

THE STRUCTURE AND FUNCTION OF THE TASTE-BUDS OF THE LARYNX.

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With 2 Plates : Plates II. and III.

ON the minute anatomy of the taste-buds of the tongue much work has been done, but relatively little on the buds of the larynx. Yet in this cavity, on account of the isolated position of the buds, their structure can be more easily discerned and the nerve supply more closely studied than in the mouth. The investigations which are described in this paper have been chiefly directed toward the morphological characteristics of the laryngeal buds, especially the nerve supply, including the nerve-endings. It was hoped that such investigations would throw some light upon the physiological action of taste-buds in general and upon any additional physiological action which the taste-buds of the larynx might possess.

The tissue examined was obtained from man, from the monkey, dog, and rabbit. The method employed was chiefly the *intra vitam* injection of methylene blue, as described in a former paper (Wilson, 1904). The tissue was usually counterstained with orange G acid fuchsin. At the same time sections were stained by the Golgi method, by iron hæmotoxylin, and by gentian violet.

In the larynx the taste-buds, first described by Verson, in 1871, are found on the laryngeal surface of the epiglottis and the medial and lateral surfaces of the arytenoids. They are usually met with in groups, but never closely packed together as in the tongue. Buds are found only in the squamous epithelium. They do not project beyond the surface, but lie in a very shallow saucer-like depression (Shofield, 1876).

They extend through the whole depth of the epithelium, and each rests on a broad papilla of relatively dense connective tissue, through which vessels and nerves enter the buds. These papillæ are not always prominent, and may be absent; when present, they are easily observed, since over the cartilage of the epiglottis the epithelium possesses relatively few papillæ.

Notwithstanding the shallow saucer-like depression of the epithelium in which the buds lie, their pores are very much exposed, and so are in marked contrast to the concealed nature of the taste-pores of the tongue (Plate II. A). Each bud is surrounded, except at its base, by a wall made up of epithelial cells, which are flattened laterally and imbricated (fig. 1; compare extrabulbar cells of Gräberg, 1899). A

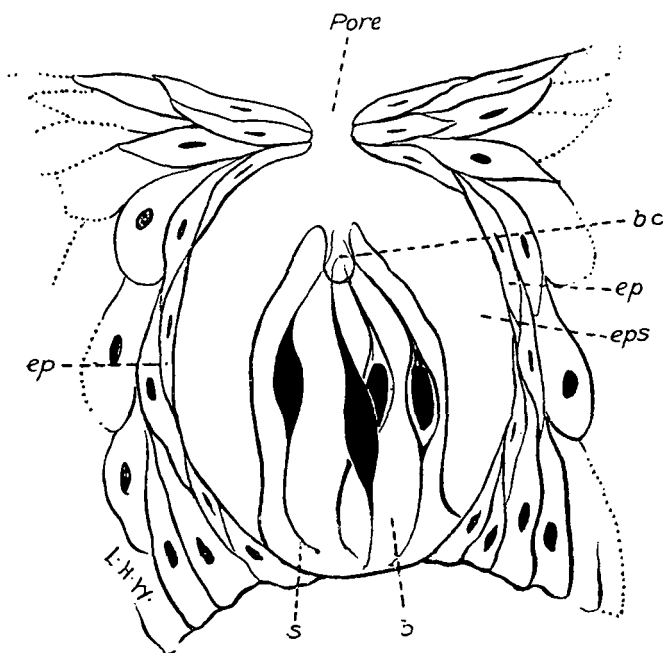


FIG. 1.

Section of the epiglottis of a dog, showing the arrangement around the bud of the epithelial cells—flattened and imbricated (*ep*). Taste-bud (*b*) retracted from the sides, but attached at base leaving a space (*eps*). Within the bud four spindle-shaped cells (*s*) project into bud cavity (*bc*).

Zeiss $\frac{1}{12}$ oil immersion. Comp. occ. 4.

condition of cornification can be observed in many of them. They fit closely to each other, and are adapted to the shape of the bud. Towards the surface the cells are so adjusted as to form a clean-cut edge around the pore, sloping slightly in a radial direction to it. The pore proper is formed entirely by these epithelial cells. Towards the subepithelial tissue the cells have their bases flattened and so extended as to embrace the papilla. There is here, therefore, such a modification of the epithelium adjacent to the bud that it may be regarded as forming a protective capsule, the closely packed epithelial cells being in marked contrast to the loosely arranged cells of the bud. To this capsule the bud is attached by protoplasmic bands, and out of this epithelial setting, after fixation, it easily drops.

The laryngeal taste-bud, like that of the tongue, has two types of cells, the spindle-shaped cell and the supporting cell, also a flasked-shaped cavity in its upper segment.

(1) The spindle-shaped cell (fig. 1 and Plate II. B) extends the whole length of the bud; it is not confined to the axial region. Its central termination, long, fine, and unbranched, reaches to the connective tissue of the papilla, but not into it. Peripherally its cytoplasm is prolonged into a very fine hairlike process which projects into the cavity of the taste-bud, and may even reach to the taste-pore. In vital staining with methylene blue, not only does the nucleus stain readily, but the facility with which the whole cell takes up the dye is in marked contrast to the non-reaction of the supporting cell and of the surrounding epithelial cells to the dye. In these cases the cell is very sharply outlined.

The evidence in support of the special sense function of the fusiform cell is based on :—

(a) The fact that it colours readily with neurotropic dyes, as opposed to the non-colourability of the supporting cell.

(b) The morphological character of the cell.

(a) Primary colourability as a test for a neuro-epithelial cell, though of great value, is subject to so many exceptions that alone it is open to objections. Methylene blue, although neurotropic, is not monotropic (Ehrlich, 1902). It is impossible to deduce from primary colourability that we are

dealing with a nerve termination. Some cells which so stain cannot be recognised as neural cells; for instance, one cell in the epithelium which readily takes up the dye is the so-called "wandering cell," a cell which has been mistaken for and described as a ganglion cell (Dogiel, 1903). In the bud, however, we have two varieties of cells, one of which, the spindle-shaped cell, shows the neurotropic character, the other does not; so we are justified in assuming that the former possesses a certain chemical constitution which allies it more closely to the nerve-cell.

(b) When to this we can add such morphological characteristics as its peripheral process with its relation to the pore, its analogy to other special sense-cells, we have support for the belief that the fusiform cell is specially engaged in the mediation of the sense of taste.

(2) The second type of cell, the so-called supporting cell, differs in no respect from the corresponding cells in the buds of the tongue. Its shape varies very greatly, but there are not two types of this cell, one peripheral and one central. The irregularity is due in some degree to fixation. The cells are loosely applied and adjusted to each other, to the taste-cells, and to the epithelium around, leaving spaces through which leucocytes may wander (Ranvier, 1888). Under fixation they readily shrink and may withdraw from each other, but chiefly as a bud from the epithelial wall from which they may separate at any point. When this shrinkage occurs, the intercellular bridges which pass from the epithelial wall to the supporting cells are easily observed and without doubt distort the cell wall. While this is so, the general relation of the supporting cell to the taste-cell and its general outline in cross-section prove that we have to do with a cell which readily adjusts its contour to the surrounding parts. In the centre of the bud it appears somewhat triangular, with the fusiform sensory cell applied to the flattened and slightly concave surface; at the periphery there is a similar adjustment of the external surface to the epithelial wall—convexity to concavity. Its general appearance and its mobility of surface suggest a cell protoplasm easily susceptible to external influences.

The cavity, first described (v. Ebner, 1897) in the taste-buds of the tongue, is generally flask-shaped (fig. 1 and Plate II. A), and has its mouth directly opposed to the taste pore. It extends but a short distance into the upper segment of the bud, and is formed by the approximation of the peripheral ends of the supporting cells. Projecting into it are the peripheral ends of the taste-cells which pass between the supporting cells. The contents of this cavity are unstainable; it probably contains, as in the tongue (Poirier et Charpy, 1902), a clear liquid, in which the terminal points of the gustatory cells are bathed.

Shrinkage of the bud from its epithelial capsule through the action of a fixing agent is more common than in the taste-buds of the tongue of the same animal. It is so constant a feature that one may well enquire whether the protoplasm of the bud is not more capable of reacting to fixatives than is the protoplasm of the surrounding cells.

From the stability of the capsule, from the minuteness of the pore, from the relative density of the subepithelial tissue at the insertion of the bud, from the ease with which shrinkage occurs, the impression is given that the bud is an organ subject to very little external pressure, and that the cells of which it is composed are capable of reacting freely to any agent which may influence them at their exposed parts in the central flask-shaped cavity of the bud.

The anatomical investigations of the relation of nerve-endings to taste-buds have been made on those of the tongue, with the exception of some work done by Arnstein (1897) on those of the larynx. There is still much doubt as to how the nerves end. It is generally admitted that there is a subgemmal plexus (Retzius, 1892), but as to the nerves that form it and how its constituent elements are distributed, we have as yet no precise information. Thus Jacques (1894) derives perigemmal, intragemmal and intergemmal fibres from a subgemmal plexus, which can thus bear no similarity to the subgemmal plexus or "cupula" of v. Lenhossék (1893) and Arnstein (1897), still less to the plexus of special sensory fibres described by Dogiel (1897). Moreover, no sufficient evidence has been advanced for the

view that certain nerves going to the bud are sensory, while others are nerves of special sensation. Again, though Arnstein (1893) appeared to have clearly shown that Fusari (1891) was mistaken in describing the actual connection of the nerve-fibre with the fusiform cell, this connection appears to be still maintained by some authors (Finocchiaro, 1904). Lastly, there is the question of the presence of a ganglion cell in the subgemmal plexus, which Jacques (1894) supports, and Roeske (1897) denies.

I find that the mode of ending of the nerves in the taste-buds of the larynx is as complex as that of the tongue. Lying under the epithelium of the laryngeal surface of the epiglottis and aryteno-epiglottic fold there is a subepithelial plexus composed of both medullated and non-medullated fibres. From this plexus there go to the taste-buds not less than two, and usually three or more, nerve-fibres, some fine varicose fibres, others, which are at first medullated, but lose their sheath at a varying distance between the plexus and the bud. These fibres divide repeatedly, so that at the base of the bud the nerves are very numerous and individual fibres are often difficult to follow (Plate II. A). But two distinct groups can, as a rule, be distinguished: (1) Those that break up to form a plexus at the base of the bud, with prolongations within the bud; and (2) those which go more or less directly round the bud. The latter may branch in the plexus, but there is no anastomosing nor interlacing of branches, as occurs with the fibres of the plexus. In this complex arrangement three groups can therefore be distinguished:—

(I.) Subgemmal plexus; (II.) Intragemmal nerve-fibres; (III.) Perigemmal nerve-fibres.

The so-called intergemmal fibres (Jacques, 1894) are nerves distributed to the epithelial cells which lie between the buds (Plate II. A). They have no direct connection with the bud, and differ in no way from the nerves to the adjacent epithelium.

(I.) The subgemmal plexus Plate III. B, and Plate II. A) lies in the subgemmal connective tissue, and may begin at some distance beneath the bud. The apex is central towards

the subepithelial plexus; the base is broad, and applied to the convex central end of the taste-bud. It is formed by branching and apparent anastomosis of one or more fibres which come from the subepithelial plexus. The winding and interlacing of these fibres are very complex, and often are made more difficult to follow because of the "Endbäumchen," which branch around and among them, but from which they are distinct. The plexus is continued within the bud, so that on cross-section the basal part of the cells of the bud appears to be embedded in the plexus.

(II.) There are two sources from which intragemmal fibres arise: (1) From the subgemmal plexus; (2) directly from the subepithelial plexus.

(1) The fibres connected with the subgemmal plexus are very irregular in their course. At the base of the bud they have a plexiform arrangement, and surround the bud cells. Two varieties of endings are seen in connection with this group (Plate II. B): (a) A branching and interlacing network around the cells. This is well marked in the lower third of the bud, less in the middle, and only slightly at the upper third. (b) Knob-like endings most marked at the upper third of the bud; they lie on the cells.

(2) A few non-medullated fibres come directly from the subepithelial plexus and take no part in the formation of the subgemmal plexus (Plate II. B, and Plate III. A, where a fibre is marked v.). They may run to the bud outside the subgemmal plexus, or they may pass through it. In the latter case they run a course more or less direct towards the bud; they may divide in the plexus, and their rami run in opposite directions, but in no case do they show such complex interlacing as do the fibres of the plexus. Their course to the bud is by no means difficult to follow. Within the bud they are not always easy to follow, but the general trend of all the branches is towards the apex of the bud.

(III.) The perigemmal nerve-fibres (Plate II. c and A) form a plexus of non-medullated varicose fibrils which lie around the bud, forming at the apex a circle around the pore (Lenhossék, 1893). They arise from medullated nerves which come from the subepithelial plexus, but which lose

this sheath before reaching the base of the bud. They may pass through and even branch in the subgemmal plexus. On cross-section branches may at times be seen to pass from the perigemmal plexus within the bud.

That some of these fibres are sensory as distinct from nerves of special sensation is demonstrated by the following ; if we assume that one nerve-fibre carries a special sensation, or if we assume that the special sense organ of taste must have, like the eye or ear, special sensory fibres: (a) There can frequently be seen a nerve-fibre dividing into two trunks, one of which goes around or within the bud, the other to the surrounding epithelial cells (Plate II. A). (b) Occasionally, and more often near the base of the epiglottis and in the aryteno-epiglottic fold, a division at a node may send one fibre to the bud, another to an unencapsulated nerve-ending, as, for instance, a subepithelial end-tree (Plate III. A). The general course of these fibres is to surround the bud. Their terminals are directed to the apex of the bud to end near the bud cavity.

There are other fibres independent of these, different in structure and mode of distribution, which lie principally at the basal part of the bud and which form the subgemmal plexus and its continuation with the bud. These we regard as nerves of special sensation.

Ganglion cells have been described in connection with the nerves of the taste-bud by many investigators—Retzius, v. Lenhossék, Jacques, &c. Lenhossék (1893) gives a very guarded opinion: "Vollentwickelte Nervenzellen, wie etwa die des Sympathicus, sind es gewiss nicht" (p. 124). In the subgemmal plexus I have never seen sufficient evidence, in vital injection preparations, to enable the deduction to be drawn that swellings which may be seen on the nerves represent ganglion cells. Nor am I convinced of their presence by the evidence afforded by such swellings as are found in Golgi preparations.

The whole question of swellings in the course of the non-medullated nerve trunks is an interesting one, and many varieties are present in connection with the nerves of the taste-bud. For example, there are the well-known varico-

Plate II.

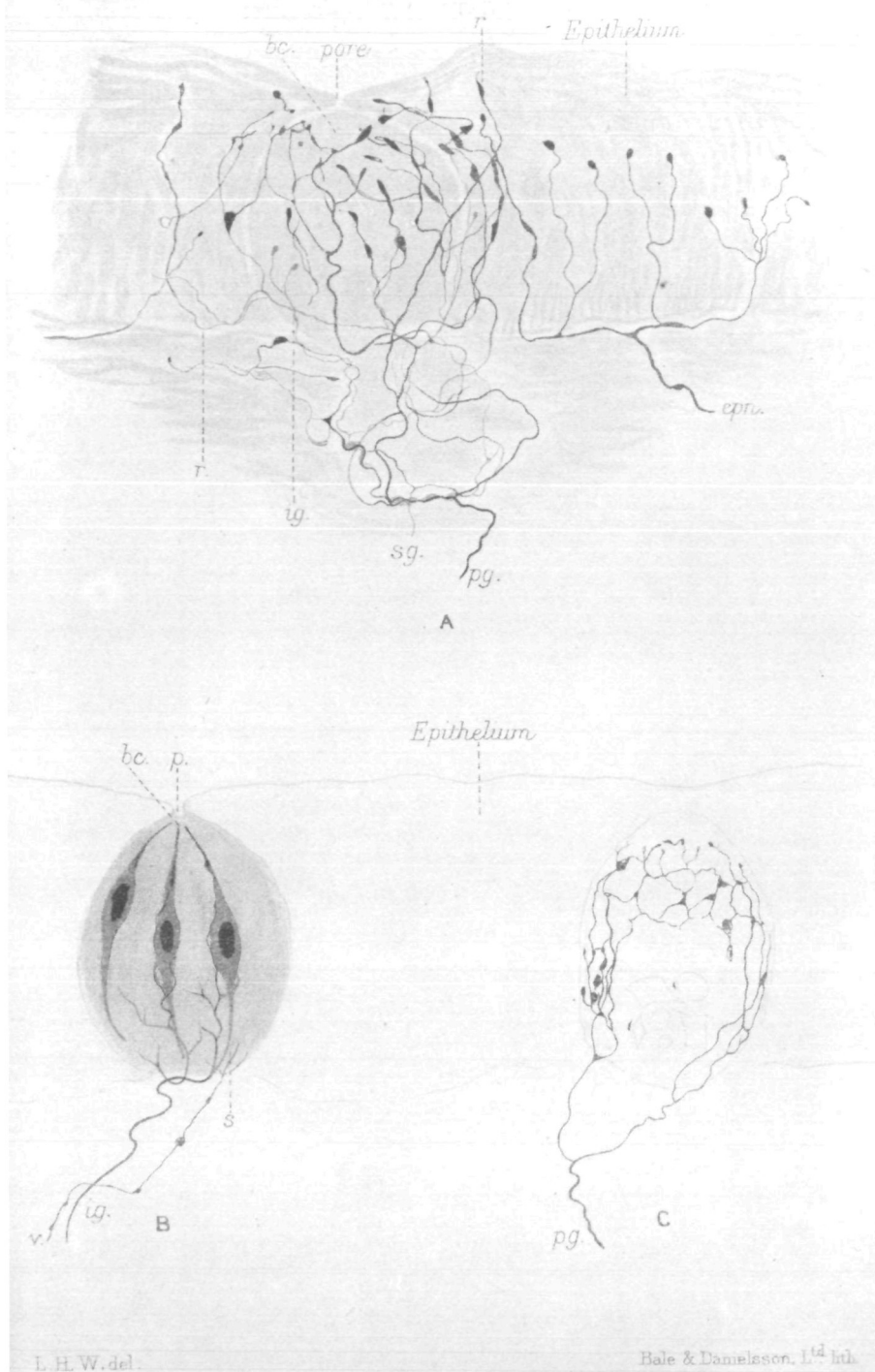
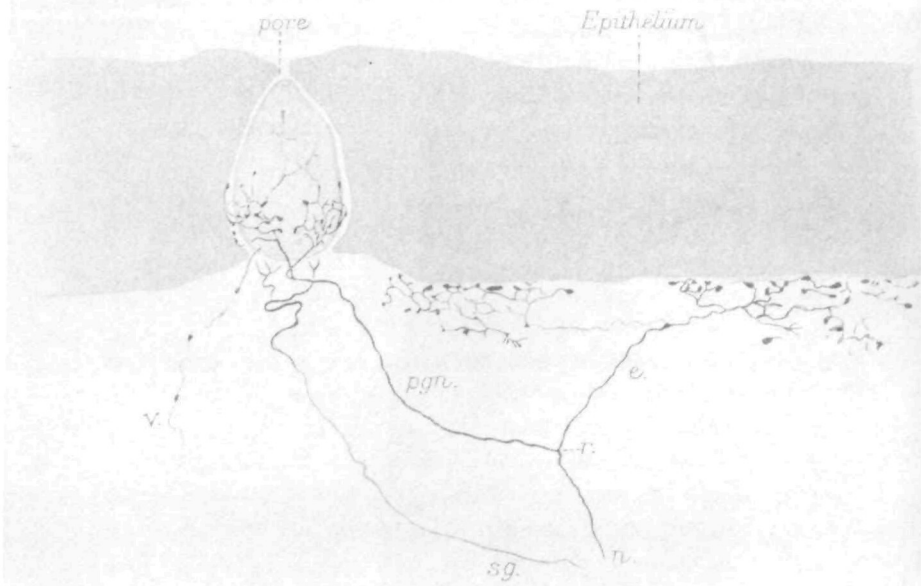
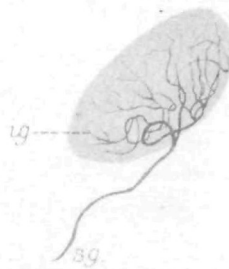


Plate III.



A



B

L.H.W. del.

Bals & Danielson, 12^d inch

sities on the fine non-medullated nerve-fibres so constant in their presence and in their form both in non-fixed and fixed preparations that they cannot be passed over as merely *artefacts* or *post-mortem* changes (Kalius, 1905), but must be regarded as representing some peculiarity of the nerve-fibre. Thus it may represent a swelling on the axis cylinder or a point where the fibre is more exposed to external influences, just as at the node of a medullated nerve, where the sheaths are interrupted, there is a tendency to a darker and more profuse staining. Another variety of swelling appears at the point of division of an axis cylinder, due to a diffuse staining where its constituent parts are separating. This swelling will be obviously accentuated if, not two fibres branch off, as is usually the case, but three, four or five, as may at times be seen in the fibre going to the bud or to an adjacent tree ending. There is also that form which occurs at the interlacing of fibres. In addition to these there are a number of swellings of many forms and sizes—oval, triangular, &c. Many of them are artefacts, but whether they can all be classed as such may be open to doubt. This, however, may be said: they are fewer in well-stained preparations and are larger and more numerous in nerves undergoing degeneration.

From the time Verson (1872) described the taste-buds of the larynx various opinions have been held in regard to their function. Verson held that the very fact that they are found in the posterior surface of the epiglottis is proof enough that they are not taste-buds. Krause believed that they were the organs "*für intensive Nachgeschmacke*."

That taste can be perceived in the upper part of the larynx cannot be doubted. My own investigations corroborate the statements of Michelson (1891) and Kiesow (1901-2) on this point. By means of the laryngoscopic mirror one can touch any desired point of the vestibulum laryngis. Taste perception is rapid and sufficiently accurate to differentiate more or less definitely the four primary tastes, though quantitatively and qualitatively inferior to the tongue.

The following hypotheses have been advanced to explain the presence of taste-buds in the larynx:—

(1) They are a phylogenetic residue.

(2) They are organs of taste whose chief function is to strengthen the reflexes which close the laryngeal cavity during the passage of food: “Die Reflexe zu verstärken wenn Geschmackstoffe in den Larynx gelangen” (Kiesow, 1901).

The first hypothesis is supported by: (a) The history of the taste-buds in the vertebrates—a history which shows a formerly widely diffused sense-organ becoming more restricted in locality; (b) the history of the taste-buds in the individual life of man, since in early life they cover a much wider area; (c) the statement that they can serve no function, as they never come into actual contact with food.

It must be acknowledged that the taste-buds have undergone a phylogenetic decrease, and that in the individual life of man their area of distribution diminishes. We have a corresponding phylogenetic decrease and restriction of area in the allied sense-organs of smell (Mann, 1905).

But restriction of area need not indicate a phylogenetic residue, and may equally well indicate a more specialised sense arising from a concentration of the area of peripheral sense. It is hard to believe that these organs have no function; their number, their abundant nerve supply, their persistence during life, their physiological activity, speak against the acceptance of this hypothesis. One feels that the reason for their continued presence here has to be sought in the intricate mechanism of deglutition.

In discussing the second hypothesis it is well to recall how great a part of the function of the larynx lies in protecting the entrance to the trachea (Anderson Stuart, 1892), and to note that the hypothesis which accounts for the closure of the larynx during deglutition as due to the mechanical lid-like action of the epiglottis cannot be upheld, and that the evidence clearly shows that closure of the *aditus laryngis* occurs by an approximation of the arytenoids,

by contraction of the soft parts together with their apposition to the inferior surface of the epiglottis (Anderson Stuart, 1892; Eykman, 1904). The primary purpose of taste was probably to select a suitable food supply, and so to act as a protective agent for the animal. What more suitable end-organ to assist in protecting the trachea during the passage of food could there be than one whose natural stimulus is the food? In the vestibule of the larynx those functionally active buds, particularly rich in their nerve supply, rest on an exposed surface in marked contrast to the concealed nature of these organs in the tongue; there is, therefore, a rapidity and facility of reaction of laryngeal buds in contrast to the persistence of functional activity apparent in those of the tongue. To this hypothesis the localisation of these organs lends additional support. They are not, as a rule, found at the apex; they become apparent near the middle and are most marked, very obviously so in the dog, on both sides of the line joining the aryteno-epiglottic fold. In man, so far as our preliminary investigations have shown, there are none at the apex of the epiglottis, but they lie round and beneath the cushion of the epiglottis. They are numerous on the medial surface of the arytenoid cartilage and on the lateral surface close to the apex. (Kalius, 1905.)

Further investigation will have to be made, especially as to whether or not a difference in intensity of closure of the larynx results from the application of sapid or non-sapid bodies; but even from the above one may well be justified in claiming some support for the hypothesis that these end-organs act as sentinels to assist in the protection of the laryngeal cavity during the passage of food.

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EXPLANATION OF PLATES II. AND III.

PLATE II. A.

Section of the epiglottis of a rabbit. Taste-bud lying in a shallow depression of the epithelium with pore (*p*) communicating with the faintly outlined cavity (*bc*) in the upper segment of the bud. (*pg*) Nerve dividing in submucous tissue and finally breaking up into numerous branches, which form a network around the bud (perigemmal plexus); branches (*r*) are seen passing into the surrounding epithelium. (*sg*) Nerve-fibre branching frequently to form a network (only partly shown) at the base of the bud; it sends branches (*ig*) within the bud (intragemmal fibres). (*epn*) Nerve with epithelial endings.

Zeiss D. Comp. occ. 4.

PLATE II. B AND C.

Section from mucous membrane of vestibulum laryngis of dog, near base of epiglottis. (B) Bud with spindle-shaped cells (*s*) stained by methylene blue, showing relation of the intragemmal fibres to the cells. (*v*) Fine varicose fibre passing into bud. (C) Bud cut obliquely with the part adjacent to the pore not seen. The perigemmal plexus is connected with the nerve (*pg*). At the base a few bud cells are seen in outline.

Zeiss $\frac{1}{15}$ oil immersion. Comp. occ. 4.

PLATE III. A.

Mucous membrane from larynx of dog near arytenoid cartilage. (*n*) Nerve-fibre which divides at (*r*) into two branches, of which one (*e*) goes to end in a subepithelial end-tree (Endbäumchen), the other (*pgn*) goes to form a plexus around the bud. The nerve (*sg*) winds spirally and branches at base; it finally sends off shoots (not shown) into bud. (*v*) Fine varicose nerve-fibre passing into the bud.

Zeiss D. Comp. occ. 4.

PLATE III. B.

From epiglottis of a dog; lower segment of bud which has been cut obliquely. The nerve (*sg*) coils and branches in subgemmal connective tissue to form a plexus around the base of the bud (subgemmal plexus). From this plexus branches (*ig*) pass into the bud (intragemmal).

Zeiss $\frac{1}{15}$. Comp. occ. 4.

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