve-fibrils, and forming the supporting cells of the bulbs.

In comparing some of the results arrived at by the foregoing observers, we notice first a want of harmony in the expressions of v. Wyss and Hermann respecting the appearance of the foliate organ in the new-born rabbit. The former says¹ that this organ is quite perfectly formed in the new-born rabbit, and that bulbs can be detected without difficulty, the latter differing in size and form only from those of the adult animal. Hermann, on the other hand, maintains² that genuine epithelial bulbs, as seen in the full-grown animal, are found only very isolated in the newly-born rabbit, and are more fusiform than those of the adult. According to Hermann, the foliate organ does not acquire its definite form until the sixth day of life, and even then the bulbs are different in their structure and arrangement from those of the full-grown rabbit.

The statements of Hermann and Lustig are likewise not entirely in accord. While the former recognised taste-bulbs, in an early stage of formation, on the free area of a foliate papilla in a rabbit embryo 54 mm. long, and found them numerous and comparatively well advanced in the same region of a circumvallate papilla of a rabbit embryo 70 mm. in length, the latter³ failed to discover them in rabbit embryos at all, and, in consequence, was led to doubt their existence during intrauterine life.

Hoffmann⁴ found embryonic taste-bulbs in a fungiform papilla of a four and one-half months' fœtus, and in the papillæ of one at the sixth month. Lustig failed to detect bulbs in the papillæ of a fœtus at the end of the fifth month,⁵ but in one at the seventh he found on the free upper surface of both circumvallate and foliate papillæ small but well-defined bulbs.

The views of most of the investigators which I have cited are somewhat at variance respecting the nature of the taste-bulbs and their mode of origin, but I will not prolong this paper by discussing them.

PRESENT INVESTIGATION.

I am greatly indebted to Dr William F. Whitney, curator of the Anatomical Museum of the Harvard Medical School, and to

¹ *Loc. cit.*, p. 254.

² *Loc. cit.*, p. 221 *et seq.*

³ *Loc. cit.*, pp. 311, 315.

⁴ *Loc. cit.*, pp. 526, 529.

⁵ *Loc. cit.*, p. 317.

Dr John G. Stanton, of New London, Conn., both of whom very kindly placed at my disposal much of the material used in this research.

The youngest tongue which came under my observation was taken from a foetus at about the end of the fourth month.

Microscopic Appearance.—The upper surface of the tongue is marked by a wide, and in places deep, longitudinal mesial groove running nearly the whole length of the organ. The posterior dorsal surface is covered with papillary elevations of the mucous membrane, which present a great diversity in size and shape. The corresponding surface of the fore part of the dorsum is comparatively smooth and level. Near the lateral contour of the tongue proliferation of the epithelium appears to be most active. Here and elsewhere the epithelial cells may be seen pushing into the mucosa, some of their nuclei showing indications of karyokinetic figures. The cells composing the outer layers of the stratified pavement epithelium are large and chiefly cuboidal or polyhedral in form. The epithelium covering the papillary elevations does not differ greatly, save in the size of the cells, from that investing the lingual papillæ of later foetuses. The superficial layer, which is more or less thin, is formed of ordinary pavement epithelium.

Internal to this layer is a much thicker one, consisting for the most part of spheroidal cells with prominent nuclei, and below this again is a deep layer, composed entirely of elongated but not true columnar cells, which are in contact with the mucosa. Quite frequently the middle and deep layers are so thoroughly blended as to obliterate completely the line of demarcation between them. The connective tissue of the mucosa and submucosa is rich in nuclei and delicate fibrils. The stroma of the submucosa is somewhat looser in texture than that of the mucosa, and at various points where the epithelium has penetrated it to a considerable depth changes are perceptible, which suggest the incipient stages of development of the serous glands and their ducts. The transverse striæ of the muscle-fibres of this tongue require a comparatively high power to resolve them.

On the posterior dorsal surface, near the base of the organ, are five papillæ of the circumvallate type. The largest and most advanced of these papillæ is situated directly in the median

line of the tongue, and measures 0·13 mm. transversely and 0·15 mm. in height. The papillæ comprising this type project but slightly from the surface. Two adjoining ones show a decided tendency to share an enclosing wall in common. Fungiform papillæ, in various stages of growth, are scattered over the posterior dorsal region, and the foliate organs, in a formative stage, are clearly recognisable in the irregular elevations of the mucosa at the sides of the base of the tongue. The upper surface of the circumvallate papillæ is flattened or slightly convex, and the sides are perpendicular, or inclined slightly inwards. The trenches are not yet differentiated, although their future position is, in most instances, clearly delineated. The mucosa filling the interior of the circumvallate papillæ is perfectly homogeneous in appearance, and does not differ in character structurally from that underlying them.

In one of the smaller circumvallate papillæ is a taste-bulb in an early stage of development. It lies vertically directly in the long axis of the papilla. Its component cells, which are separable with a high power, converge peripherally and form an apex, which penetrates the outer layers of epithelium. The base of the bulb is completely lost in the mucosa. Four sensory cells are distinguishable, each of which possesses a relatively large oval nucleus, situated in the lower half of the cell. This embryonic terminal organ measures 0·0165 mm. in length and 0·012 mm. in breadth. Here and there, in the epithelium and connective tissue of these papillæ, modifications of the cells and stroma were unmistakable, but the precise nature of these changes I was unable to determine, nor could I in all cases establish with certainty the identity of the elements themselves.

The next tongue which I examined came from a foetus four and one-half months' old, and, like the preceding, required the microscope to reveal its superficial structures.

Microscopic Appearance.—The dorsal surface of this tongue is more markedly papillose than that just described, and at its extreme posterior portion the mucous membrane is thrown into a number of irregular folds. The epithelium covering the circumvallate papillæ does not differ greatly in arrangement from that of the new-born child. The epithelium, however,

overlying the general lingual surface is relatively much thicker than in newly-born children. The external layer of stratified pavement epithelium is very thick, and fills up to a common level most of the depressions and interstices between the various papillæ. The middle epithelial layer, as a distinct layer, has in places almost ceased to exist, and the deep or internal layer is composed of true columnar cells. The mucosa and submucosa are quite readily distinguished one from the other, and in the stroma of the latter the glands have advanced to some degree, and here and there are beginning to take definite shape.

At the posterior part of the dorsum of this tongue are six circumvallate papillæ, one or two of which are undergoing transition from the fungiform type. Some of these papillæ show indications of lobation. The trenches are still filled to the level of the free surface with pavement epithelium, and that protecting the upper exposed area of the papillæ is continuous with the adjoining lingual epithelium. The epithelium of the upper surface has increased in thickness without a proportionate increase in the thickness of that investing the lateral area. The papillæ vary in size, but one of average dimensions measured 0.35 mm. in its transverse diameter and was 0.20 mm. in height. The foliate organs consist of a few folds of the mucous membrane, the spaces between which are filled up to one level with epithelium.

The greater number of the circumvallate papillæ bear embryonic taste-bulbs at their upper part, but in no instance were any detected in the epithelium of the lateral area of a papilla. The largest number visible in a single vertical section was three, and each of these represented a different stage in development. The bulbs most advanced are spheroidal in shape, and extend in a vertical or oblique direction, across the stratum of epithelium. Other bulbs, more rudimentary in character, lie partly in the epithelium and partly in the mucosa, and still others appear to be almost wholly subepithelial in position. The largest and most fully developed of these embryonic bulbs measures 0.030 mm. in length and 0.028 mm. in breadth. The nerves, which could only be recognised with great difficulty in the tongue of the fœtus of the fourth month, are here, for the most part, quite clearly shown. Medullated fibres of the glosso-

pharyngeal nerve enter the base of the circumvallate papilla, and soon after divide and subdivide, forming a rather coarse plexus at the upper part of its body. Many of the terminal branches of these fibres have lost their medullary sheath, and can be traced to the upper part of the papilla, while very few apparently are distributed to its lateral area. In the mucosa, directly underlying the deep layer of columnar cells of the epithelium, these nerve-fibrils form a fine delicate network, very similar in some respects to that which I have seen in the papillæ of the common hare (*Lepus americanus*). In the circumvallate papilla of this rodent, owing to my success with gold preparation, I found the subepithelial network very beautifully depicted, the nerve-fibrils and small ganglia, which are scattered through the membranous stroma, being stained deep violet or black. A portion of the terminal fibrils of the network enter the bulbs at their base, while others pass between the latter, and end freely in the epithelium, or possibly form an intra-epithelial plexus.¹

I failed to discover embryonic taste-bulbs in the foliate organs of this fœtus, but isolated bulbs were present at the upper part of some fungiform papillæ. They are placed vertically in the long axis of the papilla, and are almost entirely epithelial in position. One of the most conspicuous bulbs of this region was pyriform in shape, and measured 0·0185 mm. in its greatest transverse diameter, and was 0·033 mm. in length. The peripheral end of the neck of this bulb failed to pierce the outermost layer of pavement epithelium.

The third tongue which I investigated came from a fœtus at the end of the sixth month. This tongue measures 27 mm. in length, 19 mm. in breadth, and 8 mm. in thickness, and is free from the floor of the mouth for 8·5 mm. The papillæ, which can now be seen without the microscope, are distributed quite uniformly over the dorsum, and those of the fungiform variety are quite numerous near the lateral margins and upon the anterior third and tip of the organ. Some of those of the tip are encircled by a deep fossa, and in vertical sections bear a

¹ Drasch has described in detail, in the treatises already cited, the arrangement and distribution of the nerves in the foliate papillæ of the rabbit and hare. A discussion of the results of his investigations, and his deductions therefrom, would lead me beyond the scope of this paper.

striking resemblance to normal circumvallate papillæ. The papillæ of mechanical function are quite thickly placed at the fore part of the dorsum. They consist largely of conical or cylindrical-shaped elevations of the mucosa, and are covered with a thin stratum of pavement epithelium. They measure about 0.20 mm. in height, and from one-third to one-half as much transversely. The lingual epithelium has increased in thickness, and proliferation of its cells is still very active. In the mucosa and submucosa fat is quite abundant. It is mostly in the form of closely aggregated circumscribed groups of fat cells.

At the back of the tongue, and disposed somewhat in the form of a crescent, are eight circumvallate papillæ. These papillæ are not all equally advanced, but they are all lobate or compound, varying in the number of their lobes from two to eight. The epithelium covering their upper surface is thicker and more substantial than that of the lateral area. The papillary and outer wall of the trench are not yet in all cases completely differentiated, but in many of the papillæ the trench is open throughout its extent, although still very narrow. Some of the papillæ possess secondary ones, the depressions between them being filled with pavement epithelium. Serous glands are plentiful, and their ducts communicate directly with the trenches, opening into them either at the base or sides. Mucous glands are also present, but they are situated in this region externally to the serous glands, and somewhat nearer the under surface. The circumvallate papillæ vary greatly in their dimensions, depending on the number and size of their respective lobes. One measured 0.35 mm. in breadth and 0.30 mm. in height; whilst another, with three large and nearly equal lobes, had a transverse diameter of 1.20 mm.

The foliate papillæ are still in process of formation, and are less advanced than those of the fungiform or circumvallate type. Each papilla consists of six to eight folds, which differ greatly in size, shape, and appearance. Many of the folds are cleft vertically, often in several places, the clefts being wholly or in part filled with fusiform cells of the epithelium. At the anterior limits of the foliate organ the mucous membrane is thrown into a lineal series of fairly uniform papillary elevations. These

elevations are rounded at the summit and slightly constricted near the middle, and measure on the average about 0.34 mm. in height and 0.10 mm. in their greatest transverse diameter.

I will observe here that it is by no means always an easy matter to define with exactness the anterior limits of the foliate organ in man. The nearest approach to the foliate type is probably reached in later fetuses and very young children. In man the characteristic primary and secondary lamellæ of the typical foliate organ are either wanting or imperfectly developed, and the presence of taste-bulbs may or may not be of diagnostic value in determining the nature of the organ in question.

The epithelium covering the upper surface of the folds of the foliate papillæ is thicker than that of the sides, and measures 0.045 mm. in thickness. The furrows are not yet entirely free from epithelium, but the latter is for the most part confined to their lower half. Within the folds are small collections of fat cells, deposited in spheroidal or oval-shaped masses, and about their bases are serous glands and ducts in abundance.

Taste-bulbs are not very numerous in the circumvallate papillæ. They are most frequent on the exposed surface, although they occur to some extent in the epithelium of the lateral area. They measure on the average 0.039 mm. in length and 0.024 mm. in breadth. In the foliate organ the bulbs occur on both the free area and sides of the folds, but they are smaller, fewer in number, and more subepithelial in character and position than those of the circumvallate papillæ. Some of the taste-cells of a bulb were isolated sufficiently for partial study. They are long and narrow, and terminate peripherally in a very minute point. In the nuclear region of the cell they measure 0.0025 mm. in diameter. The nucleus is oval in form, and is situated in the lower half of the cell. The central end of these cells was lost in the stroma of the mucosa. Bulbs were rarely met with in the fungiform papillæ, and those that were seen were rudimentary in character.

In the anterior region of this tongue, a little back from the tip and near the lower surface, I found the mucous glands of Nuhn. They were well developed, and their ducts opened on the under surface of the organ.

The fourth tongue worked upon came from a fetus of the

seventh month. It measures 35 mm. in length, 17 mm. in breadth, and 14 mm. in thickness. Anteriorly it is free from the floor of the mouth for 10 mm. The upper surface is faintly impressed with a medial groove. The tip, which is expanded and flat, is beset with long, coarse, closely aggregated papillæ of various shapes. The mucous membrane of the anterior surface is in places thrown into fairly uniform elevations, varying somewhat in size, but resembling a series of loops. Fungiform papillæ are fairly numerous, and are most thickly distributed over the anterior third, and upon the sides of the tongue. Those about the tip are elliptical in form, and are joined to the tongue by a narrow pedicel. They measure about 0.33 mm. in height, their greatest transverse diameter being 0.15 mm. The extreme posterior dorsal surface of the tongue is obliquely furrowed, and projecting from it are quite a number of coarse, fleshy elevations, the apices of which are directed inwards and backwards. The subparallel transverse folds of mucous membrane of the lateral edges of the organ stand out prominently in this tongue. Beginning at the anterior limit of the foliate papilla they gradually decrease in size, and cease altogether just before reaching the tip of the organ. Near the lateral border on either side of the tongue, a little beyond and in line with the outermost circumvallate papilla, is an epithelial-lined recess, the floor of which is invaginated upwards into a ridge. I was at first disposed to regard these depressions of the mucous membrane as mucous crypts, but their size, position, and structure rendered this supposition doubtful, and upon a closer inspection of them I was led to conclude that they were not.

Two fetuses of this period of intrauterine life came under my observation, and each of them possessed eight circumvallate papillæ. In both, seven out of the eight papillæ were lobate. They are disposed on the tongue very much as in the new-born child, and rise slightly above the level of the general lingual surface. They vary greatly in size, and are still more or less embryonic in character. One of medium proportions measured 0.65 mm. transversely and was 0.28 mm. in height. The epithelium protecting their upper surface is a trifle thicker than that covering the sides. The trenches vary in depth and width in different papillæ, and in some instances are still undif-

ferentiated in their whole extent. Serous glands are plentiful beneath the papillæ, and frequently project between them, and more rarely extend into their interior. They form a broad belt stretching nearly across the tongue in this region, the continuity of which is here and there interrupted by bundles of muscular fibres. A band of fine and exceedingly delicate wavy fibrils of connective tissue, 0.060 mm. in breadth, extends transversely across the tongue in the anterior part, separating completely the mucosa and muscular layer.

The papillæ foliatæ consist of seven or eight folds, the largest and most developed of which are situated at the posterior limits of the organ. Some of the folds are cleft into secondary ones, the depressions between which are filled with stratified pavement epithelium. A few of the furrows are still partially filled with epithelium.

This foetal tongue offered more favourable conditions for studying the finer structure of the taste-bulbs and nerves than any of those previously examined.

The bulbs have increased greatly in number, but in their disposition they are yet very unsymmetrical and irregular. They still occur most frequently on the upper area of the papilla, and in this region their development is furthest advanced. Other bulbs, more embryonic in character, are scattered at irregular intervals around the sides, the uppermost tiers containing the most mature bulbs. In some circumvallate papillæ bulbs are wanting altogether on the lateral area, and now and then entire papillæ will be destitute of them. I have frequently found them occurring on the opposed wall of the vallum, situated usually in the upper part. Two bulbs were embedded in the lingual epithelium beyond the outer wall of the trench. They were placed obliquely to the underlying matrix of connective tissue, with their apices directed inwards. One of the most mature bulbs of this tongue measured 0.048 mm. in length and 0.036 mm. in breadth. Horizontal sections through the crest of one of the circumvallate papillæ showed it to be crowded with bulbs. I counted forty, but they exhibited the greatest difference in size and form, and many of them were partly sub-epithelial in position.

In the foliate organ the taste-bulbs are restricted to a few

folds, and are smaller, fewer in number, and less advanced structurally, than those of the circumvallate papillæ. Only a few folds bear bulbs on both their upper and lateral areas. The fungiform papillæ of the anterior third and tip of the tongue contain fairly well developed taste-bulbs, and the latter are not infrequently more advanced structurally than the papillæ which bear them. One bulb lying at the upper part of a fungiform papilla (which was situated directly on the tip of the tongue) measured 0.045 mm. in length and 0.030 mm. in breadth.

Bulbs were seldom met with on the epiglottis. A few were present in the lower part of the posterior surface, and I found one on the anterior surface. They lie deeply embedded, and are small, spheroidal, rudimentary structures. In the soft palate and uvula of one of the seven months' fetuses were several small bulb-like bodies. In a vertical section through the anterior part of the soft palate I found a single bulb, lying mostly in the epithelium, with its apex projecting slightly beyond the free surface of the latter. This appearance of the apex was doubtless due to the superficial layers of epithelium having become detached. This bulb resembled those of the epiglottis, and measured 0.035 mm. in length and 0.025 mm. transversely. Of the bulbs of the uvula, also epithelial in position, the most conspicuous measured 0.027 mm. in length and 0.019 mm. in breadth. Mucous glands were present in this region.

Transverse and vertical sections through the taste-bulbs show that the number of taste or sensory cells has, by most observers (Hermann alone excepted), been considerably underestimated. In a transverse section of a bulb (measuring 0.028 mm. in diameter) which passed through the nuclei of its component cells, I counted twenty-three sensory cells. From an examination of many sections I think the mean number of these cells is about sixteen. Two kinds of sensory cells are distinguishable. The first kind comprises the taste-cells of Lovén, with which the *stiftchenzellen* of Schwalbe are identical. The second kind, which are less numerous and less highly refractive, are those designated by Schwalbe *stabzellen*. There are other cells which do not appear to exactly agree structurally with either of the above, but these I am disposed to regard as inter-

mediate or degenerate forms of the needle-cell or staff-cell. A third element which enters into the construction of a taste-bulb is an intercalary network composed of very delicate filaments, through the meshes of which the sensory cells pass. Whether this intra-bulbous network springs from the intra-epithelial or subepithelial plexus I was unable to determine, though I am inclined to believe that it is derived from the latter.

Medullated nerve-fibres enter the circumvallate papilla through its pedicel. These divide into smaller ones, and some of the finer branches subdivide beneath the epithelium into a number of terminal fibrils. In the earlier stages of embryonic and foetal life these ultimate nerve-fibrils, as already pointed out, are more numerous at the summit of the papilla. In the later periods, however, they also stream towards the sides bearing taste-bulbs. From the delicate network, directly beneath the basal layer of epithelium, fibrils run to the bulbs, and also pass into the epithelium in the spaces between them. Precisely how these intra-epithelial nerve-fibrils terminate in all cases I unfortunately did not succeed in discovering. The very delicate intra-epithelial network which I had failed to detect in earlier foetuses was in this foetus quite well shown. It is far more probable that the terminal fibrils, or at least a portion of them, contribute to the formation of this network, than that they enter the bulbs laterally, as supposed by some observers.

The sensory cells of the taste-organs are, I believe, unquestionably developed directly from the peripheral extremities of the nerve-fibrils, this development taking place somewhat in the following way:—The incipient stages of growth are more or less completed in the mucosa beneath the epithelium. The fasciculi of nerve-fibrils, as they become more organised, penetrate the deep layer of epithelium, the columnar or basal cells of the latter being gradually forced asunder owing to the pressure exerted by the inpushing bulb. These cells, which become elongated, and gradually modified into spindle-shaped ones, proliferate into the mucosa, and are partially reflected over the nerve-cells before the latter have entirely embedded themselves in the epithelium. Ultimately they form the peripheral envelope of the bulb, and function as supporting and protecting elements. The sensory cells are not completely covered until

somewhat later, for in several bulbs lying wholly within the epithelium they can still be detected through the little chinks separating the opposed edges of the modified epithelial cells.

If the foregoing explanation of the genesis of the taste-bulb be the true one, as my experience would lead me to infer, the sensory elements of the bulb are derived from the epiblast and not from the hypoblast as supposed by some, although, of course, if the epithelial covering of the tongue be hypoblastic in origin, the peripheral cells of the bulb would spring from that.

Coming now to the newly-born, we find in a child twenty-eight days' old all of the circumvallate papillæ completely differentiated. The epithelium covering them is well organised, and their expanded summits are subdivided into many secondary papillæ. The serous glands are well developed, and here and there the ducts open directly on the free lingual surface. Where two papillæ share an enclosing wall in common, the bottom of the mid-trench separating the opposed walls of the papillæ is frequently invaginated upwards into a ridge. At the sides of the ridge serous ducts discharge. All of the circumvallate papillæ bear taste-bulbs, though not all of the lobes of an individual papilla. Isolated bulbs still occur on the free upper surface, but they are usually situated near its outer limits. The bulbs are disposed quite regularly at the sides in five to eight tiers, those of the uppermost tier being the most mature. In the upper tiers the peripheral processes of the taste-cells of several bulbs project from the pore, whilst in the lower ones many of the bulbs are still partly subepithelial in position. A typical taste-bulb of this child measured 0.057 mm. in length and 0.033 mm. transversely. Bulbs, although not abundant, are present on the posterior surface of the epiglottis.

In a child of seven weeks all of the seven circumvallate papillæ save one were lobate. The fungiform papillæ were relatively larger than in the adult. The orifices of the mucous crypts on the posterior dorsal surface of the tongue were easily distinguishable with an ordinary pocket-lens.

In a child four months' old only one of the circumvallate papillæ appeared to be lobate. The taste-bulbs have increased in size and number. In one horizontal section I counted seventy-

six bulbs, the mean of the different levels being about sixty. They are quite uniformly disposed at the sides of the papillæ, those of the lower tiers being less regular in arrangement and smaller, and lying partly in the mucosa. The most mature bulbs have a number of hair-like processes protruding through their taste-pore for a distance of 0.0035 mm. The largest bulbs measure about 0.069 mm. in length and 0.033 mm. in breadth, the average being considerably less. Serous glands and ducts are very plentiful, there being sometimes more than a score of the latter visible in a single section of a papilla. A circumvallate papilla cleft into two unequal lobes, and with its summit much below the plane of the general lingual surface, almost completely fills the foramen of Morgagni. This papilla is very rich in taste-bulbs. There are many in the epithelium of the upper and under surface, and the lateral area is crowded with them. The perpendicular wall of the foramen cæcum, corresponding to the outer wall of the trench, also bears many bulbs at its upper part. Serous and mucous glands are present in abundance, and the ducts of the former discharge into the foramen cæcum at various places. The folds of the foliate papillæ, eight or nine in number, are very irregular, but the furrows are free from epithelium. Bulbs are sparingly present on the upper surface, and have increased in number on the lateral area of the folds; but their disposition in both regions is far from regular, entire folds often being destitute of them.

With the object of comparing the taste-organs of very young children with those of full-grown individuals, I examined quite a large number of human adult tongues. The circumvallate papillæ of these tongues varied in number from seven to ten, the average being eight. More than half of the tongues possessed lobate papillæ, and in a few instances the latter were verrucose on top. I am inclined to believe that lobation of the circumvallate papillæ is a more distinctively characteristic feature in man than in the lower animals. It is certainly one less commonly met with in those which I have investigated, some twenty-five species in all.

In none of these tongues, which were from individuals presenting a considerable range in age, did the bulbs of the circumvallate papillæ appear to be perceptibly decreased in number,

although they had disappeared almost entirely from the upper surface. In horizontal sections I have seen a hundred or more, forming a zone around the papilla. In most of them the neck (or canal leading down to the bulb, as the case may be) is clearly shown, and in a number of instances nerve-fibrils can be traced directly to their basal end, with which, to all appearance, they are continuous. They vary in shape and size, some of them having the form of a peg-top, and measuring only 0.048 mm. in length and 0.033 mm. in breadth. In the circumvallate papilla, which springs from the floor of the foramen cæcum, I found bulbs plentiful, but they were small and confined to the lateral area.

In the foliate papillæ of the adult only a few folds ordinarily bear bulbs, and I have examined adult foliate organs without finding even a vestige of them. They occur on the free surface as well as on the sides of the folds, and measure 0.07 mm. in length and 0.038 mm. in breadth. I explored the folds of the posterior dorsal surface, and also various other regions of the tongue, with the hope of exposing taste-bulbs, but I failed to discover any trace of them. In the lower part of the posterior surface of the epiglottis, however, I found quite a number of bulbs. They are placed some distance apart, and the majority still retain the spheroidal shape. They measure 0.048 mm. in length. Another form, of which there were a few examples present, measured 0.060 mm. in length and 0.048 mm. in breadth.

SUMMARY OF RESULTS AND CONCLUDING REMARKS.

On the tongue of a human foetus, at the fourth month of intrauterine life, are five papillæ of the circumvallate type. These papillæ are in process of formation, and illustrate the earlier stages of development, those most advanced being still very embryonic in character. There are no trenches, properly speaking, but their future position is indicated by the prolongations of the epithelium into the connective-tissue matrix of the tongue. One of the smaller papillæ of this foetus bears on its exposed surface an embryonic taste-bulb. This bulb lies directly in the longitudinal axis of the papilla, and its base is

hidden in the mucosa. Elsewhere in these papillæ were unmistakable evidences of structural modifications, both in the basement layer of epithelium and in the underlying tissue. These changes were of a nature to suggest the incipient stages in the development of the taste-organs.

On the tongue of a fœtus, at the middle of the fifth month, are six circumvallate papillæ, some of which are lobate. One or two of these papillæ are in process of transition from the fungiform type. The trenches are not yet differentiated, and the structural continuity between the epithelium investing the free area of the papilla and that covering the general lingual surface is still unbroken. The foliate organs, which I failed to detect in earlier fœtuses, consist of a few folds of the mucous membrane, the place of the future sulci being indicated by the epithelial ingrowths which at intervals penetrate the mucosa. The majority of the circumvallate papillæ bear embryonic taste-bulbs on their exposed surface, the largest number visible in a single vertical section of a papilla being three. The more advanced among them are mainly epithelial in position, while the less mature are largely embedded in the stroma of the mucosa. Medullated nerves are fairly shown in these papillæ. The main trunks divide in the papillary axis, and form a primary plexus. Directly beneath the basal cells of the epithelium is a fine, delicate reticulated network, from which non-medullated nerve-fibrils pass upwards, penetrating the bulbs and neighbouring epithelium. No taste-bulbs were seen on any part of the lateral area of the circumvallate papillæ, and none were discovered in the foliate organs, but many fungiform papillæ bore them at their upper part.

On the tongue of a six months' fœtus are eight circumvallate papillæ, all of which are lobate. These papillæ are not all equally advanced, but in most of them the structural continuity hitherto existing between the epithelium covering their upper area and that overlying the adjacent lingual surface has become interrupted. The papillary wall and outer wall of the trench of the different papillæ have for the most part separated, leaving a very narrow fissure. Taste-bulbs are most frequent on the upper area of the papillæ, but a few immature ones are sparingly scattered over the lateral walls. The foliate organs consist of

six to eight very irregular folds, several of which are cleft vertically. The furrows, like the trenches, are open throughout their extent. On the folds of the foliate organ there are a few taste-bulbs scattered over the upper surface and sides, but they are small and partly subepithelial in character. In the anterior region of the tongue, not far from the tip and under surface, are the mucous glands of Nuhn, with their ducts opening on the lower surface of the organ.

On the tongue of a foetus at the seventh month are eight circumvallate papillæ, all but one of which are lobate. In a few instances the trenches are not completely differentiated, and some of the furrows of the foliate organs are partially filled with epithelium. The taste-bulbs have increased greatly in number on the lateral area of the papillæ, and have not decreased apparently on their upper surface. Those situated at the lower part of the papillæ are, as a rule, the smallest and least advanced. Bulbs are present on the outer wall of the trench, and even occur beyond it embedded in the lingual epithelium. Many of the bulbs of the circumvallate papillæ lie partly in the mucosa, and the ultimate nerve-fibrils or filaments, which constitute the sensory elements of these terminal organs, can be seen within the epithelial shell, where the cells of the latter have been but partially reflected over them, or where the imbrication is incomplete. In the foliate organs bulbs occur on the summit and sides of a few folds. They are also present on the anterior and posterior surface of the epiglottis, and in the epithelium of the soft palate and uvula.

In a child about a month old the taste-bulbs had increased in number, and isolated ones still occurred on the free upper surface of the papillæ. In the lower tiers of the lateral area many of the bulbs were still partly subepithelial in position.

In a child four months old the papilla of the foramen cæcum bore bulbs on its entire exposed area, they being likewise present in the wall facing the papilla.

In the circumvallate papillæ of the adult the taste-bulbs do not appear to have decreased in number, although they have disappeared almost completely from the upper surface. In the foliate organs they are less numerous than in early life, but are still normally present on the lateral and upper area of the folds.

From a study of the gustatory papillæ of the different fetuses, it appears highly probable that the nerve-fibrils given off from the network beneath the epithelium of the bulb-region of the papilla terminate either as specialised end-organs of taste, or penetrate the epithelium, to all appearance unchanged. Those fibrils which are to compose the future sensory elements of the bulbs form themselves into fasciculi of delicate filaments, the latter becoming more or less modified before penetrating the epithelium. While these changes are taking place in the mucosa there is an increased activity manifested by the contiguous basal cells of the epithelium. These become swollen and elongated, and grow downwards and inwards, gradually enveloping the newly-formed terminal organs. Eventually these cells constitute the intercalary and peripheral cells of the bulbs. A portion of the non-medullated nerve-fibrils which enter the epithelium directly doubtless take part in the formation of the intra-epithelial network. Other fibrils appear to end freely in the epithelium.

There has been a tendency on the part of nearly every investigator of the gustatory terminal organs to underrate the number of taste-cells. From my own criteria, I should place the number of sensory- or nerve-cells in a bulb of average size and maturity at sixteen; and I think that this estimate cannot be very wide of the truth.

I cannot entirely agree with those histologists who are disposed to multiply the kinds of taste or sensory cells, and I frankly admit that, after a careful search, I was unable to distinguish more than two distinct forms of these elements. The first form is identical with the taste-cell of Lovén (needle-cell of Schwalbe), to the description of which I have nothing to add. The second form, answering to the staff-shaped cell of Schwalbe, is larger, less frequently met with, and less highly refractive than the former, and, moreover, lacks the styliform process. The staff-shaped cells possess a large ovoidal body, situated in the lower half of the cell, and are usually placed more externally than the cells of Lovén, the latter having a tendency to group themselves nearer the axis of the bulb. A third element which enters into the construction of a taste-bulb is a fine network, composed of very delicate filaments, through the meshes of

which the sensory cells pass, and which may be derived from the subepithelial plexus.

It is not altogether unlikely that insufficient allowance has been made for differences in the structural details of individual cells. I have occasionally observed elements within the bulb which failed to agree structurally with either recognised form of taste-cell, but I have been inclined to look upon them as representing intermediate stages of regeneration or degeneration, as the case may be, of either or both kinds of taste-cells; and what is observed may be either the initiatory stages of cells in process of growth or the vestigial products of degenerated ones.

Some time prior to the investigation under consideration I had, from *à priori* reasoning, adopted the view of the subepithelial nature of the sensory elements of the taste-bulb, it having commended itself to me as the most acceptable explanation of the many perplexing and seemingly contradictory phenomena with which investigators of these terminal sense-organs are frequently confronted. And I had, moreover, felt assured that if it could be shown that the bulb, at any stage of its existence, was largely subepithelial in position, the subepithelial nature of its sensory cells would not be seriously questioned. Griffini has already demonstrated by physiological methods the subepithelial character of the taste-cells, and my own results coincide essentially with his. I have no wish to be understood as denying the existence in these organs of neuro-epithelial cells, only I have never knowingly observed them, and can see no obvious necessity for their presence.

Poulton¹ was the first, I believe, to direct attention to the subepithelial nature of the taste-bulbs. He based his conclusions on the appearance of these organs as presented in *Perameles*, but more especially in the ancestral *Ornithorhynchus*. In the latter type he discovered bulbs wholly embedded in the mucosa. In the case of the higher mammals this author conceived that the primitive terminal organ of *Ornithorhynchus* was replaced by one epithelial in character. That this is not, however, necessarily so I have endeavoured to show. The bulb as a terminal organ has

¹ *Quart. Jour. Micr. Sci.*, vol. xxiii. p. 470, 1883.

undoubtedly, in passing from lower to higher forms, become more highly specialised and consequently more complex, but in all likelihood its nature and mode of origin have remained essentially unchanged. Poulton, in discussing the origin of the taste areas of mammals, is inclined to regard the gustatory ridge of *Ornithorhynchus* as an intermediate form between the circumvallate and foliate types,¹ rather than as a precursory type of bulb-bearing organ.

The hypothesis that a fungiform type of papilla is always a forerunner of the circumvallate form, and that all circumvallate papillæ are but modifications of the fungiform type, is, I think, scarcely tenable. While some circumvallate papillæ unquestionably arise in this way, others, probably the greater number, have an independent origin.

What purpose the temporary taste-bulbs (for such they seem to be) of the free upper surface of the circumvallate papillæ subserve in the embryo is difficult to comprehend. With the appearance of the bulbs of the lateral area they gradually disappear, and, from all indications, perish. By the time the bulbs of the free surface of the papillæ have attained their full development, bulbs in early stages of formation make their appearance on the wall, the lowermost bulbs being the most elementary. Were it otherwise it might be conceivable, as Hermann suggests,² that by an unfolding of the papilla laterally the bulbs of the free area are shifted to the sides. In the present state of our knowledge there seems to be no better way than to believe with Hoffmann,³ that "the bulbs of the free surface perish through the proliferation of the ordinary epithelium." It is not improbable that after the bulbs have once disappeared from the upper surface that certain altered conditions of the epithelium prevent, save in rare instances, their recurrence there.

Klein⁴ has observed that in newly-born children, owing to the indistinctness of the wall in most instances, no difference is perceptible between the circumvallate and fungiform papillæ. This statement must have, I think, a somewhat restricted

¹ *Loc. cit.*, p. 471.

² *Loc. cit.*, p. 228 *et seq.*

³ *Loc. cit.*, p. 528 *et seq.*

⁴ Stricker's *Manual of Histology*, New York, 1872, p. 353.

application, for not only in tongues of new-born children, but in those of fœtuses of six and seven months the two forms of papillæ are readily distinguishable from each other, and by means of the glass can be recognised at still earlier periods of intrauterine life.

While it is possible to study the succeeding stages in the development of the taste-bulbs during the latter period of intrauterine life, and consequently to learn something of the different elements of which they are composed, yet the first appearance of the taste-organs of man must be sought in earlier embryos than those examined by me.