30. The Comparative Anatomy of the Tongues of the Mammalia.—XII. Summary, Classification and Phylogeny.

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(Text-figures 31–45.)

CONTENTS.

During the examination of the tongues described in the preceding papers of this series two main objects were kept in view. In the first place, attempts were made to discover characters which can be added to those which are employed in classification. The success which followed my efforts in this direction varied considerably, as is shown on pp. 729–733. In the second place, data were accumulated for phylogenetic purposes. Many hundreds of tongues were examined, and my own observations, coupled with those of other anatomists, gave me a good knowledge of the range of variation exhibited by the lingual structures in many species. Very few genera were not represented in my own material.

I attempted to give explanations of the meaning of the features which were observed, but I was unable to explain the significance of many conditions, for our knowledge of the comparative embryology of the tongue and mouth is very poor. So many of the features which I described must remain as recorded facts only till we know more about the development of the tongue.

A. SUMMARY OF ANATOMICAL AND PHYSIOLOGICAL CHARACTERS.

The tongue fills the mouth in all Mammals except some of the adult Odontoceti, Rodentia and *Ornithorhynchus*. In some Rodents it is excluded from the front of the mouth by inward prolongations of the hair-clad lips through the diastemata. In the young *Ornithorhynchus* the tongue reaches the end of the mandible to permit of suckling, but it lies far back in the adult because of the growth of the bill. In all Odontoceti in which I examined the parts *in situ* the tongue lay far back, but its tip overlaps the symphysis menti in the fœtus.

In many Mammals the tongue so fills the mouth that its dorsum bears the imprint of the palatal rugæ, and one must be careful not to mistake these marks for natural lingual structures. In all Anteaters except *Orycteropus* and *Manis* inwardly-projecting folds of mucous membrane derived from the gums and cheeks form a sheath for the long vermiform tongue.

Colour of the Tongue:—In several Primates and Ungulata the tongue is pigmented in whole or in part, and the colour may form a definite pattern on the dorsum or inferior surface. Sometimes the gustatory papillæ alone are pigmented. The colour varies, sometimes very considerably, in each species, so it is of no taxonomic value. In my paper on the Cebidæ (**4**), I figured several pigmentary patterns, and I pointed out that the colours vary in their resistance to the bleaching action of preserving fluids.

Sometimes the colour of the tongue is similar to that of the hairs and epidermis, the most striking illustration being the tongue of *Cercopithecus patas*. The pigment cells or granules lie in that part of the epithelium which corresponds to the stratum Malpighii of the epidermis. Sometimes the pigment cells are branched.

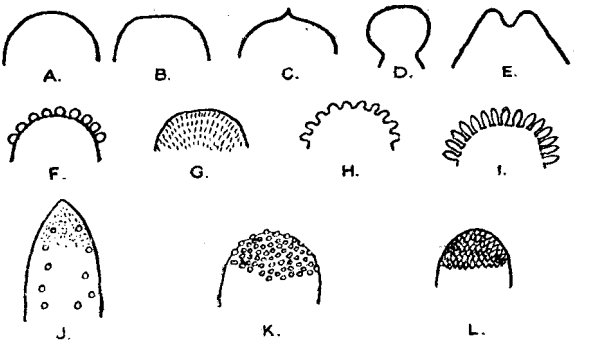
Shape of the Tongue:—The tongue is tapering, spatulate, rectangular or vermiform, the latter being the only adaptation for a particular kind of diet, namely living ants. It is thin in the Polyprotodont Marsupialia and in the Carnivora. And it is thick in the Bradypodidæ, Rodentia and Mystacoceti. In the other Orders the thickness is not unduly small or great. In the Felidæ the apex is very frequently gripped tightly by the incisor teeth after death.

Divisions of the Tongue:—The upper surface of the tongue is divided into oral and pharyngeal parts, the division between them being the circumvallate papillary area; and the lengths of these parts vary considerably. Thus the pharyngeal part or base is short in the Rodentia, Chiroptera and Hapalidæ, so that the circumvallate papillæ lie close to the epiglottis. The base is long in *Manis*, and there is a long tract of mucous membrane between the tongue and epiglottis in the Lion and Jaguar, an arrangement which is supposed to be associated with their roaring habits. In many Mammals the posterior part of the oral division is raised up to form an intermolar eminence.

When no circumvallate papillæ are present, as is the case in many of the Cetacea, it is impossible to distinguish the two parts of the tongue; so it is only by a study of development that one can observe them. In other Mammals the histological structure without any macroscopic examination will help us, because the base is glandular and the oral part is not. In many Cetacea (**7**) most of the tongue is very glandular, so histology does not help us at all, and will mislead us unless we know very accurately from what part of the tongue sections have been taken. Again,

the oral part of the tongue has conical and fungiform papillæ which are distinctive, but many Odontoceti do not possess these structures. Hence one can see that a study of development is frequently the only means of distinguishing between the two primary divisions in the Cetacea. There is no other Mammalian Order to which this condition applies, for all have characteristic papillæ on the oral part of the tongue.

Text-figure 31.



The apex of the tongue in various Mammals. A, *Homo* and *Simia*; B, Monkeys; C, *Physeter macrocephalus* (fœtus); D, Myrmecophagidæ and *Manis*; E, many Pinnipedia; F, *Tupaia minor*; G, Sirenia; H, many Odontoceti; I, some species of *Sus*; J, *Giraffa*; K, Cercopithecidæ; L, *Ornithorhynchus*.

The oral part in Man is developed from the first branchial arch, and the pharyngeal part or base springs from the second and third arches. It is probable that the same rule holds good in other Mammals. The relative proportions of these parts to one another vary greatly. The base is very short, thus bringing the circumvallate papillæ close to the epiglottis in the Rodentia, Chiroptera and Hapalidæ; the base is long in *Manis*; and there is a long stretch of mucous membrane between the tongue and epiglottis in the Lion and Jaguar, the large space at the back of the mouth being associated with the roaring habits of these animals. In many Mammals the posterior part of the oral division of the tongue is greatly thickened to form the intermolar eminence.

The *intermolar eminence* is present in *Ornithorhynchus*, *Hyrax*, and many Sirenia, Mystacoceti, Ungulata and Rodentia; and it is absent in all Marsupialia, Insectivora, Chiroptera, Edentata, Carnivora and Primates. Relatively to the size of the tongue it is largest in *Ornithorhynchus* and some Rodents. It is not a character of primary importance in classification. It is supposed to raise the food up to the level of the grinding teeth. In the

Mystacoceti it helps to expel the water containing the small Pteropods and other animals on which the Whales feed through the baleen plates. The eminence may be as wide as the tongue as in many Rodents and *Ornithorhynchus*, or it may be in the centre of the dorsum only.

The surface of the eminence is smooth, or covered with papillæ of different kinds; and it has markedly pointed structures in *Ornithorhynchus* and *Cavia cobaya*. In the former there are two strong, pointed horny structures called lingual teeth on the anterior border of the eminence; and these are supposed to direct insects and other food material into the cheek-pouches when the animal is feeding under water. No other Mammal has these structures. In *Cavia* there are rows of sharp conical papillæ on the anterior border of the eminence.

I described several individual peculiarities in the eminence in my account of the Murine tongues (**10**).

The circumvallate papillæ and lateral organs lie on the eminence, but fungiform papillæ are variable thereon.

The region in front of the eminence varies in length. Thus it is short in the Beaver, but it is long in some Ungulates. It is divisible into two parts. Most anteriorly is the tactile area including the apex of the tongue, and the posterior part is mechanical in function. In *Zaglossus* the tongue has a solid posterior part on which lie the circumvallate papillæ, lateral organs and dense spines, and a long, cylindrical, very mobile anterior part; and I believe that the posterior part corresponds to the intermolar elevation.

The *apex of the tongue* varies in shape, being rounded, truncated, pointed or globular (text-fig. 31). Sometimes it has a small notch, but it is deeply cleft in the Pinnipedia. In a fœtal *Physeter macrocephalus* it had a very pronounced median process, but I did not have the opportunity of examining an adult animal to see whether it is present or not. It certainly does not exist in any other Cetacean tongue examined by myself.

In human development the tuberculum impar, derived from the mandibular arches, becomes buried by two laminæ which fuse to form the oral part of the dorsum. Sometimes the laminæ do not unite anteriorly, so the apex of the tongue becomes cleft, resembling in a slight degree the condition which exists in Lizards and Snakes. This occasional occurrence in Man is the rule in all Pinnipedia. It must have some physiological significance, but it is not apparent to me.

The apex is bound down to the floor of the mouth in all Odontoceti, but it was free in a very young fœtus of *Physeter macrocephalus*. It has been suggested that the tongue is not very mobile in the Odontoceti because of the binding down to the floor of the mouth. Such a condition alone is not conclusive, for the tongue of the Elephant, which is mobile, has no free anterior part. When the Elephant masticates, a piece of the dorsum

becomes converted into an apex. The reason for the poor mobility in the Odontoceti lies in the condition of the muscles. In the Sirenia the mobility is slight, but I suggested (7) that the hard, retroverted apical papillæ enable it to exert its maximum mechanical action when the animals crop the vegetation on which they subsist.

The apex and the dorsum behind it may be destitute of obvious structures, but the following appearances are noteworthy:—

1. There is a marginal row of fungiform papillæ in *Metachirus opossum*, *Marmosa elegans*, *Tupaia minor* and *Cercopithecus tantalus*.

2. There is a thick cluster of fungiform papillæ in the Simiidæ, Cercopithecidæ, some Cebidæ, Lemuridæ and Ungulata. These papillæ have taste-buds and tactile nerve-endings.

3. There is a thick cluster of large conical papillæ in the Sirenia, Pinnipedia, Ungulata and *Ornithorhynchus*.

4. There are marginal lobules in *Galeopithecus* and some Cetacea. In *Tursiops tursio* there is a large blunt median lobule, corresponding perhaps to the long median process in the fœtal *Physeter macrocephalus* mentioned above.

5. There are long, pointed or club-shaped papillæ in some species of *Sus* and *Ursus*.

The apical part of the tongue is prehensile, tactile or gustatory in function, or it may perform two or all these functions, but the chief and most widespread use is no doubt touch. Nerve-endings of various kinds have been detected, and it is possible that certain types, which only occur in Man, are associated with speech. The tactile function probably reaches a high degree of perfection in the Anteaters, whose tongues are really glutinous, exploring and prehensile organs. But there are differences in the apex in various Anteaters. Thus the apex is pointed in *Zaglossus* and *Orycteropus*, but it is globular in *Myrmecophaga*, *Tamandua* and *Manis*.

The prehensile function of the tongue for solids is great in the Monotrematous and Edentate Anteaters, the Giraffe and some Bats. Owen points out that the apical papillæ in the Bat *Monophyllus* are employed for probing night-blowing flowers for insects. All these animals have very mobile tongues, but the Rodentia, Odontoceti and Sirenia have the least protrusible tongues. It will be shown later that there is a relation between the prehensile function of the tongue and the characters of the lower incisor teeth. In Mammals which drink the tongue plays an important part in the process; and it is used either for lapping or for suction. In the Primates we find that the Lemuroidea, which have cleft upper lips adhering to the gum, drink by lapping, whereas the Anthropoidea, which have entire, non-adherent upper lips, drink by suction. The degree of mobility varies in each Order, and the differences may be very striking, as can be seen by comparing the tongue of *Ornithorhynchus* with those of *Zaglossus* and *Acanthoglossus*.

In *Dasypus peba* there are two pointed structures under the apex of the tongue. Muscle fibres pass to their bases, and Mayer suggested that they are useful for killing insects.

Sulci:—The dorsum of the tongue may have a median longitudinal sulcus on its anterior part, on its base or on both parts, but there is never a complete sulcus extending from the apex right back to the epiglottis. The circumvallate papillæ interrupt the sulcus in its complete form. When an intermolar eminence is present there is never a sulcus on it. These sulci may be regarded as traces of bilateral origin of both the oral and pharyngeal parts of the tongue. In the Lemuridæ and Simiidæ there is a Y-shaped group of circumvallate papillæ, and the vertical limb of the Y lies over the position of the median dorsal sulcus on the base of the tongue.

There is frequently a median ventral sulcus; indeed, it is more often present than the median dorsal sulcus. It receives the lingual attachment of the frenum linguæ in its posterior part. In *Cœlogenys paca* alone the median dorsal and median ventral sulci are continuous round the apex of the tongue.

Permanent transverse sulci radiate from the median dorsal sulcus in *Mustela erminea*; they indent the mucous membrane, so they cannot be mistaken for the shallow, wide grooves, which are formed by the palatal rugæ. Permanent transverse ventral sulci exist in *Cœlogenys paca* and *Galeopithecus volans*. In *Manis* and *Zaglossus* there is a deep groove or tunnel on the anterior part of the tongue, and the walls are formed by the upward folding of the sides of the dorsum; in the former the floor of the groove is smooth, but it has long spines in the latter. No trace of the tunnel exists in *Myrmecophaga*, *Tamandua* or *Orycteropus*. It may act as a trap for insects. The presence or absence of sulci is of little value in classification.

Median ventral ridges occur in many Mammals. In some cases they are undoubtedly artefacts produced by the action of preserving fluids. In other cases they are vestigial structures, being remnants of the lytta or sublingua.

The *lateral borders of the tongue* are thin or massive, and they lodge the foliate papillæ or lateral organs at their posterior extremities when these organs are present (see p. 714). They have conical and fungiform papillæ, and they have lobules anteriorly in *Galeopithecus* and some Cetacea. When the apex of the tongue is fixed the lateral borders may be quite mobile. Thus the apex is bound down to the mandibular symphysis in *Platanista gangetica*, but the edges are free and mobile. The animal is blind, and burrows in mud at the bottom of rivers for small fishes and crustacea, which constitute its diet. And the sensitive edges of the tongue may be organs of exploration. The lateral lobules in the adult Cetacea are not present in some fœtuses which have been described.

Lingual Papillæ:—The mucous membrane of the mouth and

tongue is in reality the modified skin of the stomodæum, so a comparison between the cutaneous and lingual papillæ is important. There is, moreover, as far as I can ascertain, no definite account of the difference to be found anywhere. In the general skin surface the papillæ are all buried beneath the surface of the smooth epidermis. Some papillæ have blood-vessels arranged in loops, and others have sensory end-organs, but papillæ with blood-vessels have no end-organs. Nerves pass into the epidermis, but none of these have a more complicated mode of termination than a small varicosity. The sudorific and sebaceous glands do not end in close association with the special end-organs. In some special tactile areas such as the skin of the bill of *Ornithorhynchus* and the snout of the Mole there are special end-organs near the surface. In the tongue, particularly on the base, a few papillæ are buried, but most stand up prominently on the surface of the mucous membrane. The corium centres have both vessels and nerves, but all the special sense-organs lie in the epithelium. The serous glands open alongside the gustatory organs, and are never found anywhere except in close relation to these structures. Their degree of development corresponds more or less to that of the gustatory papillæ, and there is a theory that the lateral organs were evolved from serous glands. No cutaneous papillæ carry out any mechanical function. These notes show that the adequate stimuli demand that the lingual papillæ should be elevated, and have their sense-organs near the surface; in the skin that is not necessary.

From the physiological point of view the papillæ fall into two great groups as follows:—

A. Mechanical papillæ.
B. Gustatory papillæ.
   a. Fungiform papillæ.
   b. Circumvallate papillæ.
   c. Lateral organs.

Of these the mechanical and fungiform papillæ occur in several classes of Vertebrates, but the circumvallate papillæ and lateral organs are only found in Mammals. It is interesting to note that the mechanical papillæ remain, whereas the gustatory papillæ are absent or strangely modified in the Cetacea in which the tongue has degenerated.

The papillæ may be described in any order, but I have begun here with the fungiform papillæ, as they represent early stages in the evolution of the circumvallate papillæ.

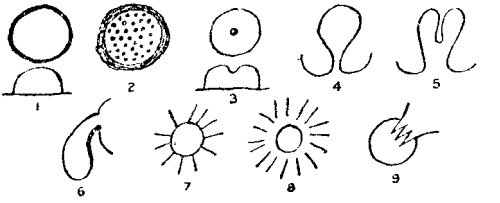
The Fungiform Papillæ (text-fig. 32).

The fungiform papillæ are bright in colour in the living tongue, but they are dead white in preserved ones; and the dead-white colour is of importance in enabling us to detect them when they

are very small, as they are in primitive Mammals. They vary in appearance, number and arrangement. They are hemispherical, globular or pedunculated bodies standing on the flat surface of the tongue, or contained within pockets in the mucous membrane. Those which lie in pockets near the junction of the oral and pharyngeal parts of the tongue are apt to be mistaken for circumvallate papillæ, and histological examination may be necessary to determine the true nature of a particular papilla. The surface is smooth, granular or umbilicated, the granules being formed by secondary papillæ.

The different forms are not characteristic of particular Orders. Thus the hemispheral form occurs in all Orders, and pedunculated forms are found in *Homo*, the Simiidæ, *Cercocebus*, *Nasua*, and the small group of Felidæ containing the Domestic, Wild and Caffre Cats, the Lynx and the Caracal. In that group of Felidæ pedunculated papillæ with taste-buds lie in the positions of the

Text-figure 32.



Types of fungiform papillæ. 1, hemispherical on plan and section; 2, granulation by secondary papillæ; 3, umbilicated papilla; 4, clavate type; 5, umbilicated clavate type; 6, depending papilla; 7–9, relations to conical papillæ.

lateral organs, and I suggested the name of papillæ clavatæ for them (8). Their value in classification is described on pages 729–733. It may be difficult or impossible to detect papillæ macroscopically, either because they are very minute, or they are concealed by overhanging conical papillæ. I could not detect them even with a powerful lens in *Galeopithecus*, some Canidæ and the Monotremata. In the Arctic Fox there are individual variations, some specimens having minute, but visible, papillæ, whereas others have none visible macroscopically. The converse condition is observable in some Rodents, the small fungiform papillæ being thrown into prominence by the small size of the conical papillæ around.

Papillæ are present on the oral part of the dorsum, the lateral borders and a greater or less extent of the periphery of the inferior surface. As none are found behind the circumvallate papillæ, they are limited to the part of the tongue which is formed from the first pair of branchial arches.

On the oral part of the dorsum the papillæ may cover the entire surface from before backwards and from side to side, but in many specimens they are absent from the central part. They may or may not exist on the intermolar eminence. The extent of the surface containing them varies with age in Man. Thus the infant has them all over the dorsum, but the adult has not. These observations on the age-changes in Man have not been supplemented by observations on other Mammals. In lower Orders the papillæ may cover the dorsum.

The central area of the dorsum which is free from fungiform papillæ may extend back into the area of the circumvallate papillæ; or it may be shut off by a posterior cluster or rows of papillæ. And the presence or absence of these groups is of value in classification.

The papillæ on and behind the apex may be sparse, or they may be irregularly grouped in a cluster of variable size. In the lower Orders the cluster is very small or absent, but in higher Orders it is small or large. Moreover, in some of the higher Orders the more primitive animals have smaller clusters than the specialized ones. These statements are illustrated in the subjoined table. On the dorsum behind the apex the papillæ are arranged in rows of varying degrees of obliquity; and they increase in size, and perhaps in number, as we proceed from the lower Orders to the higher. On the lateral borders of the tongue they are numerous or scanty, and are disposed in one or more rows.

On the bounding zone on the inferior surface of the tongue the fungiform papillæ may be scanty or numerous. They may be irregularly disposed, or they may be arranged in one or two rows. Of these rows both may have papillæ of equal size, as in the Gorilla, or the inner row may contain larger elements than the outer one. There may be a thick cluster of papillæ beneath the apex of the tongue, and this group is largest in the higher Primates.

When the papillæ in the various Orders are compared, one sees that they vary in numbers, in size, and in concentration on various parts of the tongue. Of special interest is the size of the apical cluster. The arrangements are shown in the following table, which deals with all Orders except the Chiroptera, of which too few specimens were available to enable me to draw any conclusions of value.

From a study of the subjoined table the following conclusions can be drawn:—

1. In the lower Orders the papillæ are relatively fewer and smaller than those in the higher ones.

2. As we proceed from the lower Orders to the higher ones we notice a concentration of papillæ at the apex of the tongue. The apical cluster is largest in the Cervidæ and Catarrhine Primates.

3. In some Orders the fungiform papillæ have vanished, but the tongue has otherwise undergone specialization. In *Ornitho-*

Order.	*Apical* cluster.*	*Lateral dorsal papillæ.*	*Remarks.*
Monotremata	absent.	absent.	
Marsupialia.			
a. Didelphyidæ	„	few.	Papillæ all minute.
b. Dasyuridæ	„	numerous.	Papillæ larger than in *a*.
c. Peramelidæ	slight.	„	Papillæ larger than in *a* and *b*.
d. Phalangeridæ	absent.	„	Papillæ all very small.
e. Phascolarctidæ	„	„	„ „ „
f. Macropodidæ	„	„	„ „ „
Edentata.			
a. Dasypodidæ	„	a few.	
b. Bradypodidæ	moderate.	„	Papillæ larger than in *a*.
c. Myrmecophagidæ	absent.	absent.	
d. Manidæ	„	„	
e. Orycteropodidæ	„	a few.	Papillæ larger and more than in *a*.
Insectivora	„	„	Papillæ very small.
Dermoptera	„	absent.	
Rodentia	small or absent.	variable.	Papillæ always small.
Carnivora.			
a. Felidæ	small or moderate.	„	Papillæ small or of medium size.
b. Viverridæ	small when present.	„	„ „ „ „ „
c. Protelidæ	not large.	„	Size moderate.
d. Hyænidæ	„ „	a few.	
e. Canidæ	small or absent.	„	Papillæ usually very small.
f. Mustelidæ	small.	numerous.	„ „ „ „
g. Procyonidæ	good.	„	Papillæ small.
h. Ursidæ	„	variable.	Size moderate.
Cetacea	absent.	small or absent.	Papillæ always small when present.
Ungulata.			
a. Perissodactyla	small.	numerous.	Size moderate.
b. Suina	„	„	„ „
c. Tylopoda	„	not numerous.	„ „
d. Cervidæ	large.	„ „	Papillæ large.
e. Bovidæ	absent.	numerous.	„ „
f. Tragulidæ	small.	„	Size moderate.
Sirenia	absent.	very few.	Papillæ very small.
Primates.			
a. Tarsiidæ	minute.	scanty.	Papillæ of moderate size or large.
b. Chiromyidæ	„	„	„ „ „ „
c. Lorisidæ	„	variable.	„ „ „ „
d. Galagidæ	„	„	„ „ „ „
e. Lemuridæ	moderate.	numerous.	„ „ „ „
f. Hapalidæ	„	scanty.	„ „ „ „
g. Cebidæ	„	numerous.	„ „ „ „
h. Cercopithecidæ	large.	„	„ „ „ „
i. Simiidæ	„	„	„ „ „ „
j. Hominidæ	„	„	„ „ „ „

* Small and slight mean that an occasional papilla occurs here and there.

rhynchus the conical papillæ have become highly developed; in the Monotrematous and Edentate Anteaters, except *Orycteropus*, the tongue is mainly a prehensile, exploring organ and the fungiform papillæ have vanished; in the Cetacea the reduction in or complete loss of the papillæ is part of a degenerative process, which has involved the lingual structures.

When the papillæ are examined histologically it is seen how many have secondary papillæ composed of epithelium alone, or of epithelium and corium. Taste-buds are present in animals belonging to most of the Mammalian Orders, and the nerves may be large and provided with ganglia. The taste-buds have fewer gustatory cells than the buds in the circumvallate papillæ, and are nearer the surface. No glands are connected to the fungiform papillæ. In lower Vertebrata the epithelium may consist of a single layer of columnar cells, or it may be stratified as in the Mammalia. In Oppel's 'Text-book of Microscopic Anatomy' many buds and papillæ have been figured.

The Circumvallate Papillæ (text-fig. 33).

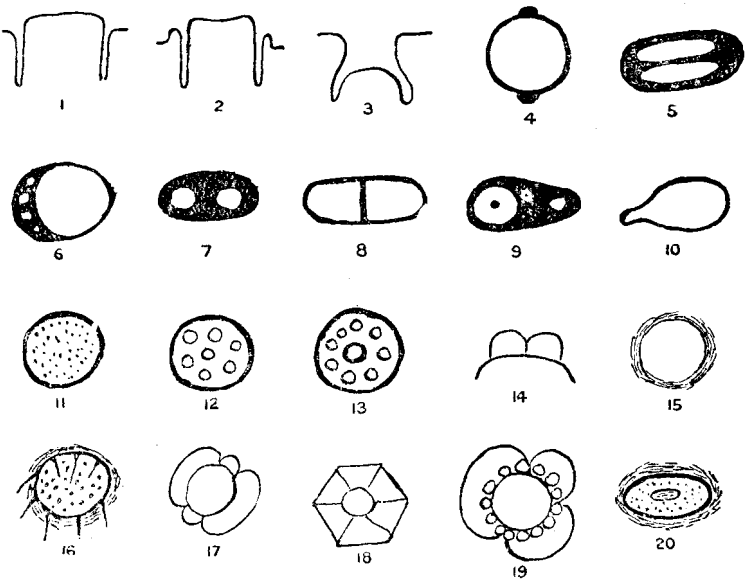
The circumvallate papillæ occur only in Mammals, but not in all species. They differ greatly in structure, number and arrangement; and there is a complete series of transitional forms between the various forms, and between them and the fungiform papillæ. In many Mammals there are transitional forms between them and the lateral organs. It is therefore necessary in the first place to describe the characters of a typical circumvallate papilla. And the papilla in question must not be selected from a Monotreme or a Marsupial.

A circumvallate papilla has a body, whose form varies considerably, lying in a hollow or fossa in the mucous membrane. The mucosa of the tongue covers the papillary body and lines the fossa. The outer wall of the fossa may be raised up to form a ridge or vallum. Serous glands always open into the depths of the fossa, and the presence of these glands is one of the features which distinguishes the papilla from a fungiform papilla. Taste-buds lie in the epithelium of both sides of the fossa, whereas they are never in the angle between the body and the tongue surface in the fungiform papillæ. It is sometimes stated that taste-buds are on the upper surface of the fungiform papillæ, but are not there in the circumvallate papillæ. That is, however, not true, for authors have described or figured them on the upper surface of the circumvallate papillæ in *Ornithorhynchus*, *Capra*, *Mus*, *Ovis*, *Talpa*, *Meles*, *Felis*, *Canis*, *Mustela* and in the new-born child. These buds are more numerous at birth than in adult life, so their diminution is one of the age-changes which occur in the tongue. The dermis component of the papillæ contains connective-tissue, blood-vessels and nerves, and the nerves may be plexiform or provided with large ganglia.

The vallate papillæ mark the boundary between the part of the tongue developed from the first arch and that arising from the second and third arches. In the higher Primates the bilateral origin of the latter may be indicated by the vertical stem of the Y-shaped group of papillæ.

The papillæ may stand up higher than, be flush with, or be recessed below the surrounding dorsum of the tongue, but the protruding form is commonest. When it is recessed, as in the Monotremata, the object attained is protection. It must, however, be noted that preserving fluids may make the papillæ contract into a smaller volume and shrink down into the vallum.

Text-figure 33.



The macroscopic characters of circumvallate papillæ.

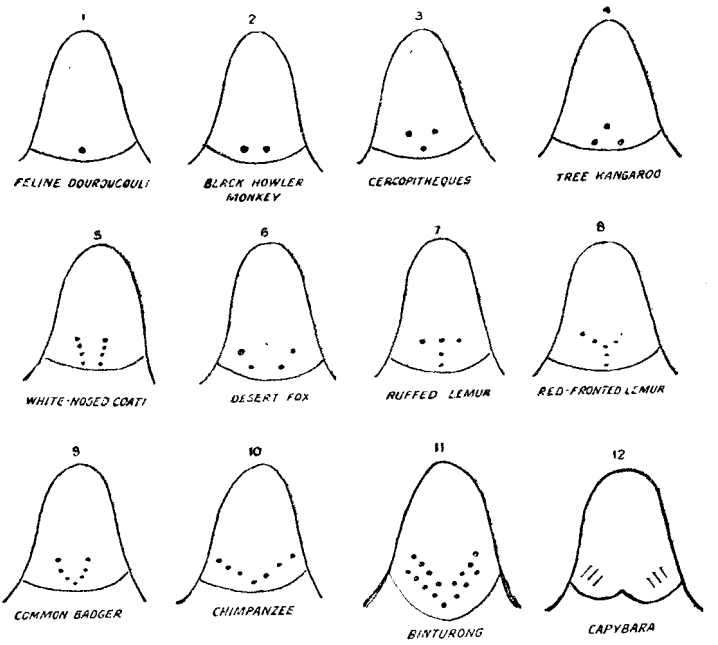
The papillary body may be hemispherical, as in *Ornithorhynchus*, globular as in *Vespertilio*, *Meles*, and *Macacus*, cylindrical or conical. In conical types the apex or base may be attached to the tongue. The fossa is shaped according to the form of the body, as it undermines the papillary body when the latter is conical with the apex attached. These forms are shown in text-fig. 33. It will be shown later that a series of phylogenetic stages includes several of these forms.

The fossa usually appears as a slit around the papillary body, but it is sometimes very patulous in tongues removed immediately after the death of the animal. And this would seem to show that variations in the fossa may accompany the act of mastication.

In *Macacus rhesus* and *M. fascicularis* the fossæ have patulous recesses at the anterior and posterior papillary poles, but these close up when the tongue is immersed in preserving fluids.

Each fossa may contain more than one papilla, and these papillæ may be completely separate, or they may be lobes of one large papilla. The two may be of the same dimensions, or the sizes may differ. These must not be regarded, however, as stages in the extra-uterine division of a papilla, for such a phenomenon

Text-figure 34.



Arrangements of the vallate papillæ. On p. 739, which deals with phylogeny, these are grouped as follows—3 = A; 2 = B; 1 = C; 9 = D; 5 = E; 1 = F; 7 = G.

does not take place. They represent the end of some process which took place in development. Probably one of the divisions is a greatly enlarged secondary papilla, and it is analogous to the long pointed summit of the papilla in *Dasyurus*.

The surface of the papillary body is smooth, polished and glistening, or it is granulated by secondary papillæ. In many Marsupials it is drawn out into a long point. Sometimes the centre is umbilicated. Secondary papillæ are very well marked on the sunken papillæ in *Manis*.

The vallum may not be raised, but when it is it is smooth and entire, or divided up into one or more concentric circles of lobules, which are circular, oval, reniform or quadrangular.

The greatest numbers of papillæ are found in the Giraffe, which has 50, and in *Antilope americana*, which has 52. On the contrary *Hyrax* and some Cetacea and Pinnipedia have none at all.

The papillæ are slit-like in *Moschus*, the Caviidæ and some Cetacea; and they are sac-like in the Sirenia and some Cetacea. The other arrangements are:—

A. *A single median papilla*:—some specimens of *Macropus* and *Phascolarctos*, some specimens of *Aotus*, the Muridæ.

B. *A pair of papillæ*:—New World Edentata, Lagomorph and Hystricomorph Rodents, Perissodactyla, Tragulidæ, Ailuroidea, Cynoidea, Mustelidæ, Chiroptera entomophaga, Lemuridæ, Cebidæ, Cercopithecidæ.

C. *Pairs of papillæ in chevron*:—Camelidæ, Cervidæ, Bovidæ, Carnivora except Ursidæ and Pinnipedia, Lemuridæ, Cebidæ, Cercopithecidæ.

D. *Three papillæ in a triangle*:—all Marsupialia and Old World Edentata, Sciuromorph Rodents, Dipodidæ, Spalacidæ, Viverridæ, Pinnipedia, Insectivora, *Chiroptera frugivora*, all Primates except Man.

E. *Several papillæ in a* V:—Tapiridæ, Pinnipedia, Arctoidea, Viverridæ, Anthropoidea except the Hapalidæ.

F. *Papillæ in line*:—Tapiridæ, *Tarsius*.

G. *Papillæ in clusters*:—Rhinocerotidæ, Giraffidæ.

H. *Several papillæ in* T:—Lemuridæ, Cebidæ, Cercopithecidæ.

I. *Several papillæ in* Y:—Lemuridæ, Simiidæ.

In the above list I have taken into account all patterns recorded by myself and others. In the following table PO= no papillæ; PI, a single median papilla; PP, a pair of papillæ; CH, pairs in chevron; LI, papillæ in line; PS, slits; PCL, clusters. The lateral organs are also shown.

	Y.	T.	V.	Δ.	CH.	PP.	LI.	PS.	PCL.	PI.	PO.	*Lateral organs.*
Order MONOTREMATA.	—	—	—	—	—	+	—	—	—	—	—	+
Order MARSUPIALIA...	—											
Didelphyidæ	—	—	—	+	—	—	—	—	—	—	—	—
Dasyuridæ	—	—	+	+	—	—	—	—	—	—	—	—
Peramelidæ	—	—	—	+	—	—	—	—	—	—	—	—
Phalangeridæ	—	—	—	+	—	—	—	—	—	—	—	+
Macropodidæ	—	—	—	+	—	—	—	—	—	+	—	+
Phascolarctidæ ...	—	—	—	+	—	—	—	—	—	+	—	+
Order EDENTATA.												
Dasypodidæ.....	—	—	—	—	—	+	—	—	—	—	—	variable.
Bradypodidæ	—	—	—	—	—	+	—	—	—	—	—	—
Myrmecophagidæ .	—	—	—	—	—	+	—	—	—	—	—	variable.
Manidæ	—	—	—	+	—	—	—	—	—	—	—	—
Orycteropodidæ ...	—	—	—	+	—	—	—	—	—	—	—	variable.

	Y.	T.	V.	Δ.	CH.	PP.	LI.	PS.	PCL.	PI.	PO.	*Lateral organs.*
Order INSECTIVORA.												
Erinaceidæ	−	−	−	+	−	+	−	−	−	−	−	+
Centetidæ	−	−	−	+	−	−	−	−	−	−	−	+
Solenodontidæ	−	−	−	+	−	−	−	−	−	−	−	−
Potamogalidæ	−	−	−	+	−	−	−	−	−	−	−	−
Chrysochloridæ	−	−	−	+	−	−	−	−	−	−	−	−
Soricidæ	−	−	−	+	−	+	−	−	−	−	−	−
Talpidæ	−	−	−	−	−	+	−	−	−	−	−	−
Tupaiidæ	−	−	−	+	−	−	−	−	−	−	−	−
Order DERMOPTERA	−	−	−	−	−	+	−	−	−	−	−	+
Order RODENTIA.												
Sciuridæ	−	−	−	+	−	−	−	−	−	−	−	+
Castoridæ	−	−	−	+	−	−	−	−	−	−	−	+
Myoxidæ	−	−	−	+	−	−	−	−	−	−	−	+
Muridæ	−	−	−	+	−	−	−	−	−	+	−	variable.
Spalacidæ	−	−	−	+	−	−	−	−	−	−	−	+
Dipodidæ	−	−	−	+	−	−	−	−	−	−	−	−
Octodontidæ	−	−	−	−	−	+	−	−	−	−	−	+
Hystricidæ	−	−	−	−	−	+	−	−	−	−	−	variable.
Chinchillidæ	−	−	−	−	−	+	−	−	−	−	−	−
Dasyproctidæ	−	−	−	−	−	+	−	−	−	−	−	+
Caviidæ	−	−	−	−	−	−	−	+	−	−	−	+
Leporidæ	−	−	−	−	−	+	−	−	−	−	−	+
Order CARNIVORA.												
Felidæ	−	−	−	−	+	+	−	−	−	−	−	variable.
Viverridæ	−	−	+	+	+	+	−	−	−	−	−	variable.
Hyænidæ	−	−	−	−	+	+	−	−	−	−	−	+
Protelidæ	−	−	−	−	+	+	−	−	−	−	−	+
Canidæ	−	−	−	−	+	+	−	−	−	−	−	variable.
Mustelidæ	−	−	+	−	+	+	−	−	−	−	−	variable.
Procyonidæ	−	−	+	−	+	−	−	−	−	−	−	variable.
Ursidæ	−	−	+	−	−	−	−	−	−	−	−	variable.
Pinnipedia	−	−	+	+	−	−	−	−	−	−	+	variable.
Order CETACEA	−	−	+	−	−	−	+	+	−	−	+	−
Order UNGULATA.												
Equidæ	−	−	−	−	−	+	−	−	−	−	−	−
Tapiridæ	−	−	+	−	−	−	+	−	−	−	−	variable.
Rhinocerotidæ	−	−	−	−	−	−	−	−	+	−	−	−
Suidæ	−	−	−	−	−	+	−	−	−	−	−	variable.
Phacochœridæ	−	−	−	−	−	+	−	−	−	−	−	+
Tragulidæ	−	−	−	−	−	+	−	−	−	−	−	+
Camelidæ	−	−	−	−	+	−	−	−	−	−	−	−
Bovidæ	−	−	−	−	+	−	−	+	−	−	−	−
Giraffidæ	−	−	−	−	−	−	−	−	+	−	−	+
Order PROBOSCIDEA	−	−	−	−	+	−	−	−	−	−	−	+
Order HYRACOIDEA	−	−	−	−	−	−	−	−	−	−	+	+
Order SIRENIA	−	−	−	−	−	−	−	+	−	−	−	variable.
Order PRIMATES.												
Lemuridæ	+	+	−	+	+	−	−	−	−	−	−	+
Lorisidæ	−	−	−	+	−	−	−	−	−	−	−	−
Galagidæ	−	−	−	+	−	+	−	−	−	−	−	−
Chiromyidæ	−	−	−	+	−	+	−	−	−	−	−	−
Tarsiidæ	−	−	−	+	−	−	+	−	−	−	−	−
Cebidæ	−	−	+	+	+	+	−	−	−	+	−	+
Hapalidæ	−	−	−	+	+	−	−	−	−	−	−	+
Cercopithecidæ	−	+	+	+	+	+	−	−	−	−	−	+
Hylobatidæ	+	+	−	+	−	−	−	−	−	−	−	+
Simiidæ	+	+	+	+	−	−	−	−	−	−	−	+
Hominidæ	−	−	+	−	−	−	−	−	−	−	−	+

The following table contains observations of Tuckerman and myself relative to the number of taste-buds in the vallate papillæ and lateral organs :—

	Number of vallate papillæ.	*Number of buds in the papillæ.*	*Number of buds in the lateral organs.*
Perameles nasuta	3	2,160	no organs.
Didelphys virginiana ...	3	2,900	„ „
Phascolomys wombat	3	3,500	
Phascolarctos cinereus ...	3	4,200	
Dasypus peba	2	2,400	organs variable.
Dasypus villosus	2	2,500	„ „
Fiber zibethicus	1	520	800
Lepus cuniculus	2	2,400	14,500
Lepus campestris	2	1,200	16,800
Cynomys ludovicianus ...	2	1,100	
Tamias striatus	3	750	
Vespertilio subulatus.....	2	800	
Pteropus pselaphon	3	3,500	
Sus scrofa	2	10,760	4,800
Ovis aries.....	24	9,600	organs absent.
Calf	24	35,200	„ „
Capra hircus	12	15,400	„ „
Antilocapra americana ...	52	48,000	„ „
Felis domestica	6	600	
Canis vulpes.....	4	9,500	
Canis familiaris	4–7	8,000	
Canis lupus	2	2,900	
Canis latrans	7	5,000	
Mephitis mephitica	2	4,000	
Putorius vison.....	4–5	2,000	
Lutra canadensis	7–8	2,400	
Macacus cynomolgus	4	4,000	
Macacus rhesus	3	1,800	
Homo sapiens	9	6,000	3,000

A series of observations was made to determine whether the members of an Order, which are primitive or specialized in other features of bodily structure have differences in the patterns of the vallate papillæ, and the following table contains the results of the investigation. The examples selected were those chosen by Pocock in his studies of the relations of the various tactile arrangements in the Mammalia. I have omitted the Cheiroptera, for the material at my disposal was scanty, and I have left out the Cetacea, in which the papillæ have been lost as the result of degenerative processes.

Order.	A. *Primitive species.*	B. *Specialized species.*	*Remarks.*
Marsupialia	*Trichosurus.*	*Dendrolagus.*	Patterns identical in A & B.
Edentata	*Dasypus.*	*Tamandua.*	„ „ „
	„	*Bradypus.*	„ „ „
Insectivora	*Centetes.*	*Sorex.*	B has more patterns than A.
Rodentia	*Atherura.*	*Erethizon.*	Patterns identical in A & B.
Carnivora	Viverridæ.	Felidæ.	A has more patterns than B.
	Procyonidæ.	Ursidæ.	„ „ „
	Canidæ.	„	„ „ „
Ungulata	*Tajassu.*	*Hippopotamus.*	Both have one pattern.
	Tragulus.	Pecora.	„ „ „ „
	Tapiridæ.	Equidæ.	A has more patterns than B.
	„	*Rhinoceros.*	„ „ „
Primates	*Tarsius.*	Lemuridæ.	A has fewer patterns than B.

In the above selected forms of Marsupials, Edentates and Rodents the number of papillæ is identical in each Order. But in the Ungulata the single pattern and the number of papillæ in each varies.

There are transitional types between the fungiform and circumvallate papillæ.

The conclusions regarding the circumvallate papillæ are given on page 718.

The Lateral Organs (1, text-fig. 16).

Like the circumvallate papillæ these gustatory organs are found only in Mammals, but not in all species. They vary in appearance and development. They are found at the posterior extremities of the lateral borders of the tongue or on the sides of the intermolar eminence. Sometimes they are replaced by rows of club-shaped fungiform papillæ containing taste-buds.

In the table on page 714 it is seen how lateral organs are absent in all Polyprotodont Marsupials, the vast majority of Lipotyphlous Insectivora, some Rodents and Ungulates, the Cetacea, the Tarsioidea and the Lorisiform Lemuroidea. They show individual variations in most of the animals formerly grouped in the Edentata, the Carnivora and some of the Ungulata. They are invariably present, though differing in type in the Monotremata, Diprotodont Marsupials, most Rodents, Hyracoidea, Proboscidea, Lemuriform Lemuroidea and Anthropoidea.

In some Marsupials (e. g. *Halmaturus* and *Macropus*) there appears on each side of the tongue at the posterior extremity of each lateral border a row or rows of small orifices like the mouths of the ducts of glands, and the row may be straight or curved.

Some of these orifices are glandular, but others represent the lateral organs. The organs are arched over by a fringe of long filiform papillæ. When sections are made through the tongue it is seen how each duct receives ductules and has taste-buds in its wall. Poulton points out that horizonial sections show that the narrow ducts, which open into the circular depressions on the surface of the tongue, are really slit-like. The taste-buds are in tiers, and nerves approach them from the sides; and the nerves have small ganglion cells. The secreting alveoli are of the serous type. The gland-ducts which receive the secretions of alveoli of the mucous type have no taste-buds. In *Macropus* the organs are more like depressions than gland-ducts. In *Trichosurus vulpecula* the organ is a row of slits, but none of the tongue in or around the organ is elevated. Taste-buds are on each side of the slits, and serous glands open into the bases. The slits are not absolutely regular as in higher Mammals The Marsupial forms are shown in P. Z. S. 1921, p. 556, text-fig. 58.

In the higher Mammals the organs may be identical, or one may be larger than the other. They consist of fissures separating laminæ of varying degrees of prominence. In a former paper (1) I called these sulci primary fissures for they separate laminæ, and I named fissures partially cleaving the laminæ secondary fissures. The primary fissures are disposed in a straight line or in an arc. The laminæ may be long and narrow, or they may be small oval bodies. Finally the whole organ may be raised up to form a body of an oval, crescentic or wedge shape. These forms occur as follows:—

A. Laminæ not elevated—*Cœlogenys*, *Simia*, *Gorilla*.
B. Laminæ elevated—most Mammals.
C. Lateral organs elevated in toto—*Lemur*, *Lepus*.

The form of the organs is of value for purposes of classification, as is shown in section 2 of this paper.

The slits may have no diverticula from them, or there may be several recesses, which, as they are lined by bulb-containing epithelium, extend the surface available for the performance of the gustatory function. These are very well marked in the Racoon.

In all adult animals the taste-buds lie down in the laminæ bounding the sulci. In the new-born child they also occur on the summits of the laminæ (11, and text-fig. 36), but they diminish as age advances. So we have here another example of the degenerative changes which occur with advancing years in the human tongue. It probably occurs in other Mammals as well.

In the Caviidæ the vallate papillæ and lateral organs resemble one another macroscopically.

The following conclusions can be drawn from a study of the circumvallate papillæ and lateral organs:—

1. The commonest pattern is three vallate papillæ in a triangle with the apex directed backwards. These have been termed the

central or apical papilla and the basal or lateral papillæ. This type is present in members of all Orders except the Monotremata and Ungulata, and it is the primitive type. Next in frequency is a pair of papillæ, the central papilla being absent. The type in which the central papilla alone is present is not very widely distributed, for it only occurs in the Muridæ and in some examples of *Macropus*, *Phascolarctos* and *Aotus*. The remaining types of most frequent occurrence are the V and several pairs of papillæ in a chevron. These can be derived from the triangle by filling in of the side limbs by papillæ, thus giving the V-type, and by loss of the apical papillæ of the V, thus forming the chevron.

2. In the lower Orders the number of patterns is small, whereas it is large in the higher ones, as can be seen by comparing the Monotremata, Marsupialia, Insectivora and Edentata with the Carnivora, Ungulata and Primates. Not only so, but the species in the lower Orders have a smaller range of individual variation than those in the higher ones.

3. When a group of animals has one fixed papillary pattern, the number of papillæ may vary in individuals.

4. It is impossible to correlate the papillary pattern with the type of food, as can be seen from the following examples:—

a. Man consumes a more varied diet than any other Mammal, and he never has any other pattern than a V; the only variations which he exhibits is the number of papillæ in the V.

b. Animals which consume one kind of diet may have several patterns.

c. The same pattern exists in frugivorous, phyllophagous, carnivorous or insectivorous animals. And that type is usually the primitive triangle.

5. There is no fixed relation between the papillary pattern and the degree of specialization of the species in each Order. Thus a primitive species may have more patterns than a specialized one, or *vice versa*; or the type may be the same in all species. In the Marsupialia, Edentata and Rodentia the primitive species have the same patterns as the specialized ones; in the Carnivora there is no fixed rule; in the Insectivora and Primates the primitive species have fewer patterns than the more advanced forms; and in the Ungulata the variations affect only the number of papillæ.

6. In the Marsupialia the pattern is constant, but the papillæ themselves show grades of specialization. Some papillæ are of the low Marsupial type, but others approximate to those in the higher Mammalia.

7. The Y and T types occur only in the Lemuridæ and Simiidæ.

8. The number of taste-buds in the vallate papillæ and lateral organs have been counted in many animals, but no generalizations can be made from the figures given.

9. There is no relation between the number of vallate papillæ and the presence or absence of lateral organs. Many species have

both structures, some have vallate papillæ and no organs, and *Hyrax* has organs and no papillæ. Nor can one associate the presence or absence of organs with particular kinds of diet.

10. The taste-buds in the human lateral organs diminish as age advances.

11. From the above it will be seen that there is no relation between the arrangement, presence or absence of the main gustatory organs (vallate papillæ and lateral organs) and diet, but there are varying degrees of persistence of primitive features.

12. There are probably, though we do not know them, differences in the physiological conditions of the taste-buds in animals consuming different kinds of diet.

The Conical Papillæ.

These papillæ are present in members of all Vertebrate Classes, and they are the most numerous of all lingual papillæ in the Mammalia. From the physiological point of view they are tactile or mechanical, but never gustatory in function. They vary in size, character, and arrangement. They occur on the oral part of the dorsum in all Mammals except the Cetacea, which have none. Sometimes they occur on the base of the tongue and on a bounding zone of the inferior surface.

Arrangement:—In most Mammals the papillæ are aggregated in a cluster of variable size on and behind the apex of the tongue; they are disposed in transverse rows on the middle of the dorsum; and they are in oblique chains posteriorly. They are thus disposed in a manner very similar to that exhibited by the fungiform papillæ, but they are also present on the centre. In *Pteropus* they are all in transverse rows, in *Mustela erminea* all the rows are oblique, and in *Cercopithecus æthiops* there are no regular rows. In the Primates, Sirenia and many Ungulata the apical cluster is large. On the base of the tongue there may be no definite arrangement or the papillæ may be in oblique chains.

Size:—There are various groupings according to size, and these are of value in classification. This matter is more fuliy considered in section 2 of this paper, so only a list of the types is given here:—

1. There is a steady increase in size from the apex of the tongue to the base and from the edges to the middle line. This is the commonest form.

2. The papillæ are small all over.

3. The papillæ on the oral part of the dorsum are small and those on the base are large.

4. The papillæ on the oral part are large, but those on the base are small or absent.

5. There are no papillæ.

6. The largest papillæ form a central patch on the oral part of the dorsum or on the apex of the tongue.

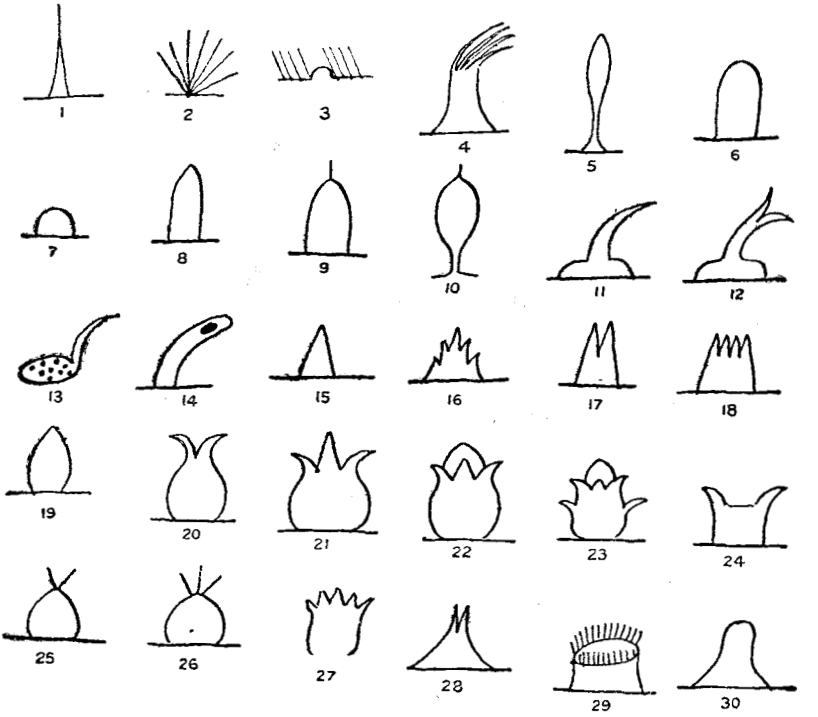
7. There is a gradual decrease from before backwards.

8. Papillæ may be present or absent on an intermolar eminence.

The grouping of papillæ on the sides and inferior surface of the tongue has no taxonomic value.

Cornification:—The conical papillæ are cornified to a variable extent, and confer a rough feeling on the dorsum. One side alone may be strongly cornified, or the whole papilla may be surrounded

Text-figure 35.



The macroscopic characters of the conical papillæ.

by a horny sheath, and the sheet is frequently thickest on its posterior aspect (e. g. *Ornithorhynchus*, *Canis*, *Erinaceus*). In *Erinaceus* there is also a horny septum passing down into the epithelium from the back of the papilla, and a smaller one descends from in front. Oppel reproduces Carlier's illustration showing the relation of the keratin sheath to the eleidin-containing cells in the deeper part of the epithelium. I have been unable to discover an account of the transformation of the eleidin into the keratin in the tongue.

Form of the Papillæ:—Numerous kinds of papillæ exist, but no form is characteristic of any Order, and transitional forms occur. Each group has simple and compound types, the latter possessing secondary papillæ.

Group. I. Filiform Papillæ.

Division A. Simple Papillæ (text-fig. 35):—

a. *Hair-like papillæ* (1). They taper from base to apex. A number may radiate from a single fixed point on the dorsum (2). They occur in several Orders. They help to distinguish *Halmaturus*, *Macropus*, *Petrogale* and *Dasyurus* from other Marsupials.

b. *Papillæ spinosæ* (11–13) in which horny spines project from an elevated base. Seen in *Didelphys* and Ailuroid Carnivora.

Division B. Compound Papillæ.

The stout papillary body is surmounted by a bunch of hair-like papillæ (fasciculate type) (4) or by a ring of hairs—the *coronate form* (29).

Group II. Cylindrical and Fusiform Papillæ.

Body cylindrical or fusiform and may have no secondary papillæ—simple type (5–8), or an apical hair may be present—the compound type (9, 10).

Group III. Globular Papillæ.

Only compound forms exist (20–23).

Group IV. Triangular Papillæ (15–18).

Simple forms have no secondary papillæ, but compound types have these papillæ or a divided apex.

In most Mammals the points of the papillæ are directed backwards, or backwards and inwards. But in many Ruminants there is an area on the back of the tongue in which the papillæ point in all directions.

The relations between the epithelium and the connective-tissue core of the papillæ vary in complexity. They are considered fully in section 3 of this paper.

When we consider the papillæ in the various Orders some interesting conclusions can be made. Thus:—

1. The lower Orders have simpler papillæ and a smaller range of types than the higher ones.

2. The increase in the complexity follows the same rules as the vallate and fungiform papillæ.

3. In some of the higher Orders the primitive species have simpler papillæ and a smaller range of types than the higher ones. This can be demonstrated as follows in the Primates:—

1. Lorises and Galagos have a less complex arrangement than the Lemuridæ.
2. The Platyrrhini are less complex than the Catarrhini.
3. The Lemuroidea are less complex than the Anthropoidea.

)n the inferior surface of the tongue the following structures
ıand consideration :—

1. Bounding papillary zone.
2. Frenal lamella.
3. Sublingua.
4. Plicæ fimbriatæ.
5. Lingual combs.

The *bounding papillary zone* is best marked in the Primates.
varies in extent and in its degree of development beneath the
x of the tongue. It has conical papillæ in every case, but
giform papillæ may be absent. The arrangement of the fungi-
n papillæ, when these are present, has been described above
e p. 709). Sometimes the zone is pigmented.
The *frenal lamella* is present in all Primates except Man and
ıe specimens of Orang. And it is absent in all other Mam-
lia. It is a triangular or complicated fold of mucous membrane
ich is set astride the frenum, and Wharton's ducts traverse it
ɔpen on its anterior border upper surface or under surface.
e apex is frequently cleft and one salivary duct opens on each
f. It is not to be mistaken for the sublingua, and some
hors including Burmeister have made that mistake. In *Nycti-*
us there are supplementary lamellæ. Pocock points out that
lamellæ overlie the ducts of the submaxillary and sublingual
nds, but I passed bristles through the ducts and lamellæ in
ny Primates.
. suggest that the occurrence of the lamellæ in the Lemuroidea,
'sioidea and Anthropoidea links these animals together as
isions of the Order Primates, and is against the view that the
nuroidea and Tarsioidea form a separate order Prosimiæ. And
s observation is to be added to existing observations on the
in and fœtal membranes which led anatomists to a similar
clusion.
The lamella is formed partly from the mucosa of the tongue
l partly from the mucosa of the floor of the mouth. It is not
ɛmnant of the sublingua, for it is present in a well-developed
m in the Lemuroidea, which have the best sublingua. I am
ıble to explain its true nature, for we do not possess a good
ɔwledge of the comparative embryology and comparative
'siology of the Mammalian mouth. It is, however, certain
t there is no structure in lower Vertebrata with which it can
homologized. It is probably connected in some way with the
elopment of the salivary apparatus. In Man and the Orang
ıay have been absorbed into the floor of the mouth, leaving
y the points projecting as the salivary papillæ.
Sublingua:—On the under surface of the tongue in some
rsupials, Rodents and Primates there are to be found complete
ıctures representing a complete sublingua or remnants thereof.
ey are of great importance, for they help us to understand

the phylogeny of the tongue. In the present section only the anatomical data are considered, the phylogenetic aspect being described later (p. 744).

The sublingual structures are as follows:—

1. A sublingual plate which is large or small.
2. A central ridge and plicæ fimbriatæ.
3. Plicæ alone.
4. A ridge alone.

All these varieties are really stages in the degeneration of the sublingua, and the stages can be seen in members of families, and at different periods in the age of individuals.

In the Marsupialia the sublingua is soft, and its apex is bound down to the under surface of the tongue. It shows various degrees of reduction even in genera of the same family. In the Didelphyidæ it is complete in all genera except *Philander*; its apex reaches as far forwards as the apex of the tongue, and it is split up into processes; on the ventral surface there is a median keel, and the edges are free posteriorly. In *Philander* the median keel alone exists. In the Peramelidæ the keel reaches the apex of the tongue, and the lateral parts are slightly reduced. The Dasyuridæ have a median keel reaching the apex of the tongue, and the lateral parts are reduced, but not as much as in the Peramelidæ; but the reduction is greater in *Sarcophilus* than in *Dasyurus*. It is thus evident that the reduction of the sublingua in the Polyprotodontia proceeds in the order Didelphyidæ, Dasyuridæ and Peramelidæ. It will, however, be shown later that, taking all characters of the tongue into consideration, the Dasyuridæ have more primitive tongues than other Polyprotodontia. In no forms is the reduction such that plicæ fimbriatæ are present, so the reduction involves the lateral parts of the sublingua, leaving the central parts alone.

In the Diprotodontia the sublingua presents greater variations than that in the Polyprotodontia. In *Cænolestes* and the Phalangeridæ the conditions are most primitive, there being a good central keel and lateral flanges. In the Macropodidæ the keel is present and the lateral parts are greatly reduced. In *Phascolomys* there is no keel, the central part of the sublingua is thin and the lateral parts are exceedingly thick. And in *Phascolarctos* there are merely diminutive plicæ fimbriatæ. Hence *Phascolomys*, and to a greater extent *Phascolarctos*, make a nearer approach to the Primates than to other Marsupialia in the characters of the sublingua.

In no Marsupial does the sublingua perform any function. It has no gustatory organs, and although muscle fibres pass into it in some species it is immobile. So we must regard it as entirely vestigial.

Gegenbaur did not observe any trace of the sublingua in the Insectivora, but Vogt and Yung saw it in several species. In

Talpa and *Rhynchocyon* there is a median ventral ridge which may be a remnant. Owen and Garrod described sublingual structures in *Tupaia*, and I found that it had a mixture of Lemuroid and Tarsioid features. Owen described plicæ fimbriatæ, but Garrod described a complete sublingua similar to that in *Chiromys*. Possibly *Tupaia* shows variations dependent on age.

Gregory stated that the sublingua in *Galeopithecus* is similar to that in *Tupaia*, but I did not see any trace of it in young or adult animals.

In all Chiroptera examined by myself there is no trace of the sublingua or its rudiments.

In the Rodentia I observed a sublingua in the Dormice alone, and this is the first occasion that the sublingua has been seen in this Order. In characters it resembles that in the Marsupialia, particularly *Phascolomys*. That is to say, it is a thick, soft, adherent, immobile plate without a median ventral keel.

The Edentata and Sirenia have no trace of the sublingua or of plicæ fimbriatæ.

In the Cetacea the sublingua is absent in the adult animal, but Schulte described a small triangular plate in the fœtus of *Balænoptera borealis*. In the young fœtus of *Physeter macrocephalus* examined by myself there were two ridges of mucous membrane which may represent plicæ fimbriatæ.

No sublingua nor plicæ fimbriatæ have been seen in the adult Carnivora, but Nussbaum observed plicæ in fœtal dogs measuring 4–5 cm.

In the Primates there is a great range of variation in the characters and degree of reduction of the sublingua.

In the Lemuroidea it is a structure which has become specialized for the purpose of cleaning the backs of the procumbent lower incisor teeth, which are used for combing the fur, the nails being useless for this action. It is consequently better developed than that in other Mammals, in which it is purely a vestigial structure. It is a strong, horny plate of a lyrate or quadrangular shape, whose apex anterior border is divided up into a variable number of strong, pointed denticles, which fit in between the teeth. On one or both of its upper and lower surfaces there is a ridge. In *Chiromys* the anterior border is smooth, but there is in its centre a strong hooked process. In many species it is quite free from the tongue, but in the others it adheres to it by its central part. The anterior part is always free. The consistence of the plate and the freedom of the anterior part distinguish it from the sublingua in the Marsupialia. The Lemurs can be distinguished from the Lorises, Galagos and *Chiromys* by the characters of the sublingua. In the fœtal *Chiromys* the sublingua is well developed, but its characters differ from those in the adult; they resemble the less specialized state in the Lemurs. The anterior border is serrated, and the strong hook is replaced by a soft, straight point.

When a section is made through the sublingua in the Lemuroidea it is seen how the stratum corneum is greatly thickened on the under surface of the sublingua, particularly in the median keel or keels. Muscle fibres pass into the sublingua. In *Stenops* and *Chiromys* there is an internal cartilaginous rod, but in *Lemur* that structure is absent.

In the Tarsioidea the lower incisor teeth are not procumbent, nor are they entirely used for combing the fur as in the Lemuroidea. The sublingua is reduced, soft, and only delimited laterally from the under surface of the tongue by a groove on each side. Anteriorly it has no denticles, but there is a small knob or blunt point lying in the position of the hook in *Chiromys*.

In none of the Platyrrhini examined by me was there any trace of the sublingua or its remnants. As regards the Cercopithecidæ I only saw plicæ fimbriatæ in one young *Cercopithecus patas* which still had its milk dentition. The Gibbons have neither a sublingua nor plicæ in the post-natal state, but Deniker saw a sublingua in the fœtus.

In all other Simiidæ and in the Hominidæ there is a well-marked sublingua or there are plicæ fimbriatæ, and these structures are better marked in youth than in adult life. In the Hominidæ they are better marked in the lower than in the higher races. In the child they have taste-buds, but these organs disappear, and that is one of the reasons why the child has a more acute gustatory sense than the adult. When the sublingua is reduced the central parts suffer more than the lateral parts, and a median ventral keel is usually absent.

The part played by the sublingua in evolution will be described later (p. 744).

From the above remarks the following conclusions can be drawn:—

1. The sublingua is functionless in the Marsupialia.
2. In the Lemuroidea it is functional throughout life.
3. In Man it is a gustatory organ in the early years.
4. Sufficient observations have been made to show that it is present in the fœtus in animals born without any trace of it. In existing works on the tongue one gets a disjointed view, for it is only described in Marsupials and Primates, as these observations make things more harmonious.
5. In the Marsupialia and Primates the primitive species have larger sublinguæ than the specialized ones.
6. The lower human races have larger sublinguæ than the higher ones.
7. Diminution in the sublingua is, therefore, a sign of specialization; and the degradation involves the central or lateral parts of the plate.
8. The Monotremes, in having no sublingua, are specialized animals.

Sublingual Combs:—In the Lemuroidea the sublingual plate has its apex or anterior border divided up into a variable number of sharp denticles, which fit into the interstices below the postero-superior aspects of the procumbent lower incisor teeth. And it appears, from the writings of Flower and Pocock, that their function is to free the teeth, which are employed for combing the fur, from scurf and other foreign material.

In many Ungulata there is a denticulated fold of mucous membrane on each side under the tongue. It is formed from the mucosa of the tongue and floor of the mouth. The processes into which the free edge is divided fit into the grooves between the backs of the incisor teeth. The processes are triangular in the Tylopoda and Tragulidæ, but they are long, sharp, spiny processes in the Bovidæ and Cervidæ. These folds are absent in the Perissodactyla, Suina, Proboscidea and Hyracoidea. So they exist in ruminating Ungulates.

Lingual Glands:—Three glandular masses may occur in the Mammalian tongue:—

1. Basal serous glands (Ebner's glands).
2. Basal mucous glands.
3. Apical gland of Nuhn or Blandin.

Serous glands, it is said, are related to the papillæ which bear taste-buds. But it is only in relation to the circumvallate papillæ and lateral organs that they are found. There are none connected to the fungiform papillæ. This is probably related to the position of the taste-buds. The buds in the fungiform papillæ come into close relation to the food while it lies on the surface of the tongue, but the constituents of the food can only excite the deeply-placed buds in the vallate papillæ and lateral organs after they have been dissolved in the glandular secretions. The glands open into the bases or outer sides of the fossæ of the vallate papillæ and into the bases of the sulci in the foliate papillæ. In a very few animals the glands are found up in the bodies of the papillæ. Their cells have large nuclei. Podwisotzky regarded them as salivary glands, but Ranvier considered them to be sensory rather than salivary in function. Flemming detected a granular structure in the cells, which he likened to appearances in the pancreatic cells.

Ranvier detected serous glands which have no relation to gustatory organs.

The *mucous glands* are found on the base of the tongue. Their cells have small nuclei and a thick basement membrane. They are modified tubular glands, whereas the serous glands are of the acinous type.

In many animals glandular orifices and pits are visible to the naked eye on the base of the tongue. And the following list shows some examples drawn from various Orders:—

Order Primates:—A few pits are present in the Hominidæ and

Simiidæ. They are numerous in the Cercopithecidæ, and they may be large or small, diffused all over or concentrated close to the tonsils and faucial pillars. They are particularly large in the Langurs and Guerezas. No pits are present in the Platyrrhini nor in the Lemuroidea and Tarsioidea.

Order Ungulata:—The Perissodactyla have numerous pits, but the Artiodactyla, Hyracoidea and Proboscidea have few or none.

Order Sirenia:—Dorsum has orifices singly or in pairs. None on inferior surface.

Order Cetacea:—Orifices more numerous than in any other Order. They are present all over the dorsum.

Order Carnivora:—Orifices numerous, scanty or absent.

Order Edentata:—Orifices only seen in *Bradypus*.

Rodents, Insectivores, Marsupials and Monotremes have few or no orifices.

It must, however, be emphasized that orifices do not demonstrate the true extent of lingual glands.

The Lytta.

Under this heading authors have included a number of more or less supporting structures, which have different origins and structure. They are present in very many, but not in all Mammals. They can be arranged in three groups:—

1. Lyttæ which are only specialized portions of the mucous membrane of the dorsum of the tongue—Horse.
2. Lyttæ which are differentiated parts of the septum of the tongue—Mole.
3. Lyttæ which are remnants of the os entoglossum of lower vertebrates. It is the only group which should really be termed the lytta. They are of two kinds:—

   a. Lyttæ of the tongue.
   b. Lyttæ of the sublingua.

The structural elements contained in the lytta are variable, for they include in each case one or more of the following—muscle, fat, fibrous tissue and cartilage.

The following list shows the presence or absence of lyttæ of the third group in the tongues of Mammals:—

Monotremata—Lytta present.
Marsupialia—Lytta absent.
Edentata—Lytta only present in *Manis*.
Rodentia—Lytta absent.
Carnivora—
Ailuroidea:—Small lytta lying in the anterior third of the tongue.
Cynoidea:—Large lytta may have a thread running back to the hyoid bone.

Arctoidea :—Lytta very large in *Cercoleptes* (*Potos*).
Pinnipedia :—Lytta absent.

Cetacea—Lytta absent.
Ungulata—No lytta of the third group. First type in Horse.
Hyracoidea and *Proboscidea*—No lytta.
Sirenia—No lytta.
Insectivora—Lytta of second type present in *Talpa*.
Primates—*Chiromys* has lingual and sublingual lyttæ.
Stenops has a sublingual lytta.
Tarsius has two lingual cartilage rudiments. None in sublingua.
Lyttæ absent in Lemuridæ and Anthropoidea.

B. The Value of the Tongue in Classification.

It must be strongly emphasized at the outset that lingual characters must not be used alone for purposes of classification. And any system which, based on them alone, would be suspect, especially if it differed from one which was drawn up after organs chosen from many parts of the body had been examined.

Several animals have such characteristic tongues that they can be recognized at a glance. And it is a curious fact that these animals are of particular interest from other points of view. They are *Ornithorhynchus*, *Phascolomys*, *Manis*, *Orycteropus*, *Hydrochœrus*, *Castor*, any Cetacean and Sirenian, *Hyrax*, *Proteles*, *Hyœna*, *Galeopithecus*, *Tarsius*, *Tupaia*, *Chiromys* and *Homo*.

Order **Primates.**

With the exception of *Homo* and some specimens of Orang all Primates have well-marked frenal lamellæ, and there are other points in which the tongue of the Orang is most similar to that in Man (2). If one finds in a given tongue that there are many fungiform papillæ at the tip, no papillæ at all on the base, several vallate papillæ in a V, presence of lateral organs and traces of a soft sublingua one can decide that it belongs to *Homo* or *Simia*. And one distinguishes between them by the characters of the lateral organs (2). If one gets an Orang tongue with frenal lamellæ the distinction is still further emphasized.

The other Primates from *Lemur* up to *Gorilla* have well-marked frenal lamellæ.

The Lemuroidea differ from the Tarsioidea and Anthropoidea in the characters of the sublingua as follows :—

Lemuroidea—sublingua functional, is free and has a variable number of processes on its anterior border.

Tarsioidea—sublingua not functional, is fixed and has one process.

Anthropoidea—sublingua not functional, is absent or only in traces.

The Lemuridæ can be distinguished in several ways from the Lorisidæ, Galagidæ and Chiromyidæ (**5**). But I am unable, from lack of material, to say anything about the Indrisidæ.

It is difficult, and in the case of some specimens, apart from the characters of the sublingua, to distinguish the tongues of the Lorisidæ and Galagidæ from that of *Tarsius*.

As regards the Anthropoidea the tongues fall into four groups:—

1. Platyrrhini.
2. Cercopithecidæ.
3. Hylobatidæ.
4. Gorilla and Chimpanzee.

The separation of the Gibbons is not in accordance with text-book teaching, but many anatomists believe that the Gibbons should form a separate family.

The Platyrrhini, Cercopithecidæ and Gibbons have no sublingua whatsoever. The Platyrrhini are distinguished from the Cercopithecidæ by the characters of the lateral organs and the absence of a thick apical cluster of fungiform papillæ. The Cercopithecidæ are distinguished from the Gibbons by the characters of the lateral organs, and by the fact that the Gibbons have their vallate papillæ in a Y, a form unknown in the Cercopithecidæ. The genera of the Platyrrhini and Cercopithecidæ have special lingual differences (**3**, **4**), but one cannot distinguish the species of the first three groups by lingual characters.

The Y type of vallate papillæ occurs in both Hylobatidæ and the Simiidæ except *Simia satyrus*.

The tongues of the Gorilla and Chimpanzee can be distinguished from one another by the characters of the lateral organs (**2**).

It is thus evident that the lingual characters support other views on the divisions of the Order Primates, and they are of value for distinguishing the genera of Monkeys from one another.

Anatomists have drawn attention to the resemblances between *Tupaia* and the Lemurs. On examining the tongues one finds that the characters present are a mixture of those in the Lemuroidea and *Tarsius*, together with some of those in the primitive Mammalian tongue.

Order **Insectivora.**

Of the suborder Menotyphla I could only examine the tongue of *Tupaia*, and I found that the good sublingua distinguishes it from the tongues of the Lipotyphla. As regards the Lipotyphla the tongues are not sufficiently distinctive for taxonomic purposes. Some structures are constant, but others vary; and I found that classifications of the tongues conflicted with those based on skeletal characters. The only forms which stand out prominently are *Erinaceus* and *Chrysochloris*.

Order **Chiroptera.**

Insufficient material was available for me to draw any conclusions of value.

Order **Dermoptera.**

Galeopithecus has Insectivore and Primate characters in the tongue, the Insectivore which it resembles being *Tupaia*.

Order **Carnivora.**

The value of the tongue in the classification of the Ailuroidea, Cynoidea, Arctoidea and Pinnipedia varies considerably (8).

In the Ailuroidea the tongue is of great value in classification. Indeed, it is of greater value in the classification of these animals than of any other Mammalian group. It enables us to distinguish the families from one another. In the Felidæ it enables us to arrange the large number of species in a number of groups. The most striking feature is the separation of the Domestic and Wild Cats, the Lynxes and the Caracal from the others. The grouping of the species by their lingual characters is almost identical to that drawn up by Pocock as the result of the examination of external and craniological characters.

In the Cynoidea the tongues present such homogeneous features that they are quite useless for classification. In the Arctoidea it is possible to distinguish the families from one another; it is possible to distinguish between the subfamilies; and it is possible to group the genera in each subfamily. The genera of the Pinnipedia have definite lingual characters, and these mark off *Trichechus* from the others.

Thus it can be seen that the value of the tongue in the classification of the Carnivora is considerable, and it agrees with classifications based on external and skeletal characters.

Order **Cetacea.**

It is only possible to distinguish the Mystacoceti from the Odontoceti by lingual characters, for the tongue gives no assistance in the characterization of families and genera.

Orders **Sirenia, Hyracoidea** and **Proboscidea.**

As regards the tongues the Sirenia and Hyracoidea have some features in common, but the Proboscidea differ entirely from the others. In fact, *Elephas* has peculiarities not found in other Mammals (7). The Sirenia have characteristic tongues, and one can distinguish that of the Manatee from that of the Dugong.

Order **Ungulata.**

It is a simple matter to distinguish between the tongues of the Perissodactyla and those of the Artiodactyla.

Of the Perissodactyla the Rhinocerotidæ have lingual characters which differ from those of the Equidæ and Tapiridæ.

with better binocular vision than *Lemur*. Its colour sense is probably absent. When inspecting food it moves its head about whereas *Lemur* usually keeps it steady. What it does in the dark we do not know, but the apex of the tongue does not get so much work to do as in *Lemur*. *Tarsius* is similar to *Nycticebus* in its lingual characters.

Lemur can use its tongue as an explorer and detector of taste impressions because of its procumbent lower incisors. The human infant can do so because of its toothless jaws, and its fungiform papillæ are more numerous than those in the adult. When teeth develop the hand places the food past the teeth and the tongue touches it.

The observations recorded in this paper demonstrate the close inter-relation of eye, tongue and hand; and the progressive increase in these structures is intimately related to the loss of olfaction and the steady increase in the neopallium.

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