

33. The Comparative Anatomy of the Tongues of the Mammalia.—VII. Cetacea, Sirenia, and Ungulata.
By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

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(Text-figures 25–30.)

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INTRODUCTION.

In papers * on the tongues of the Primates, I showed that the mobility is well marked, the gustatory and secretory organs are well developed, and the papillæ are not specialised for one kind of food. In the remaining mammalian orders one or more of these characters is highly developed, or greatly diminished, in accordance with the nature of the diet and mode of feeding. As the literature contains many descriptions of individual tongues, the remaining papers of this series will be limited to general descriptions of the different types, and special attention will be paid to physiology and classification.

The present paper is based on the examination of specimens in the Society's Prosectorium, the British Museum (Nat. Hist.), and the Museum of the Royal College of Surgeons.

Order CETACEA.

List of specimens examined.

Suborder MYSTACOCETI (Baleen Whales).

Pieces of tongue of *Balaena* and *Balenoptera*.

Suborder ODONTOCETI (Toothed Whales).

Sperm Whale (*Physeter macrocephalus*), Sowerby's Beaked Whale (*Mesoplodon bidens*), Beluga (*Delphinapterus leucas*), Porpoise (*Phocæna communis*), *Cephalorhynchus eutropia*, Risso's Dolphin (*Grampus griseus*), Common Dolphin (*Delphinus delphis*), Bottle-nosed Dolphin (*Tursiops tursio*), White-beaked Dolphin (*Lagenorhynchus albirostris*).

* P. Z. S. 1922, pp. 1–29, 277–322, 407–524, 741–767.

backwards, but there is a distinct intermolar eminence. In *Halicore*, on the other hand, the posterior two-thirds are greatly elevated as in some Ungulata.

The apex is rounded and entire in both genera, and the lateral borders are entire and devoid of lobules which characterise the Cetacean tongue. Neither notches nor sulci are present.

The mucosa on the oral part is plain, but that on the pharyngeal part has many folds. The base has glandular openings arranged singly or in pairs. There are no glands on the inferior surface, and no apical gland of Nuhn is present. The glands are less developed than in the Cetacea.

Papillæ:—In both genera there is, behind the apex, a cluster of retroverted cuticular spines. And as the tongue is not very mobile they are of great assistance in cropping the vegetation on which the animals live. Behind that cluster the dorsum is plain in *Manatus*, but covered with a velvety pile of small papillæ in *Halicore*. Owen (27) figures a plain dorsum behind the spines in the latter.

In *Manatus*, according to Owen (27), there are many vallate papillæ. In *Halicore* they are represented by clusters of pits.

Lateral Organs:—In *Manatus* (4) these are well-developed and appear as large cushions with numerous fissures. In *Halicore* these are absent.

The *Inferior Surface* has many large orifices in *Manatus*, and many embedded cylindrical bodies in *Halicore*, but I was unable to examine the latter microscopically.

The *Frenum* is slight, and there is no frenal lamella, foramen cæcum, lytta, sublingua, or plicæ fimbriatæ. No comb-like structures are found on the infero-lateral aspect.

Order UNGULATA.

Suborders PERISSODACTYLA and ARTIODACTYLA.

In most species the tongue is long, comparatively narrow, and very mobile. But it is broad and flat in *Rhinoceros*. It has the greatest mechanical power in *Giraffa*.

The apex is truncated, pointed or rounded, and may or may not have a notch. In many species it has clusters of hard mechanical papillæ, as in the Sirenia. It is free in all forms, and this gives it considerable mobility.

The lateral borders are full and rounded. They may be comparatively smooth, or covered with prominent conical and fungiform papillæ. But *Sus* is the only genus with lateral lobules similar to those in the Cetacea.

The anterior part of the tongue is flat and very mobile. Posterior to that is an intermolar eminence which raises the food up to the molar teeth. Most posteriorly is a flat, thin, more or less glandular part.

The intermolar elevation is present in all families. It is entire

in all except the Rhinoceros in which it is cleft. And it is covered with papillæ belonging to one or more of the conical, fungiform, and vallate series.

In the Perissodactyla it is well-marked, but low and flat. It has only conical papillæ in *Equus caballus*. In *Tapirus indicus* it has both conical and fungiform papillæ. In *Rhinoceros* clusters of vallate papillæ cover its halves.

In the Suina it is also flat. And both conical and fungiform papillæ are present.

The Camelidæ have well-marked eminences. And they possess large vallate and very hard projecting conical papillæ in the Llama.

In the Cervidæ and Bovidæ the prominent eminence has very hard conical and fungiform papillæ, and the former vary considerably in size and shape. Clusters of vallate papillæ may invade the sides of the eminence. I did not examine a sufficiently large series of tongues to draw conclusions as to their value for purposes of classification.

The eminence is prominent in *Tragulus*, but flat in *Hyomoschus*.

When the posterior third of the tongue is examined it is seen how glandular orifices are numerous in the Perissodactyla, but few or absent in all other forms. And the characters of these structures in the different Mammalian orders, with special reference to the relation between their size and that of other parts of the oral glandular apparatus, have already been described.

It is seen in this paper that the Cetacea, which have no salivary glands, have large lingual glands; the Sirenia, which have small salivary glands, have fewer glands; and the Ungulata, with good salivary glands, have few lingual glands. Also the Perissodactyla have larger lingual glands than the Ruminantia.

Circumvallate Papillæ (text-fig. 30 A):—The number and arrangement vary, and the following patterns were observed by myself:—

1. No papillæ.
2. A pair of papillæ.
3. Several papillæ in a straight line, or wide-angled V.
4. Rows of papillæ on each side of the tongue.
5. Clusters or fields of papillæ.

In the Perissodactyla there are two large papillæ in *Equus caballus*, *E. asinus*, and *E. chapmani*, but several observers noted three in *E. caballus*. Mayer (22) described a pair in *Tapirus americanus*, but I noted several in a straight line or wide-angled V in *T. americanus*, *T. indicus*, and *T. bairdi*. In *Rhinoceros* there is a field of ten papillæ on each side of the tongue.

In the Suina there is a pair of papillæ in *Sus scrofa*, *S. babi-russa*, *Potamochoerus penicillatus*, *Phacochoerus celiani*, and *Dicotyles torquatus*. Schwalbe (30) recorded three papillæ in *Sus scrofa*.

The Tylopoda have the largest vallate papillæ, and they are arranged in two converging lines on the narrow intermolar eminence. In *Camelus dromedarius* there are seven on each side in a single chain. But Mayer (22) stated that the seven in *C. bactrianus* are in two rows on each side—an inner one with three papillæ, and an outer one with four. In *Auchenia* the numbers of papillæ are not identical in each row.

The Tragulidæ have types of papillæ which are not found in any other group. There is a pair of long furrowed papillæ surrounded by a patulous fossa in both *Tragulus* and *Hyomochus*; but Flower (14) described many small papillæ in the latter.

The tongue in *Giraffa* has more papillæ than that of any other mammal. Münch and Tuckerman counted fifty, and Owen (27) described two fields, each with 15-20 elements.

In the Cervidæ the papillæ are usually arranged in two rows on each side. And the following numbers were observed by myself, or recorded by others:—

<i>Muntiacus muntiac</i>	6	on each side.	
<i>Cervus elaphus</i>	26-28		(26).
" <i>axis</i>	15-20	" "	
" <i>dybowski</i>	20	" "	
" <i>humilis</i>	10	" "	
<i>Capreolus caprea</i>	7-8	" "	(24).
<i>Rangifer tarandus</i> ...	5-6	" "	(22).
<i>Alces machlis</i>	18-20	" "	(33).
<i>Curiaacus virginianus</i>	13	" "	(33).
" <i>toltecus</i>	10-11	" "	(33).

In the Bovidæ there are rows of small papillæ on each side, and the number of rows are shown in the classification given below.

The following list contains the number of papillæ:—

<i>Bos taurus</i>	10-17	on each side.	
<i>Bison americanus</i>	18	" "	
" <i>bonasus</i>	11	on one side, and 6 on the other	(33).
<i>Bibos indicus</i>	17-19	on each side	(33).
<i>Budorcas taxicolor</i>	14	" "	(36).
<i>Connochætes gnu</i>	20	" "	(36).
<i>Cephalophus maxwelli</i>	7	" "	
" <i>dorsalis</i>	12	" "	
<i>Antilope mergens</i>	18-20	" "	(6).
<i>Rupicapra rupicapra</i>	10	" "	(19).
<i>Antilocapra americana</i>	36	" "	(33).
<i>Capra hircus</i>	12	" "	
" <i>ibex</i>	13	" "	
<i>Ovis aries</i>	12	" "	
<i>Ammotragus</i>	8	" "	

It is frequently difficult to determine by the naked eye whether a certain papilla is of the vallate or fungiform variety.

It appears, therefore, that the papillary patterns are distributed as follows:—

No papillæ	Hyracoidea.
A pair of papillæ	Equidæ, Suidæ, Phaco- cheridæ, Tragulidæ.
Papillæ in a line or V	Tapiridæ.
Papillæ in rows	Camelidæ, Cervidæ, and Bovidæ.
Papillæ in fields	Rhinocerotidæ and Giraffidæ.

The papillæ are oval, cylindrical, or conical with the bases of the cones projecting beyond the vallums. And the surface is smooth, granular, or lobulated (text-fig. 30 B.). The fossa is closed or patulous, and the vallum varies in prominence. Taste-buds are usually well-marked.

Fungiform Papillæ (text-fig. 30 C.E.F.):—The distribution on the dorsal and ventral surfaces varies in the different families. In appearance they are hemispherical, or almost pedunculated, and the surface is smooth, granular, or covered with processes. Many have rich supplies of taste-buds.

In the Perissodactyla they are not very numerous, but have the usual mammalian arrangement in clusters and rows; and those on the lateral borders are very numerous. In *Equus* there are none on the intermolar elevation, but there are prominent ones there in *Tapirus*. In neither genus is there a marked ventral papillary zone.

The tongues of the Suina have many papillæ on the dorsum, but few on the ventral surface. And those on the lateral borders may be very prominent.

In the Tylopoda the papillæ are not numerous on the dorsum, but they form a very wide ventral papillary zone. And in no other family is the latter so large.

In the Cervidæ there is a prominent cluster of papillæ behind the apex. Between it and the anterior extremity of the intermolar eminence there is an area possessing very few papillæ, but the latter is bounded laterally by papillary bands. The ventral papillæ are numerous, but small.

In the Bovidæ there is no thick apical, dorsal cluster, and the papillæ stretch right back from the apex to the intermolar eminence. They are only absent from a thin central strip of the dorsum. They are very regularly arranged. They are not numerous inferiorly in *Bison*, but they are numerous, small, and closely packed in *Antilope*, *Capra*, and *Ammotragus*.

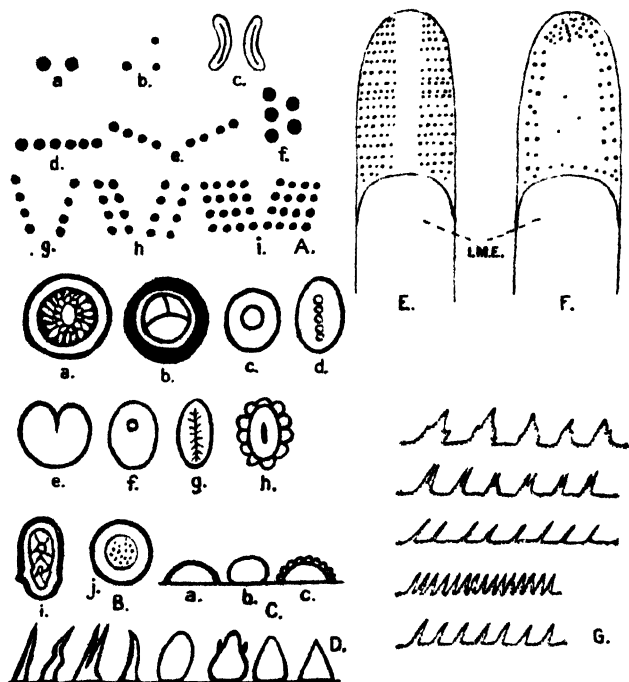
In the Tragulidæ the papillæ are numerous on the dorsum, and have the usual arrangement. They are absent only from a narrow central strip.

Conical Papillæ:—The teeth in the Ruminants are assisted by the action of the hard conical papillæ comminuting the food against the prominent palatal ridges.

In the *Perissodactyla* they are innumerable, slender, silky, and set very closely together. And their characters are similar over the entire dorsum.

In *Sus* the lateral borders of the tongue have innumerable long, club-shaped conical papillæ, as in the *Cetacea*. But no other genus of the *Suina* possesses them. In *Potamochoerus* the

Text-figure 30.



Tongues of the Ungulata. A (a-i): vallate papillary patterns; B (a-j): naked eye appearances of the vallate papillæ; C (a-c): fungiform papillæ; D: conical papillæ; E: fungiform papillæ of the Bovidæ; F: fungiform papillæ of the Cervidæ; I.M.E.: intermolar eminence; G: sublingual combs.

conical papillæ on the base are very large, pointed and directed backwards. In *Dicotyles* all the papillæ are very minute. The characters of the conical papillæ and lateral organs are useful for classifying the *Suina* (page 653).

In the *Camelidæ* the anterior part of the tongue has minute closely-set papillæ. But those on the intermolar elevation are large, flat, hard, and separated into two groups by a smooth central strip.

The Bovidæ and Cervidæ have papillæ similar to those in the Camelidæ, but those on the eminence are smaller, more numerous, and not divided into two groups.

In the Tragulidæ the conical papillæ on the dorsum are all small in *Tragulus*, but in *Hyomoschus* those on the base of the tongue are large, pointed, closely set, and directed backwards. Those on the base are not so disproportionately large in *Tragulus*.

The ventral papillary zone is narrow in the Perissodactyla, but wide in the Artiodactyla, especially the Tylopoda.

The conical papillæ are shown highly magnified in text-fig. 30 D.

Lateral Organs:—As Oppel (26) has collected the various published accounts, it is only necessary to show here their value for purposes of classification. They are frequently absent, and I would suggest that the lateral rows of circumvallate papillæ replace them in these cases.

In the Perissodactyla they are absent, according to Boulart and Pilliet (5), in *Tapirus americanus*, *Equus caballus*, and *Rhinoceros*. But they are well-marked in all the Tapiridæ examined by myself. Complete accounts of the organs have been published by Sertoli (32) and Hönigschmeid (19).

In the Suina they are present in *Sus*, *Phacochoærus*, and *Potamochoærus*, but they are absent in *Dicotyles*. The Babirusa has circular organs, but those in the other forms consist of rows of laminæ and sulci.

In the remaining Artiodactyla they are present in the Giraffidæ, Tragulidæ, and *Antilope mergens*, but they are absent in all others examined.

The *Lytta* is represented by a median ventral ridge, which varies in width and prominence, but it is not at all like that in the Carnivora. And sections show that it has a central core.

In *Tapirus indicus* it is narrow, prominent, and firm. But it is wide, flat, and softer in *Equus*; and the structure in the latter has already been described by Brühl (7). Owen (27) recorded its presence in *Rhinoceros*. In all Perissodactyla it does not widen much from before backwards.

In *Dicotyles* it forms a long, narrow isosceles triangle.

The Tylopoda, as exemplified by the Llama, have short, prominent crests with very thick mucosa.

In the Tragulidæ it is broad and flat, especially in *Hyomoschus*. But it is most variable in the Cervidæ and Bovidæ. In these it is narrow and sharp, low and broad, or absent. The appearances, however, are of no value for purposes of classification.

On the infero-lateral aspects of the tongue there may be long bands with divided free edges, or rows of separate processes. They may help to keep the interstices between the teeth clear, or they may help to mix the food and saliva. They have not been named, so I suggest the term "sublingual combs" for them. They are restricted to the attached part of the inferior

surface of the tongue. The following arrangements have been observed:—

1. Combs absent—*Perissodactyla*, *Suina*, *Hyracoidea*.
2. Edges divided into triangles—*Tylopoda*, *Tragulidæ*.
3. Long, more or less separate processes—*Bovidæ* and *Cervidæ*.

Some forms are shown in text-fig. 30.

The *frenum* is always present, and permits the tongue to be very mobile. But there is no trace of a frenal lamella.

There is no trace of a foramen cæcum, sublingua or plicæ fimbriatæ, and the apical gland of Nuhn is present only in *Ovis aries*.

It has been the object of the above summary of the characters of the tongues of the Ungulata to show their value for purposes of classification. And they have been arranged schematically as follows. From that system it will be seen that the characters of the tongue are a useful addition to the external and skeletal characters at present in use.

Classification.—The following characters are valuable for purposes of classification:—1. Character of the orifices of glands on the base. 2. Nature of the intermolar eminence and its papillæ. 3. Arrangement of the vallate papillæ. 4. Lateral organs. 5. Sublingual combs. 6. Distribution of conical and fungiform papillæ.

Suborder PERISSODACTYLA.

Numerous orifices of glands on base. No combs. Conical papillæ silky and closely-set. Ventral papillary zone very small or absent.

- | | |
|--|--------------------|
| A. Intermolar eminence cleft. Vallate papillæ in fields. No lateral organs | <i>Rhinoceros.</i> |
| B. Eminence low, flat, and entire. | |
| <i>a.</i> A pair of vallate papillæ. No lateral organs. No fungiform papillæ on eminence | <i>Equus.</i> |
| <i>b.</i> Vallate papillæ form a row or V. Lateral organs present. Large fungiforms on eminence..... | <i>Tapirus.</i> |

Suborder ARTIODACTYLA.

Few or no orifices of glands on base. Combs variable. Conical papillæ hard and not so closely set. Ventral papillary zone well-marked.

- | | |
|---|----------------------|
| A. No sublingual combs. Two vallate papillæ. | |
| <i>a.</i> Edges of tongue have long processes | <i>Sus.</i> |
| <i>b.</i> No long processes present. | |
| <i>i.</i> Papillæ on base immense | <i>Potamocharus.</i> |
| <i>ii.</i> Papillæ on base not immense. | |
| <i>a'.</i> Lateral organs present | <i>Phacocharus.</i> |
| <i>b'.</i> No lateral organs | <i>Dicotyles.</i> |

B. Sublingual combs present.

- a. A pair of long, narrow vallate papillæ.
- i. Basal conical papillæ small..... *Tragulus.*
 - ii. Basal conical papillæ very large *Hyomochus.*
- b. A single row of immense vallate papillæ on each side... *Camelus, Auchenia.*
- c. One or more rows of small vallate papillæ on each side.
- i. Fungiform papillæ absent from an extensive area in front of the intermolar eminence. Two rows of vallate papillæ CREVIDÆ.
 - ii. Fungiform papillæ stretch right back to eminence, but are absent from a central strip on the anterior part of the dorsum.
 - a'. One row of vallate papillæ on each side *Cephalophus.*
 - b'. Two rows on each side *Bos, Ovibos, Bison, Connochaetes, Strepsiceros, Antilope.*
 - c'. Four rows on each side *Budorcas, Ovis.*

Suborder HYRACOIDEA.

The tongue in *Hyrax* has a low, flat elevation similar to that in *Halicore*, and the lateral organs are well-marked. There is no vallate papilla in several specimens examined by myself, and by Brücher (6), Gmelin (16), Munch (24), and Tuckerman (33). And there is no trace of a lytta. All conical papillæ are minute. The basal lingual glands have few orifices on the surface. It is evident, therefore, that the tongue has some affinities with those of the Sirenia. No sublingual combs are present.

Suborder PROBOSCIDEA.

The tongue is short and wide, and it corresponds to the intermolar elevation of the other Ungulata. The apex is bound down to the floor of the mouth, as in the Cetacea. In *E. indicus* Mayer (22) observed six papillæ, but Miall and Greenwood (23) recorded four. In the specimen examined by myself there were two on the right side and one on the left. In *E. africanus* Forbes (15) saw four papillæ on the right side, and three on the left, but Münch (24) observed three on each side. The lateral organs are well-developed, but their contained taste-buds are sometimes very few. No sublingual combs are present.

SUMMARY AND CONCLUSIONS.

1. The Cetacea have simpler tongues than any other mammals.
2. The tongues do not support the view of some authorities that there are affinities between the Cetacea and Ungulata. But the differences between them are due to the nature of the diet and the mode of feeding. And the nature of the food causes the Sirenian tongues to resemble those of the Ungulata in some points.

The essential differences between the Cetacea, Sirenia, Artiodactyla, and Perissodactyla are :—

Cetacea—Mobility slight. No gustatory organs. Glands numerous. An intermolar eminence is only present in some Mystacoceti. Few or no mechanical papillæ.

Sirenia—Mobility greater. Slight gustatory organs. Glands fewer. Small intermolar eminence. Mechanical papillæ present.

Artiodactyla and Perissodactyla—Mobility great. Well-marked gustatory organs. Glands variable, being numerous in the latter and few in the former. Intermolar eminence well-marked, but variable in size. Mechanical papillæ well-marked.

3. The characters of the tongue have several points in common in the Artiodactyla and Perissodactyla, but those of the Hyracoidea and Proboscidea are such as to separate them into groups by themselves. Of these the Hyracoidea have some resemblance to the Sirenia.

4. The Cetacea are the only mammals in which the tongues may lie far back in the mouth.

5. The tongues of the Mystacoceti differ from those of the Odontoceti.

6. The tongues of the Mystacoceti contain large quantities of oil, but this is absent in all other mammals.

7. The excessive development of cuticular spines on the anterior part of the tongue in the Sirenia allows great use to be made of the moderate mobility.

8. The Perissodactyla differ from the Artiodactyla in the characters of the glands on the base of the tongue.

9. Sublingual combs are only present in the Camelidæ, Tragulidæ, Cervidæ, and Bovidæ.

10. It is impossible to distinguish the genera of the Cervidæ from one another by the characters of the tongue.

11. The distribution of the fungiform papillæ is a good means of telling the Cervidæ from the Bovidæ.

12. The Hyrax and Cetacea are the only mammals in which I was unable to detect vallate papillæ.

13. The sheep (*Ovis aries*) is the only mammal below the Primates which possesses the apical gland of Nuhn.

14. The characters of the fungiform papillæ distinguish the deer from the antelopes.

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