
[Received August 8, 1921: Read November 8, 1921.]

INTRODUCTION.

In the five preceding papers of this series I described the structure of the tongues of the Primates and gave a short account of the physiology of the lingual glands. I also drew attention to a number of points bearing on the phylogeny of the tongue. In the present paper I have summarised these observations and pointed out how the lingual characters support systems of classification which have been based on external and skeletal characters.

SUMMARY.

Pigmentation.—Most of the pigmented forms are included in the Cebidae. The colour, which is yellow, green, brown or bluish-black, especially the latter, is uniformly distributed all over the dorsum, or the pigmented and colourless parts may form definite patterns; in Ateles griseus, for example, there is a white cross on a brown background. The vallate and fungiform papillae may be pigmented (e.g. in Hylobates lar) or colourless, but the lateral organs and central parts of the inferior surface of the tongue are always white. If several examples of each pigmented species are examined it will be seen that the colour varies considerably, so is of no value for purposes of classification. Most specimens of Cercopithecus patas, for example, have reddish-yellow tongues, but some tongues are colourless, and the fungiform papillae of Cercopithecus tantalus are yellow or colourless.

The bluish-black colour persists longest in preserving fluids.

Form and Proportions.—Most tongues are conical, but a few are oval, spatulate or rectangular; and shape is of no value for comparative purposes.

In most of the Primates the tongue is long and comparatively narrow, but in Anthropopithecus troglodytes and Gorilla gorilla the tongue of the young animal is relatively wider than that of the adult. I did not, however, see such variations in Cercopithecus patas or Macacus sinicus, of which I examined very young and adult examples.

Cunningham showed that the tongue of Simia satyrus resembles that of Homo most closely in the relative proportions of length and width.

The Apex is round, truncated or pointed, and may or may not have a notch, but the latter is usually absent from the fresh tongue. It is comparatively smooth, or roughened and tubercu-
lated by small conical and fungiform papillae. The relative quantities of fungiform papillae on and immediately behind the apex vary; in the Simiidae and Cercopithecidae they are numerous and thickly clustered, but in the other families they are few and discrete.

In some species of Lemur the apex exhibits a number of sharp-pointed processes prolonged forwards from ridges on the inferior surface of the tongue, but these vary even in different examples of each species.

Sulci and Ridges.—Few fresh tongues have median dorsal sulci on the oral part of the dorsum, but many preserved specimens do; and I observed a well-marked median sulcus on the pharyngeal part in Anthropopithecus troglodytes alone. The most pronounced mesial dorsal sulcus which I observed occurred in Mystax ursulus. Median dorsal ridges are present in some Lemuroidea and Hapalidae.

Wide, shallow transverse sulci separating low wide transverse ridges are present on the fresh tongues of Lemur catta and Hapale jacchus; and fine narrow sulci are seen in Gorilla gorilla and Perodicticus potto. Some of the fine sulci and ridges remind one of the patterns of fissures and ridges on the finger-tips.

The median ventral sulcus is present in most tongues, and is never an artefact induced by preserving fluids as is the dorsal one in bottled specimens. It is narrow and deep, or wide and shallow, and it frequently opens posteriorly into a triangular fossa which receives the upper end of the frenum. In some of the Lemuroidea it receives the median dorsal crest of the sublingua, and it recesses the crest on the dorsal surface of the frenal lamella of Cebus jatuellus.

In Gorilla gorilla, some species of Hylolates and some of the Lemuroidea it contains a fixed crest; and it has been stated that the crest is a remnant of the sublingua, but the presence of both these structures in some Lemurs would seem to disprove that theory.

Lateral Borders.—The edges of the tongue are sharp, or full and rounded, and increase in thickness from before backwards in most species. Those of Chiromys madagascariensis are more massive in proportion to the size of the tongue than those of any other species of the Primates. Of the Pithecoids Simia satyris and Anthropopithecus have the most massive lateral borders.

In Tarsius spectrum, Microcebus, Chiromys, and all Lorising and Galagidae the lateral borders are devoid of lateral organs and, as I hope to show in a future paper, this has an important bearing on phylogeny. In Gorilla gorilla and Simia satyris only small parts of the lateral organs are found on the lateral borders, but in all other Primates the greater part is found there.

The conical and fungiform papillae on the lateral borders are arranged in vertical rows and the points of the former are directed backwards.
Distribution of the Papillae.—In all Primates except some specimens of *Simia satyrus* and *Symphatangus syndactylus*, some Lemuroidea and *Homo*, papillae cover the entire dorsum, apex, lateral borders, and a bounding zone of the inferior surface. In all these species there are smooth non-papillary areas on the base of the tongue, and in the Lemurs the area is bisected by the median glosso-epiglottic fold.

The *ventral papillary zone* varies greatly in width, and its characters are of limited value for purposes of classification. It is wide in the Simiidae, Cercopithecidae, and in *Cebus, Ateles*, and *Lagothrix*, but is narrow or absent in all other Primates. In species with a wide zone the conical and fungiform papillae are numerous, but in those with a narrow zone there are few or no fungiforms. In *Gorilla gorilla* many of the fine transverse sulci on the dorsum cut the lateral borders and run inwards on the ventral papillary zone.

The *Circumvallate Papillae.*—In my paper on the tongues of the Cercopithecidae I showed that all the papillary patterns present in the family will be seen in most species if sufficient examples of each are examined. The whole series may quickly appear or it may be necessary to examine many. I am not prepared, however, to apply this rule to any other family except the Hapalidae, as insufficient specimens have come to hand.

In the following list of papillary patterns, P means two papillae forming a pair, and D.P. indicates four papillae arranged in a double pair. The Y type means that there are several papillae present and does not include forms in which the four papillae of a double pair are arranged in a Y.

<table>
<thead>
<tr>
<th>Family</th>
<th>Patterns of vallate papillae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simiidae</td>
<td>Y. T. V. Δ.</td>
</tr>
<tr>
<td>Cercopithecidae</td>
<td>T. V. Δ. D.P.</td>
</tr>
<tr>
<td>Cebidae</td>
<td>V. Δ. P. D.P.</td>
</tr>
<tr>
<td>Hapalidae</td>
<td>Δ.</td>
</tr>
<tr>
<td>Lemuridae</td>
<td>Y. Δ. D.P.</td>
</tr>
<tr>
<td>Lorisidae</td>
<td>Δ.</td>
</tr>
<tr>
<td>Galagidae</td>
<td>Δ. P.</td>
</tr>
<tr>
<td>Chiromyidae</td>
<td>Δ. P.</td>
</tr>
<tr>
<td>Tarsiidae</td>
<td>Three papillae arranged in a line.</td>
</tr>
</tbody>
</table>

One can see, therefore, that the Simiidae and Lemuridae are the only families whose tongues possess more than four papillae arranged in a Y, and it will be shown later that they differ from all other Primates in other respects.

The papillae are round or oval on plan and conical on elevation, with the bases of the cones projecting beyond the valleys.

The *Fungiform Papillae* stretch right across the dorsum, or are absent from the centre thereby forming a dorsal bounding zone. They form a cluster behind the apex, but are arranged in rows
of varying degrees of obliquity behind that. The apical cluster
is large in the Simiidae and Cercopithecidae, but in all other
families the transverse rows extend far forwards at its expense.
In the majority of tongues with large apical clusters there are
many fungiform papillae on the ventral papillary zone.

It has been shown by Tuckerman that the fungiform papillae
of the apical cluster have many taste-buds.

In some specimens of Anthropopithecus troglodytes there is a
row of prominent fungiform papillae occupying the mid-dorsal
line of the tongue and replacing the median dorsal sulcus.

It is sometimes impossible to tell whether a papilla at the
posterior part of the oral division of the dorsum is a large
fungiform or small vallate form, for fossa and vallum may be
indistinguishable even through a strong lens. Histological
examination is the only proof. The fungiform papillae may have
no taste-buds or these, if present, lie on the free upper surface of
the papilla; in the vallate papillae, on the other hand, the taste-
buds never lie on the free upper surface of the papilla, but are
deep down on one or both sides of the fossa.

In some tongues there are more fungiform papillae than are
visible to the naked eye, for some are entirely concealed by
overhanging conical papillae (e.g. Anthropopithecus troglodytes).

The fungiform papillae on the ventral zone may be thickly
clustered at the apex of the tongue and scanty further back, or
vice versa, and the examples, and the rows in which they are
arranged are close together or discrete.

From the point of view of classification the most important
features are the size of the apical dorsal cluster and the presence
or absence of the fungiform papillae on the ventral papillary zone.
Although their presence or absence in the centre of the oral
part of the dorsum varies greatly, it is not a character of
sufficient distinctness to be of value for purposes of classification.

The Conical Papillae vary in size and arrangement in the
different families, and there are three types of the former:

1. The papillae on the pharyngeal part of the tongue are
small: — Homo, Simia satyrus.

2. The papillae on the oral part of the tongue are compara-
tively small, but those on the pharyngeal part are large and
prominent: — Gorilla gorilla, Anthropopithecus troglodytes, all
species of Hylobates, all species of Lemur, Chiromyrs madagas-
cariensis, and Tarsius spectrums. This type also occurs in some
lower Mammalia.

3. The papillae gradually increase in size from the apex of the
tongue back to the epiglottis: — Cercopithecidae, Cebidae, Hapalidae,
Lorisidae, and Galagidae. This arrangement is also present in
Microcebus in which the vallate papillae form a triangle, so the
papillae are of value for distinguishing it from Lemur.

The arrangement of the papillae distinguishes most of the
Cebidae from all other families. In the latter they form a cluster
behind the apex and rows of varying degrees of obliquity behind
that, but in the Cebidae they are dotted irregularly all over the dorsum.

The tongues with smooth non-papillar areas on the pharyngeal part of the dorsum have been enumerated above.

In most Primates the points on the oral part of the dorsum look backwards or backwards and inwards, but in some specimens of *Simia satyrus* and *Cercopithecus ethiops* those on the centre of the oral part run in all directions.

In the Cebidae, Hapalidae, Lemuroidea, and Tarsioidea the conical papillae are mostly pointed, and cylindrical and globular forms are uncommon. In the other families there is a good admixture of all types.

The *Lateral Organs* present numerous forms and are of value for purposes of classification:

1. Organs absent: *Microcebus, Chiromys, Tarsius, the Lorisiidae and Galagidae*.

2. The laminae and sulci form ladder-like patterns on the dorsum of the tongue, and only their outer ends cut the lateral borders of the tongue: *Gorilla gorilla* and *Simia satyrus*.

3. The organs are convex towards the lateral vallate papillae: *Anthropopithecus troglodytes, Hylobates* (all species), *Lemur* (all species).

4. There are rows of short laminae and sulci on the lateral borders of the tongue: *Cercopithecidae*.

5. The inner borders of the organs are concave towards the lateral vallate papillae: *Cebidae*.

6. A few faint irregular laminae and sulci are present on the lateral borders of the tongue: *Hapalidae*.

In very few specimens did I find an equal number of laminae and sulci in the two organs of the same tongue. But one must be careful not to mistake simple folds of the mucosa at either end of the organs for laminae. Histological examination is the only true test in doubtful cases, for it reveals the presence of taste-buds in the true laminae.

In a few species of *Cercopithecus* one may find fungiform papillae situated on the laminae of the lateral organs.

The degree of protrusion of the laminae and depth of the sulci vary not only in different animals but in several examples of each.

The *Lingual Glands* are divided into apical and basal parts, but the former is most variable.

The *Apical Gland of Nuhn* is present only in *Homo* and *Simia satyrus*. Oppel believes that it is a piece which has become cut off from a forward prolongation of the basal glandular mass. The basal mass in the Marsupialia sends forwards two prolongations of variable stoutness, and it is possible that the Apical Gland of Nuhn has been cut off from one of these. If that were so it would support Gegenbaur's view that the tongues of the Primates have evolved from those of the Marsupialia.

The serous and mucous glands on the pharyngeal part of the
tongue are developed to an equal degree in the Primates, but the degree of development of the entire basal mass varies.

The pharyngeal part of the tongue possesses a variable degree of development of lymphoid nodules, and a variable number of orifices of pits and the ducts of glands; and the latter are of value for distinguishing the tongues of the various genera of the Cercopithecidae from one another. Orifices are visible in all Cercopithecidae, but are absent from most Cebidae, so are of classificatory importance when taken in conjunction with the characters of the lateral organs and mode of arrangement of the conical papilla. The following are the characters of the orifices in the Cercopithecidae:

Genus Presbytes:—Orifices larger and more patulous than in any other genus, and lie in the centres of large round glandular areas. The salivary glands are enormous.

Genus Cercopithecus:—Orifices well-marked, discrete and not patulous, and no white areas present around them.

Genus Macacus:—Orifices like pin points.

Genus Cercocebus:—Small duct orifices present at the sides of the base of the tongue.

Genus Papio:—Large duct orifices present at the sides of the base of the tongue.

In many of the Cebidae the nodules on the base form zones, with concave anterior borders, in front of the epiglottis, but I did not observe a similar condition in any other family.

The Frenal Lamella varies greatly in the Primates, and appears to belong to the floor of the mouth rather than to the tongue. It varies even in several examples of the same species, so is of limited value for purposes of classification.

In Homo, Simia satyrus, and some specimens of Symphatangus syndactylys it appears as two simple folds over Wharton's Ducts; but Mr. Pocock informs me that he observed two well-marked processes in a young Simia satyrus. I cannot believe, however, in conformity with my observations on the tongues of other animals, that reduction in the lamella is a change due to advancing years. In other species the lamella appears as a triangular or tongue-shaped process with an entire or divided apex and with both edges entire, serrated, or bearing small sharp points. The sharpest and most prominent points on the edges occur in Cercopithecus preussi and some specimens of Cebus fatuellus.

The Orifices of Wharton's Ducts vary in their position on the lamella as follows:

1. On the upper surface—Gorilla gorilla.
2. On the apex—Anthropopithecus troglodytes.
3. On the under surface—Pithecia satanas.

The apical position is the commonest form, however.

Tuckerman described a rich nerve plexus with peripheral nerve endings in the lamella of Ateles ater, and Gegenbaur considered that the endings were tactile in function. As this condition has
not been found in any other tongue there is insufficient material in which to work out its phylogenetic significance.

The Sublingua.—The various Lemuroidea are differentiated from one another by the shape, mobility, and characters of the crests and denticles as follows:—

1. Sublingua triangular or lyrate, has three ventral crests, and is very mobile. The apex is divided into a brushwork of denticles:—Lemur, Hapalemur, Indrisida.

2. Sublingua a large flat plate adherent to the under surface of the tongue by its central parts; no denticles present, but a strong keel-like ridge on its under surface projects forwards in the middle line:—Chiromys.

3. Sublingua large, tongue-shaped, but not quite so free as that of Lemur. There is only one median ventral crest, but the dorsal surface has a crest of variable prominence. This crest, the characters of the denticles, and the variations in the consistence of various parts of the sublingua are important:—

In Microcebus the sublingua is uniformly thick, the median dorsal crest is slight, and the denticles are moderately long.

In Nycticebus and Loris the central parts of the sublingua are thicker than the lateral parts, the median dorsal crest is small and the denticles are of moderate length; they are discrete in the former and close in the latter, but there is no essential difference between the sublingua of these genera.

In Perodicticus the median ventral crest is bifurcated posteriorly, the median dorsal crest is very prominent, and the denticles are long and slender.

In Microcebus, Galago, and Hemigalago the anterior border of the sublingua is broad, but in Loris and Nycticebus it is more or less pointed.

The Plicæ Fimbriatæ of the Simiidae are derived from the sublingua by a process of phylogenetic reduction, and I showed that the plice of Anthropopithecus troglodytes, with the intervening piece of mucosa form a soft triangular field resembling a sublingua; this is even more marked in the tongue of the new-born child, as described and figured by Gegenbaur. The plice of Phascolarctos cinereus, however, do not bound such an area.

The tongues of the Gibbons, Cercopithecidae, Cebidae, and Hapalidae illustrate the ultimate stage of reduction, for no traces of the sublingua or plica are present as a rule in the extra-uterine stage. In the fætal Gibbon, as shown by Deniker, there is a well-marked sublingua; and I observed two minute plice in a young Cercopithecus petae, so it is probable that the fætuses of all Primates have sublingual.

If one examines a series of human tongues at different ages, one finds that the new-born child has well-developed plice or an actual sublingua provided with taste-buds. As age advances the buds disappear and the plice diminish in size. These taste-buds probably account for the more acute sense of taste in the child. Experimental methods also demonstrate that the sense of taste
elicited by applications of solutions to the centre of the oral part of the dorsum diminishes as age advances.

This atrophy of structure following loss of function may have played an important part in the reduction in and ultimate loss of the primitive Mammalian tongue.

The Lytta.—Two forms are to be recognised:—The lytta of the tongue and the lytta of the sublingua. And Gegenbaur showed that the latter, when present, appears in one of two forms. In *Stenops* it forms a strong central supporting rod, but in *Tarsoidea* it is double. In *Lemur* it is absent altogether. Owen described the keel on the ventral surface of the sublingua as the lytta, but sections through the tongue show a well-marked lytta inside; it is connected in the middle to the sublingua.

**Classification.**

The structures which are of value for purposes of classification are:

1. The number and arrangement of the vallate papillae.
2. The arrangement of the conical papillae on the oral part of the dorsum.
3. The mode in which the conical papillae increase in size from before backwards.
4. The size of the cluster of fungiform papillae on the dorsum behind the apex of the tongue.
5. The characters of the lateral organs.
6. The width of the ventral papillary zone, with the number, characters, and arrangement of its papillae.
7. The presence or absence and characters of the lyttae of tongue and sublingua.
8. The presence or absence of the apical gland of Nuhn, and the characters of the orifices of ducts and pits on the pharyngeal part of the dorsum.
9. The sublingua and plicae fimbriatae.

These features are of specific value in the case of all the Simiidae, except *Hylobates*, and many of the Lemuroidea, but they are of generic value only in all other Primates. They lend additional weight to some schemes of classification based on external and skeletal characters; in some cases they help us to settle points which are not supported by a large body of very conclusive evidence.

The tongue of *Simia satyrus* resembles that of *Homo* most closely. Both have rounded apices, and their form and general proportions are similar. They have no large conical papillae on the base of the tongue, and their vallate papillae form a V. The frenal lamellae are two small folds over Wharton's Ducts, and their plicae fimbriatae are equally developed, but smaller than those of other Primates; and they are the only Primates possessing an Apical Gland of Nuhn. In *Simia satyrus* the lateral
organs are better developed, and the conical papillæ on the oral part of the dorsum include more pointed forms, but Homo alone of all the Primates possesses a foramen cecum.

The ladder-like patterns formed by the lateral organs distinguish Simia satyrus and Gorilla gorilla from all other Simiæ which have organs convex towards the lateral vallate papillæ, but the tongue of Gorilla gorilla has enormous conical papillæ on the pharyngeal part of the tongue, large plica fimbriata, a median ventral crest, and a large triangular frenul lamella; it has no Apical Gland of Nuhn, and its vallate papillæ form a V or Y.

The only character which really differentiates Anthropopithecus troglodytes on the one hand from Hylobates and Symphalangus on the other is the possession of plica fimbriata, for there is a similarity between them in all other features; and Hylobates has a well-marked, triangular, bifid lamella, whereas Symphalangus syndactylus has two small folds over Wharton's Duets similar to those of Homo and Simia satyrus. Their vallate papillæ form a Y.

In the Cercopithecidae, Cebidae, and Hapalidae the vallate papillæ never form a Y, the conical papillæ on the base of the tongue are never disproportionately large, and the lateral organs are neither ladder-like nor convex towards the lateral vallate papillæ. The chief differences between them lie in the characters of the lateral organs, the size of the apical cluster of fungiform papillæ, and the mode of arrangement of the conical papillæ on the oral part of the dorsum.

In the Cercopithecidae the lateral organs form rows of laminae and sulci on the lateral borders, the apical cluster of fungiform papillæ is large, and the conical papillæ on the oral part of the dorsum are regularly arranged. The genera are distinguished by the characters of the orifices of ducts and pits on the pharyngeal part of the dorsum (page 762).

In the Cebidae the inner borders of the lateral organs are concave towards the lateral vallate papillæ, the conical papillæ on the oral part of the dorsum are crowded together without any definite arrangement, and the apical cluster of fungiform papillæ is small.

The vallate papillæ are two in number, and there is a well-marked median sulcus on the pharyngeal part of the dorsum in Aotus, but in all other genera there are more than two vallate papillæ, but no basal dorsal sulcus.

The ventral papillary zone is wide, and has few fungiform papillæ in Lagothrix, but it has many papillæ in Ateles and Cebus. In Ateles the ventral fungiform papillæ are most numerous round the apex, but in Cebus they are most numerous farther back.

The ventral papillary zone is narrow in Pithecia, Alouatta, Callicebus, and Cacajao. It has many fungiform papillæ in Pithecia but few or none in the others; and Alouatta is the only
genus possessing large glandular orifices on the base of the tongue. Callitriches has many nodules and few orifices on the base, but Cacajao has neither.

The Hapalidae always have a vallate triangle and a few irregular laminae and sulci in their lateral organs. The pharyngeal part of the tongue occupies a relatively small part of the whole, and the ventral papillary zone is small or absent. The conical papillae are regularly arranged and the apical cluster of fungiform papillae is small. The lingual characters are not sufficiently distinctive to classify the genera.

The Lemuridea and Tarsiidea differ from the Simiae in the possession of a sublingua whose size, consistence, mobility, denticles, and minute structure vary in different families.

In the Tarsiidea the sublingua is soft, small, devoid of denticles, and only delimited at the sides from the under surface of the tongue by a narrow groove. There are no lateral organs, no large conical papillae, and few apical fungiform papillae.

In the Lemuridea the sublingua is large, horny, denticulated, and is more or less movable.

In Lemur and Hapalemur the sublingua is triangular or lyrate, very free, and has three ventral crests. No lyrta is present. The vallate papillae form a Y, and the conical papillae on the base are disproportionately large. The lateral organs are convex towards the lateral vallate papillae.

In Chiromys the sublingua is tongue-shaped, adherent by its central parts, has one ventral crest which is keel-like and nodulated. It has a lyrta inside the tongue. Vallate papillae form a pair or triangle, but never a Y. Conical papillae on base of tongue large. No lateral organs.

In Microcebus, the Lorisidae and Galagidae the sublingua is a flat plate with one median ventral crest and a variable dorsal crest. It varies in mobility, consistence, and denticles, and the value of these characters has already been described (page 763). The vallate papillae form a triangle, but never a Y, the conical papillae on the base of the tongue are not disproportionately large, and lateral organs are absent.

The special points arising from these notes on classification are:

1. The tongue of Simia satyrus resembles that of Homo.
2. Simia satyrus and Gorilla gorilla differ from all other Simiidae in the characters of the lateral organs, but there the resemblance between these two species stops.
3. The tongue of Hylabates differs from that of Anthropopithecus troglodytes in having no plicae.
4. The separation of Symphatangus from Hylabates.
5. The great value of the lateral organs for purposes of classification.
6. The value of the lingual glands for distinguishing between the genera of the Cercopithecidae.
7. The genera of the Hapalidae cannot be distinguished from one another by the characters of the tongue.
8. The tongues of *Lemur* and *Hapalemur* resemble those of the Simiidae most closely.
9. It is impossible to ally the tongue of *Microcebus* with those of *Lemur* and *Hapalemur*, but it resembles those of the Lorisidae and Galagidae.
10. The characters of the tongue at once distinguish the Lorises, Galagos, and Pottos from *Lemur*.
11. The tongue of *Tarsius* resembles neither those of the Simiidae nor of *Lemur*, and is hard to distinguish from those of the Lorisidae and Galagidae. It has three vallate papillae in a line, but these may be elements of a triangle which has been flattened out.
12. The keel on the under surface of the sublingua is not the true lytta as described by Owen.

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