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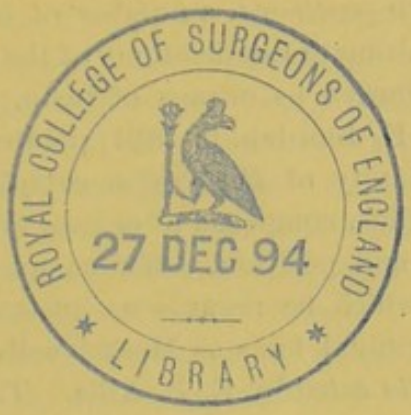

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ON THE GUSTATORY ORGANS OF THE MAMMALIA.

BY FREDERICK TUCKERMAN.

Before taking up for consideration the gustatory organs of mammalia, it may perhaps be as well to review very briefly what is known respecting the homologous organs of fishes, batrachians, and reptiles.

In 1851, Franz von Leydig discovered in the external skin of fresh-water fishes peculiar goblet-shaped bodies, which he was disposed to regard as organs of a tactile nature. In 1863, Franz Eilhard Schulze redescribed the goblet-shaped bodies of fishes, and considered them organs of taste. He found them in greatest number where the fibres of the glosso-pharyngeal nerve are most thickly distributed, *i. e.*, in the mucous membrane of the palate, upon the gums and tongue rudiment, on the inner side of the gill arches, and upon the lips. In structure he found them to agree, in most respects, with the end-discs of the frog. The goblets he described as composed of two kinds of cells, viz., *Sinneszellen* and *Stützzellen*, or sensory and supporting cells; the former having a peripheral and central process. In 1867 Schulze observed that the peripheral extremity of the taste-cell bears a fine hair-like process, as in mammals.

In 1870, he discovered in the mouth of a larval amphibian (*Pelobates fuscus*) bodies resembling in structure the goblet-shaped organs of fishes, which he considered taste-organs. In 1872,

Francesco Todaro described, in the papillæ covering the rudimentary tongue of *Trygon pastinaca*, a number of club-shaped bodies connected with the ultimate ramifications of the glosso-pharyngeal nerve, which he regarded as organs of taste, and analogous to those of mammals. E. Jourdan, in 1881, pointed out on the gills and in the buccal cavity of *Peristedion cataphractum* and other fishes cup-shaped bodies, composed of central and peripheral cells, which, in structure and position, differ completely from the organs of touch, and which he regards as gustatory organs. The goblet organs, or terminal buds as Merkel calls them, have been lately studied in *Amia calva* by E. P. Allis. They are present in large numbers on the external surface of the head, including the operculum, gular plate, and branchiostegal rays. They occur in the mouth and branchial cavities, and also extend on the top of the body as far as the dorsal fin. From the fact that the goblet-shaped sense-organs of fishes are not confined to the mucous membrane of the mouth, but occur in the skin at different parts of the body, Jobert, Merkel, and the later observers were led to regard them as organs of a tactile nature.

Leydig, in 1857, described in the epithelium covering the upper exposed surface of the fungiform papillæ of batrachians, peculiar end-organs of the glosso-pharyngeal nerve. These sensory terminal organs, which received the name of taste-discs, have been studied in the Urodela and Anura. According to Key and Engelmann, the upper surface of each papilla fungiformis of the frog bears a taste-disc (or, as Merkel terms it, end-disc). These discs are composed of three kinds of cells, viz., cup-shaped, cylinder and forked, the latter alone being sensory in function. The fork-cells Engelmann considered the end-organs of the gustatory nerve, and probably directly continuous with non-medullated nerve-fibres, which, in their chemical reaction, they resemble. The taste-discs rest upon a stratum of modified connective tissue, the so-called "nerve cushion," to which medullated nerve-fibres run, and within which they lose their medullary sheath.[1]

[1] Fajersztajn, in a recent paper on the terminations of the nerves in the end-discs of batrachians (*Arch. de Zool. exp. et gén.*, t. vii, 2e Serie, 1889, p. 705), describes four kinds of cells in the disc, viz., cylinder, winged, forked, and staff-shaped. The forked cells, and not the staff-cells of Merkel, he regards as the true sensory elements of the disc. He believes in the contiguity, but not in the direct continuity, of nerve-fibrils and the central processes of the sensory cells. Contiguity being effected either by the terminal buds of the nerve-fibrils applying themselves to the bodies of the sensory cells, or by the central processes of those cells adhering to the nerve-fibrils of the subepithelial plexus.

Leydig was likewise the first to call attention to the goblet-shaped sense-organs of reptiles. He found them in the skin and mouth of various snakes. According to Merkel, they are present in the Saurians only. They have been found in *Anguis* and *Lacerta*, on the inner side of the upper and lower jaw, on the tuberculum palatinum, and on the tongue. Structures homologous to the goblet-shaped organs of fishes and reptiles, the end-discs of batrachians and the taste-bulbs of mammals have not yet, as far as I am aware, been discovered in birds.

There is still some difference of opinion among physiologists as to what regions of the mouth are endowed with taste; but at all places where experiment has shown this sense to be present, there have been found, concealed in the stratified epithelium of the mucous membrane, small ovoidal or flask-shaped bodies. These structures are the peripheral organs of the gustatory nerves (that is, of the glosso-pharyngeal and of certain fibres of the lingual, the latter being probably primarily derived from the chorda tympani). These organs were discovered almost simultaneously, but quite independently, in 1867, by Otto Christian Lovén, of Stockholm, and Gustav Schwalbe. Schwalbe, now professor of anatomy in the university of Strassburg, was at that time a student in the laboratory of Max Schultze, at Bonn. To these newly discovered sensory terminal organs of mammalia Lovén gave the name taste-buds or taste-bulbs, while Schwalbe called them taste-goblets, from their likeness to the homologous goblet-shaped bodies present in the epidermis of fishes. They have also been called epithelial-buds by Krause, end-buds by Merkel, and taste-knobs by Henle. Lovén found them in the epithelium of the circumvallate papillæ of the rat, rabbit, pig, sheep, calf, horse, dog and man, and in the fungiform papillæ of the rat, rabbit and calf. Schwalbe studied them in the circumvallate papillæ of the guinea-pig, rabbit, hare, pig, deer, sheep, ox, horse, dog, cat and man. He at first denied their existence in the fungiform papillæ, but afterwards found them there. He also detected them in the rudimentary papillæ foliatæ of the pig. The anatomical description of these organs, as given by Schwalbe, agrees in the main with the slightly earlier account of Lovén.

Within a year or so following the discovery of the taste-bulbs of mammals, Verson called attention to somewhat similar structures on the posterior surface of the epiglottis of man. Engelmann and v. Wyss discovered in 1869, but independently of each other,

taste-bulbs in the papillæ foliatæ of the rabbit and hare. v. Wyss also studied them in many mammals, including the hedgehog and squirrel, and at the same time made some attempt at grouping them. Krause observed taste-bulbs in the fungiform and foliate papillæ of man, and also found bulb-like structures on the posterior surface of the epiglottis of the sheep and rabbit. Ditlevsen made a comparative study of the taste-organs of mammals, investigating in all some twenty-five species. About one-half of these, however, had already been studied. Hoffmann found taste-bulbs on the anterior surface of the soft palate and on the upper part of the uvula. Schofield has described them in the lower half of the posterior surface of the epiglottis of the dog and cat. Davis studied the bulb-shaped organs in the epiglottis of the rabbit, pig, calf, dog, cat and man, and found them on the upper and lower part of the posterior surface of that organ. In the dog he found them on the inner side of the arytenoid cartilages, on the ary-epiglottic folds, and in the epithelium of the true vocal cords. Later observers have found them on one or both surfaces of the epiglottis in the musk-rat, squirrel, mink, fox and other mammals. In 1873, v. Ebner pointed out that certain glands, differing in many respects from the mucous glands, and which he classed with those of the serous type, always occur in the parts of the tongue which contain taste-organs, and their ducts open into the furrows and trenches lined by the taste-bulbs.

To recapitulate, the taste-bulbs of mammals have been found on the lateral area of the circumvallate and foliate papillæ (and more rarely on their free surface), in the epithelium of the outer wall of the trench facing the circumvallate papilla, at the upper part of the fungiform papillæ, in the soft palate and uvula, at the upper and lower part of the anterior and posterior surface of the epiglottis, on the inner side of the arytenoid cartilages, on the ary-epiglottic folds, on the vocal cords, and in other parts of the larynx. Of all these regions the lateral area of the circumvallate and foliate papillæ is preëminently the place where the taste-bulbs are found. The bulbs have been demonstrated in all mammals in which a careful search has been made for them. In addition to those already mentioned they have been found in the Insectivora, Chiroptera, Marsupialia, and Monotremata. They have yet to be studied in detail in the Quadrumana, Cetacea, Sirenia, and Edentata.

It may be of interest at this point to say a word about the gus-

tatory papillæ themselves. In the highly ancestral *Ornithorhynchus* we find the primitive form of the circumvallate papilla. At the posterior region of the tongue of this mammal are two pairs of gustatory areas. The anterior pair lie below the surface in a furrow, the floor of which is invaginated upwards into a ridge. The ridges of the posterior pair reach the surface. The ridges of both areas bear taste-bulbs over the whole of their convexity. Ascending in the scale, we find in the gustatory ridges of *Belideus* structural characters which are common to both the circumvallate type of taste-area and the bulb-bearing ridges of *Ornithorhynchus*. The ridges of *Belideus* furnish us with an intermediate stage in the process of development of the former from the latter, the more recent from the more primitive form of taste-area. In the higher mammals it is probable that in some cases, the number of the circumvallate papillæ may be added to by direct development from fungiform papillæ. The hypothesis, however, 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, no longer tenable.

In marsupials and in some rodents, as the squirrels, beaver and prairie-dog, there are but three papillæ of the circumvallate form, and they are nearly always arranged in a triangle, the apex of which looks towards the epiglottis. Frugivorous bats, apes and monkeys, have also three circumvallate papillæ similarly arranged. Edentates, hares and rabbits, moles and shrews, usually have two circumvallate papillæ, while the musk-rat and pouched gopher have but one. Among the domesticated animals the horse and pig have each two circumvallate papillæ, the calf and sheep twenty to thirty each, and the goat twelve. The elephant has six and the giraffe fifty. In the Carnivora the number varies from two to twenty. Man has usually eight, and sometimes twelve, but never less than four. The only mammals in which the circumvallate papillæ are apparently wanting, as far as known, are the *Hyrax*, or coney of "Scripture," and the guinea-pig. Both of these forms, however, possess the lateral organs of taste (papillæ foliatæ), those in the *Hyrax* being very beautifully developed.

The papillæ foliatæ, or lateral organs of taste, were described by Albinus in 1754 as degenerated papillæ. In 1832 Rapp observed on the hinder part of the tongue in different mammals a series of transverse fissures lying close together, and found them also in

man. The function of these fissures, however, remained unknown to him. Two years later Elsässer observed that the sense of taste was most intense on the papillæ circumvallatæ and at a place on the hinder part of the lateral edge of the tongue. This place he called, quite correctly, the "gustatory fissures" of the tongue. In 1842, Mayer, unaware of the observations of Rapp and Elsässer, described folds in the lingual mucous membrane of man and many mammals, and called them *papilla lingualis foliata seu interlocularis*. These folds he regarded as nerve-papillæ. It was not, however, until 1869 that the true nature of these organs was demonstrated by v. Wyss and Engelmann.

The lateral gustatory organs have been found in the Marsupialia, Edentata, Insectivora, Rodentia, Chiroptera, Proboscidea, in several of the Carnivora, and in the Quadrumana. Of the Ruminantia but three are known to possess them, *Tragulus javanicus*, *Cephalolophus mergens*, and *Camelopardalis giraffa*. In the bandicoots, kangaroos, and phalangers of Australia the lateral gustatory organ may be studied in its most primitive form. In *Perameles* it consists of a single gland-duct, in the walls of which scattered bulbs are developed. In *Halmaturus*, *Macropus*, *Petrogale* and *Dasyurus*, there are several of these ducts, with a proportional increase in the number of bulbs. In *Phalangista*, *Belideus* and *Acrobates*, the organ is less simple, and gland-ducts open at the bottom of slit-like furrows. Between the complex lateral gustatory organ of rodents (in which there is but little to suggest its true origin) and these simple types, there are many intermediate forms.

The microscopic structure of the end-organs of taste of mammals varies according to their location, and according to the different species of animals. In general they are not unlike a flask or bulb with a short neck; and they occupy cavities in the epithelium, which they completely fill. Their inner part or base rests upon the connective tissue of the mucous membrane. Their outer, and more slender portion, perforates the superficial layers of the epithelium and opens on the surface with a minute, circular or slightly oval aperture. This opening is called the taste-pore. The margin of the pore is usually formed by three or four cells, though it may be formed by two, or, more rarely, as in the fungiform papillæ, by a single epithelial cell being perforated about the centre. The diameter of the taste-pore varies from 0.002 to 0.0045 of a millimetre. In the circumvallate papillæ the bulbs are disposed

at the sides in a zone several tiers deep, the uppermost tier usually being about opposite the middle of the trench. In the papillæ foliatæ they are as a rule restricted to the sides of the folds, which they sometimes very nearly fill. In the fungiform papillæ the bulbs are smaller and more irregular in their distribution. They are embedded in the epithelium at the upper part of the papillæ and, not infrequently, communicate with the free surface by a minute canal, which leads from their apex to the taste-pore. The bulbs vary greatly in size and shape, even in the same individual; but their length always exceeds their greatest transverse diameter. (The dimensions of the bulbs of a number of mammals are given in the table appended to this paper.)

The mammalian taste-bulb consists of two distinct kinds of cells, the outer or investing cells, which appear to function as supporting and protecting elements, of which there may be several layers, and which are modified epithelial cells; and the inner, sensory, or taste-cells, which lie in the interior of the bulb, and which are doubtless directly continuous with the terminal branches of the gustatory nerves. The outer or cover cells are elongated, slightly flattened fusiform structures, with an oval nucleus containing nucleoli. The outer end of these cells is generally drawn out into a point. The inner or basal end, which rests on the mucosa, is usually slightly rounded, though it may be notched or even branched.

Of the taste or sensory cells, of which there are probably from twelve to sixteen in a bulb of average size and maturity, several forms have been described, but the majority of observers distinguish but two forms. The first form comprises the taste-cells of Lovén, with which the *Stiftchenzellen* of Schwalbe are identical. These are highly refractive elements consisting of an elliptical-shaped nucleated enlargement, usually situated near the middle of the cell, and two poles or processes. The peripheral process is cylindrical in form, and frequently terminates in an obliquely truncated apex from which projects a very delicate hair-like or styliform process. In successful preparations the styliform process may be seen protruding through the taste-pore. The central process of the taste-cell, more slender than the peripheral, and occasionally slightly varicose, sometimes divides below the cell-body into two or more branches, but more commonly it terminates in a somewhat pointed extremity. The second form of taste-cells Schwalbe called *Stabzellen*, or staff-cells. They differ from those just described in being

slightly larger, less numerous, and less highly refractive; and, moreover, they lack the styliform process. They are also placed more externally than the cells of Lovén, the latter having a tendency to group themselves nearer the axis of the bulb. A third form of taste-cell, quite similar in structure to the fork-cells of the end-discs of batrachians has been described by Ditlevsen and Krause, but this form has not been very generally recognized by later observers. 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 nerve plexus.

Hermann, a recent writer on the gustatory organs of mammals, describes three kinds of supporting cells in the taste-bulb of the rabbit. First, the outer or "pillar cells," which constitute the true supporting element of the bulb; second, the inner supporting cells, which resemble the "staff-cells," of Schwalbe and heretofore supposed to be sensory in function; and, third, "basal cells" which he regards as compensating cells for the bulbs.

The cells within the bulb which fail to conform structurally to either the taste-cell of Lovén or the staff-cell of Schwalbe, may possibly represent intermediate or degenerate forms of the one or the other, as the case may be, and what is observed may be either cells in process of growth or the remains of degenerated ones. As far as the finer structure of the bulbs is concerned subsequent research has really done little more than confirm the results reached by the early investigators. Of late years, however, something has been accomplished towards a better understanding of the nature and distribution of the mammalian taste-organs, and something, too, has been learned about their mode of development.

The gustatory papillæ of the back of the tongue are supplied by the glosso-pharyngeal nerve. Fine medullated branches of this nerve, containing small groups of ganglion cells, are distributed to the circumvallate papillæ and break up in their interior, ramifying in all directions. After dividing and subdividing they form a plexus at the upper part and sides of the papilla. Many of these branches have lost their medullary sheath, but retain the primitive sheath. In the mucosa directly underlying the layer of columnar cells of the epithelium, the nerve-fibrils form a fine delicate network. In the common hare, in gold preparations, the subepithelial network is very beautifully shown, the nerve-fibrils and small ganglia, which

are scattered through the membranous stroma, being stained deep violet or black. Engelmann early called attention to the resemblance in their chemical reaction of nerve-fibrils and the central processes of the taste-cells. Hönigschmied, by means of chloride of gold, traced the nerve-fibrils directly into the taste-cells in the fungiform papilla of the cat, the investing cells not being stained, while the taste-cells were. A portion of the terminal fibrils of the subepithelial network (probably axis cylinders) enter the bulbs at their base, while others pass between them to end freely in the epithelium, or form an intra-epithelial network.

Within the circumvallate papillæ of *Perameles nasuta* and *Fiber zibethicus* a large and distinct ganglion has been found. It is in the form of a thick axial column, making up a great part of the bulk of the papillary body. It is surrounded by a clearly defined connective tissue capsule, which enters the body of the ganglion and gives it support. Above the ganglion, and also at the sides, branches radiate outwards towards the sloping side containing the taste-bulbs. The nerves are non-medullated, but possess a distinct primitive sheath. It thus appears almost certain, as Poulton observes, that nerve-cells are intercalated in the course of sensory impulses from the peripheral organs to the nervous centres. This is of interest in bringing these terminations into closer connection with the related terminal organs of sight and hearing, where ganglion cells similarly intervene.

Drasch has lately published the results of an investigation of the intimate structure of the papilla foliata, or lateral gustatory organ, of the rabbit and hare. Speaking of the nerves, he says: "Beneath the basal membrane of the secondary lamella of the papilla foliata is a plexus formed of medullated nerve-fibres. From this plexus, fibres, corresponding in number to the sum of the sensory cells, go directly to the bulbs. Other fibres, more numerous, pass between the bulbs to the epithelium situated above them. Many fibres, however, terminate in the membranous stroma beneath the epithelium. Below the bulb region, in the entire width of the lamella, is found a connected stratum of ganglion cells which contribute to the multiplication of the fibres."

The experiments of v. Vintschgau and Hönigschmied, carried on conjointly (and afterwards repeated, and with similar results, by Ranvier), appear to prove beyond question a direct continuity be-

tween nerve-fibrils and taste cells. Their experiments show that after section of the glosso-pharyngeal nerve the taste-bulbs of the papillæ on the corresponding side entirely disappear, while in those on the normal side (where the nerve remained intact) no change takes place. The bulbs of the side supplied by the divided nerve, degenerate within a short time and disappear completely by the fortieth day, while the investing cells are changed in a few months into ordinary epithelial cells.

The experiments of v. Vintschgau and Hönigschmied have quite lately been reconfirmed and added to by Griffini, who studied the reproduction of the gustatory papillæ and regeneration of the taste-bulbs in the rabbit and dog. From his experiments, it appears that after excision of a foliate papilla of the rabbit, the area, corresponding to the part removed, is shortly revested 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 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 two hundred and ninth day, their development was still incomplete.

The development of the taste-organs has been studied to some extent in the rabbit and in man. Hoffmann investigated the human embryo and new-born child for the purpose of studying the distribution of those organs in man. The earliest gustatory structures 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 fœtus, and also in the papillæ of one at the sixth month, taste-bulbs were present. 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 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 or permanent 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 permanent 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.

Recently the tongue of the human embryo has been reëxamined for gustatory structures by the present writer. In an embryo of about the tenth week (the earliest investigated) the gustatory papillæ, and the lingual papillæ in general, were undeveloped nor was it possible to determine with any degree of certainty their future position. In the tongue of a fœtus of the fourteenth week several papillæ of the circumvallate type, in the early stages of development, were present. The trenches of the papillæ were undifferentiated, but their future position was clearly indicated. The proliferations of the epithelium also marked the future position of the glands and their ducts. Fungiform papillæ in various stages of growth were scattered over the dorsum, and at the sides of the back of the tongue the lateral gustatory organs (the papillæ foliatæ) were sufficiently advanced to be perceptible. A few bulbs were detected in the circumvallate papillæ of this fœtus, but un-

fortunately, little could be learned of their structural details. The best marked bulb was spheroidal in shape, and in some respects resembled those of the soft palate and epiglottis. It measured 0.030 mm. in length and 0.027 mm. in breadth, and was placed vertically in the long axis of the papilla, with its lower two-thirds resting in a cavity of the mucosa. The outer extremity of the bulb penetrated the superficial layers of the epithelium. While embryonic taste-bulbs were wanting in the tongue of a ten weeks embryo, it is not improbable that they may yet be found in the incipient stages of growth in one of the twelfth week of intrauterine life.

The same observer has also found bulbs in the human fœtus at the fourth month, the middle of the fifth, and at later periods of intrauterine life. They always make their appearance first at the upper part of the papilla, that is on the exposed surface. The more advanced among them being epithelial in position, while the less mature are largely embedded in the stroma of the mucosa. By the sixth month of fœtal life, bulbs begin to appear on the lateral area of the papilla, but they are much less advanced than those of its free surface. In the new-born child, and until the fourth month of life, isolated bulbs may still be found on the free area of the papilla; at a later period they occur but rarely there.

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, 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, 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, certain altered conditions of the epithelium prevent, save in rare instances, their recurrence there.

TABLE.[1]

	NUMBER OF CIRCUMVALLATE PAPILLÆ.	NUMBER OF BULBS IN CIRCUMVALLATE PAPILLÆ.	MEAN DIMENSIONS OF BULBS.		PAPILLÆ FOLIATÆ OR LATERAL GUSTATORY ORGANS.	NUMBER OF BULBS IN PAPILLÆ FOLIATÆ.	MEAN DIMENSIONS OF BULBS.	
			LENGTH.	GREATEST TRANSVERSE DIAMETER.			LENGTH.	GREATEST TRANSVERSE DIAMETER.
			mm.	mm.			mm.	mm.
Bandicoot (*P. nasuta*).	3	2,160	0·070	0·043	Present.	. . .	0·060	0.030
Bat (*V. subulatus*).	2	800	0·026	0·014	?	. . .	. . .	. . .
Musk rat (*F. zibethicus*).	1	520	0·050	0·027	Present.	800	0·046	0.027
Woodchuck (*A. monax*).	3–5	800	0·060	0·032	Do.	. . .	0·057	0·035
Porcupine (*E. dorsatus*).	2	. . .	0·054	0·024	Do.	. . .	0·048	0·027
Gray squirrel (*S. carolinensis*).	3	750	0·057	0·032	Do.	2,200	0·052	0·028
Red squirrel (*S. hudsonius*).	3	1,200	0·054	0·024	Do.	4,500	0·051	0·021
American hare (*L. americanus*).	2–3	1,200	0·051	0·033	Do.	8,000	0·056	0·035
Rabbit, . .	2	2,400	0·050	0·033	Do.	14,500	0·055	0.036
Horse, . .	2–3	. . .	0·080	0·070	Do.	. . .	. . .	. . .
Pig, . .	2	10,760	0·092	0·036	Do.	4,800	0·066	0·033
Sheep, . .	24	9.600	0·085	0·045	Wanting.	. . .	. . .	. . .
Ox, . .	24	35,200	0·100	0·040	Do.	. . .	. . .	. . .
Goat, . .	12	15,400	0·062	0·030	Do.	. . .	. . .	. . .
Cat, . .	6	600	0·070	0·032	Do.	. . .	. . .	. . .
Dog, . .	4–6	. . .	0·071	0·040	Present.	. . .	. . .	. . .
Fox (*V. vulgaris*).	4	9,500	0·042	0·020	Do.	. . .	0.045	0·021
Skunk (*M. mephitica*).	2	4,000	0·045	0·028	Wanting.	. . .	. . .	. . .
Mink (*P. vison*).	4–5	2,000	0·039	0·024	Rudimentary.	. . .	. . .	. . .
Raccoon (*P. Lotor*).	7–10	14,400	0·055	0·023	Present.	. . .	0 045	0.021
Man, . .	9	6,000	0·079	0·040	Do.	3,000	0.070	0.038

[1] The bulbs of the circumvallate papilla of the flying phalanger (*B. ariel*) measure 0.042 mm. in length and 0.022 mm. in breadth. On one of the gustatory ridges of *Ornithorhynchus*, Poulton estimated the number of bulbs to the square millimetre of surface at about 500.

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