THE UPPER LIP IN PLACENTAL MAMMALS

Observations on the Morphology of the
Upper Lip and Related Structures

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INTRODUCTION

The superior labial frenum in man is apparently of little or no functional importance, yet it is occasionally found as a large fleshy mass tethering the upper lip to the alveolar process between the upper central incisor teeth. The only explanation put forward to account for its presence (Bolk, 1921; Boyd, 1933) is that the frenum represents the vestiges of a structure found in the lower Primates. In an attempt to find out more about the human superior labial frenum, the morphological variations of the frenum in several other species of mammals were examined. However, as the initial enquiry developed, it became clear that the frenum could not be studied in isolation from surrounding structures such as the upper lip and the alveolar process supporting the incisor teeth. It also became apparent that several features of the human upper lip, including the philtrum and the vertical ridges on either side of it, are not found in other mammals. In order therefore to obtain a better understanding of the morphology of the human upper lip a systematic survey was made of the upper lip and its associated midline structures in as wide a range of mammals as possible. The findings of this survey are presented and then the upper lip and frenum in man are examined in the light of the variations found in other mammals.

REVIEW OF THE LITERATURE

Literature concerning the superior labial frenum is limited to that on the frenum in man except for passing references to its presence or absence as part of a general description of a particular species. Tait (1929) has established that the human superior labial frenum is relatively much more prominent in the infant than in most adults and that it is not necessarily associated with spacing between the central incisor teeth as was thought to be the case. The literature on the human superior labial frenum has been reviewed by Ceremello (1953) and Adams (1953) but these reviews simply confirm Tait's findings. Of the other features of the human upper lip, Monie and Cacciatore (1962) have shown that the philtrum does not represent the line of fusion of the paired fronto-nasal processes but appears some time after lip formation is complete. Duckworth (1910) has compared sagittal sections of the lips in man and several advanced Primates, showing that an extensive vermilion border of the lip is unique to man, while Dannenberg, Leider and Bass (1958) have shown that the labial tubercle is only a transient feature of the vermilion border of the upper lip in human infants.

The standard reference on the morphology of the upper lip in mammals is the article by Boyd (1933). He considers that the most primitive arrangement of the upper lip is where the hair-bearing skin is confined to the lateral portions of the lip and the central portion is composed of moist, naked skin - the rhinarium - extending down from the nares to fuse with the oral mucosa at the edge of the lip. In species showing an advance on this simple pattern there are differing degrees of encroachment, by the hairy skin of the lateral aspects of the lip, onto the central rhinarial skin until, in those species possessing the most advanced level of lip development, there is an unbroken strip of hairy skin separating the nares from the edge of the lip.

Apart from Boyd (1933), other references to the relationship of the upper lip and the rhinarium are confined to descriptions of a particular species e.g. Pocock (1914b) or Osman Hill (1953). The functional behaviour of the lip and snout in mammals does not appear to have been described in any detail except for the work of Hafez (1962) on domestic species.

Lip behaviour in man has been comprehensively discussed by Lightoller (1925). Other references to various aspects of the upper lip and rhinarium are given at appropriate points in the text.

MATERIAL AND METHODS

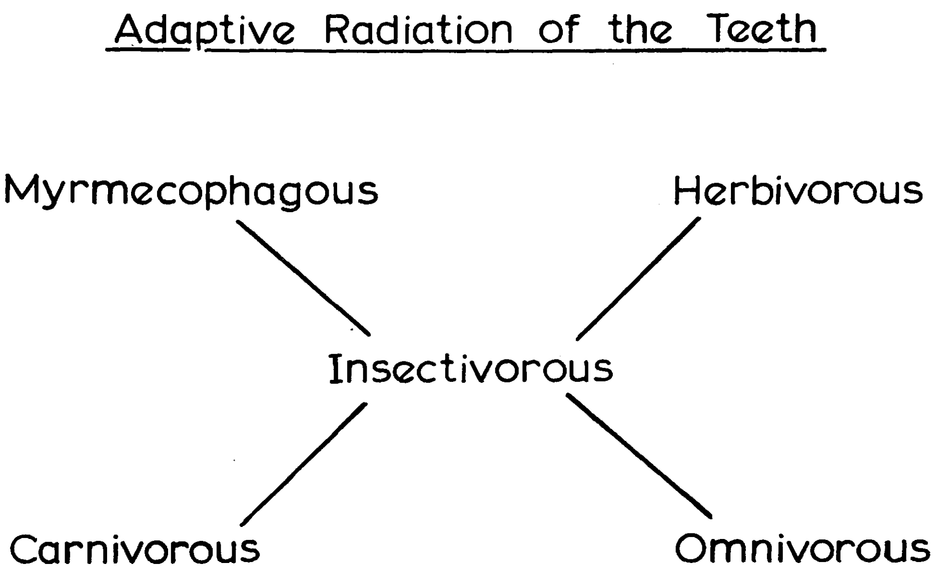
Whenever possible, use has been made of several different methods of studying each species. These methods include examination of (a) living specimens, (b) fresh dead specimens, (c) wet-preserved specimens, (d) dried or mounted specimens. Dissection has been undertaken where conditions allowed but, in the case of some of the smaller, more fragile specimens, fixation and sectioning has been employed. A definitive survey of all placental mammals is obviously not possible but it is felt that sufficient species have been described to provide a reasonable basis for discussion.

Several techniques of illustrating the material have been employed. Where sufficient detail can be shown in a photograph this has been the method of choice but in many instances, particularly in the case of smaller animals or where dissection has been done, half-tone drawings are used. Where sectioning has been necessary, a photomicrograph of a stained section is given in most instances.

In a systematic survey of this type, one or other of two approaches is possible. The order of presentation of the material may adhere strictly to that found in a given taxonomic system e.g. that of Simpson (1945). Alternatively, since a composite group of structures is being examined, species may be arranged in sequence to illustrate gradations of change in the structures. The second method has been employed in this study.

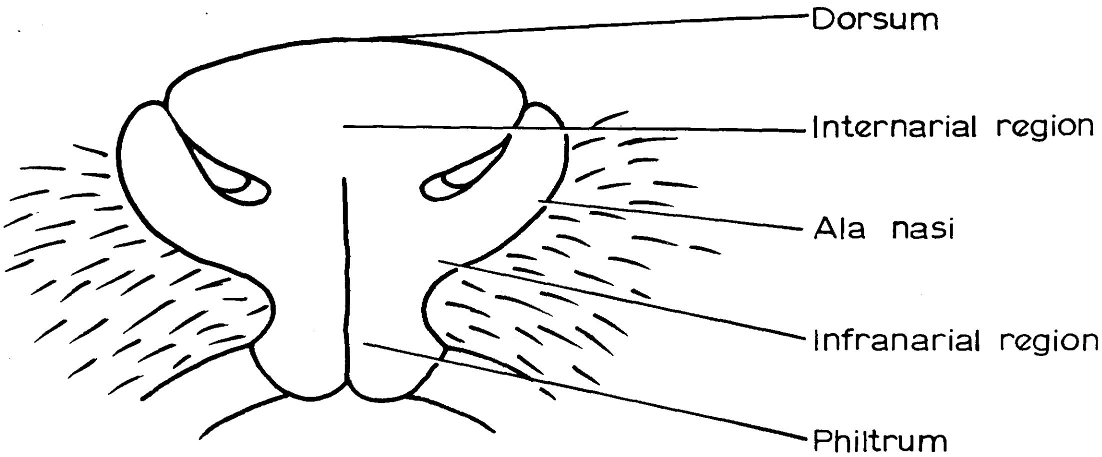
Lull (1948), when discussing adaptive radiation of the teeth in mammals, gives a plan of the main lines of development according to the dietary variations (Fig. 1). Since the structures under examination in this study are also involved in the process of feeding, the same general plan has been employed. It is not possible, however, to keep rigidly to this arrangement without creating some confusion. Each species is therefore placed in the dietary grouping predominant in its particular Order e.g. the Bear although more correctly described as omnivorous is grouped with the Carnivores. Similarly the Mole, which is predominantly carnivorous, is placed with the Insectivores. Each exception is dealt with as it arises.

The nomenclature employed is that of Simpson (1945) since this is currently widely accepted. The popular name of a species or genus is used where it is sufficiently accurate but in all such instances the correct



Redrawn from
R. S. Lull's "Organic Evolution" 1948.

Fig. 1.



SCHEME of PARTS of the RHINARIUM

Fig. 2. Diagram of the anterior surface of the snout of a typical Strepsirhine Primate.

zoological name is also given when the species is first mentioned. A glossary of some of the terms used is given below, together with a diagrammatic representation of the anterior part of the snout of a typical Strepsirhine Primate (Fig. 2), to assist identification of the parts. The definitions are those of Osman Hill (1953).

Rhinarium The area of naked moist skin around the external nares in most lower mammals. It can be divided into different parts as follows:-

Dorsum An area of variable extent on the dorsum of the apex nasi.

Infranarial Region This extends around the lower border of the external nares and varies considerably in size.

Internarial Region The area, continuous with the dorsum above and the infranarial region below, which separates the external nares.

Philtrum The median strip of rhinarial tissue which extends down from the infranarial area to the margin of the upper lip.

Detailed descriptions of lower mammals, such as those by Dobson (1882), are not available for every species discussed. Nomenclature of the muscles in some instances has therefore been arrived at by a process of analogy and an assessment of the probable action of each muscle.

OBSERVATIONS

INSECTIVOROUS SPECIES

Insectivorous placental mammals are mostly found in one Order, the Insectivores, although species which are partially insectivorous are found in other Orders. The Insectivores are a diverse assemblage of ancient mammals each specialised to some extent but with an underlying primitiveness which makes them extremely difficult to classify logically (Simpson, 1945). They are diphyodont and heterodont with a dental formula similar to or slightly reduced below that of the primitive mammalian formula i.e. $I\,\frac{3}{3}\;C\,\frac{1}{1}\;PM\,\frac{4}{4}\;M\,\frac{3}{3}$. An elongated, protruding snout is characteristic of most of the Insectivores (Huxley, 1880) and for the purposes of this study the species are arranged according to the extent of this protrusion with the short-snouted species being considered first.

Tree Shrews

Tupaia

One fresh dead specimen and two live specimens of *Tupaia minor* were examined. The rhinarium in *Tupaia* occupies a large portion of the anterior part of the upper jaw (Fig. 3). There is a shallow sagittal

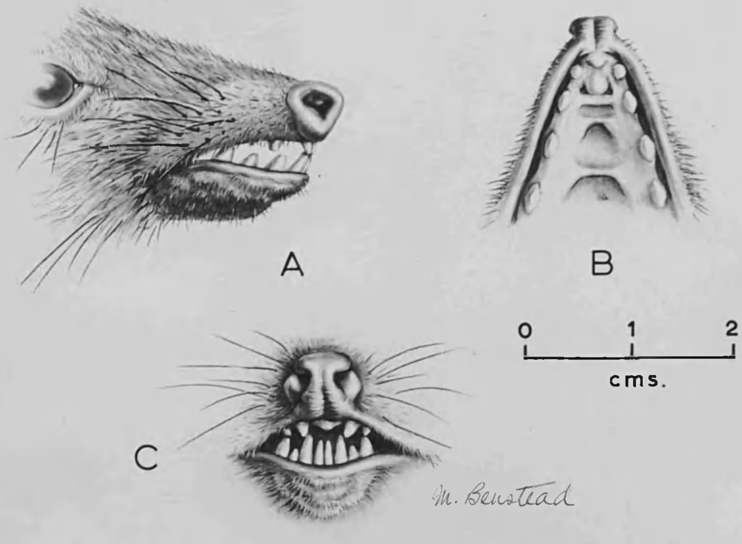


Fig. 3. Tree Shrew (Tupaia minor). Teeth not in occlusion.

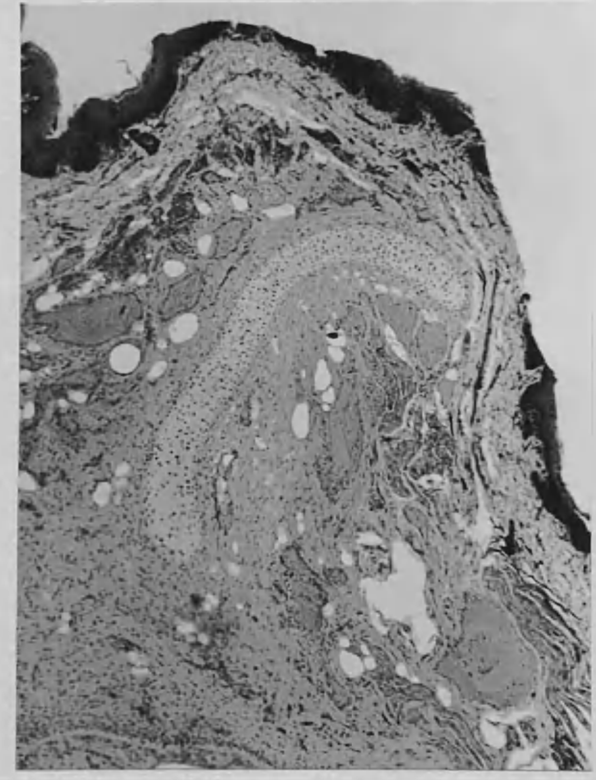


Fig. 4. Tree Shrew. Transverse section through upper lip. The superficial surface is at the top of the field with the central rhinarial groove to the left. Some transverse muscle fibres, cut longitudinally, can be seen on the lower right, stopping well short of the anterior surface. x32.

midline groove extending down the rhinarium from the internarial region to the lower border of the lip. At this point the groove is lost and the rhinarial mucosa fuses with the oral mucosa. There is no labial sulcus deep to the rhinarial portion of the upper lip. Just palatal to the rhinarium, in the midline, is the incisive papilla which forms a well-defined raised mass. It lies midway between and slightly labial to the two large central incisor teeth. These teeth have a simple conical shape but they are rather larger than the upper lateral incisors. The lower incisors, which are proclined, occlude between the upper central incisors when the teeth are brought together.

One specimen was fixed, sectioned in a plane parallel to the palatal surface and stained (Fig. 4). The loose fibrous tissue deep to the sagittal groove on the rhinarium lies anterior to the cartilage of the snout. This central zone has a number of wide, thin-walled blood vessels, probably venous sinuses, containing haemorrhagic debris. There is no muscle in this central area but some muscle fibres terminate near the lateral edge of the cartilage. These fibres are the most medial strands of the Orbicularis oris muscle which fails to reach the midline in *Tupaia* (Lightoller, 1934). The muscles of the upper lip are therefore confined to the lateral borders of the rhinarium.

Ptilocercus lowii

Only one mounted specimen was available. In the Pen-tailed Tree Shrew (*Ptilocercus lowii*) the relationship of the rhinarium to the upper incisor teeth and alveolar process is similar to that in *Tupaia* (Le Gros Clark, 1926) and apart from a greater degree of elongation of the bony snout in the Pen-tailed Tree Shrew the two species are very similar as regards the general morphology of the head.

Limnogale

One preserved specimen of *Limnogale* was examined. *Limnogale* is a true insectivore but unlike most of the Order it is an amphibian. This fact accounts for the modification observed in *Limnogale*. Instead of a sharp protruding snout there is a broad spatulate muzzle of considerable depth (Fig. 5). The rhinarium is much reduced in size and occupies a small area on the upper aspect of the muzzle. There is a narrow, grooved

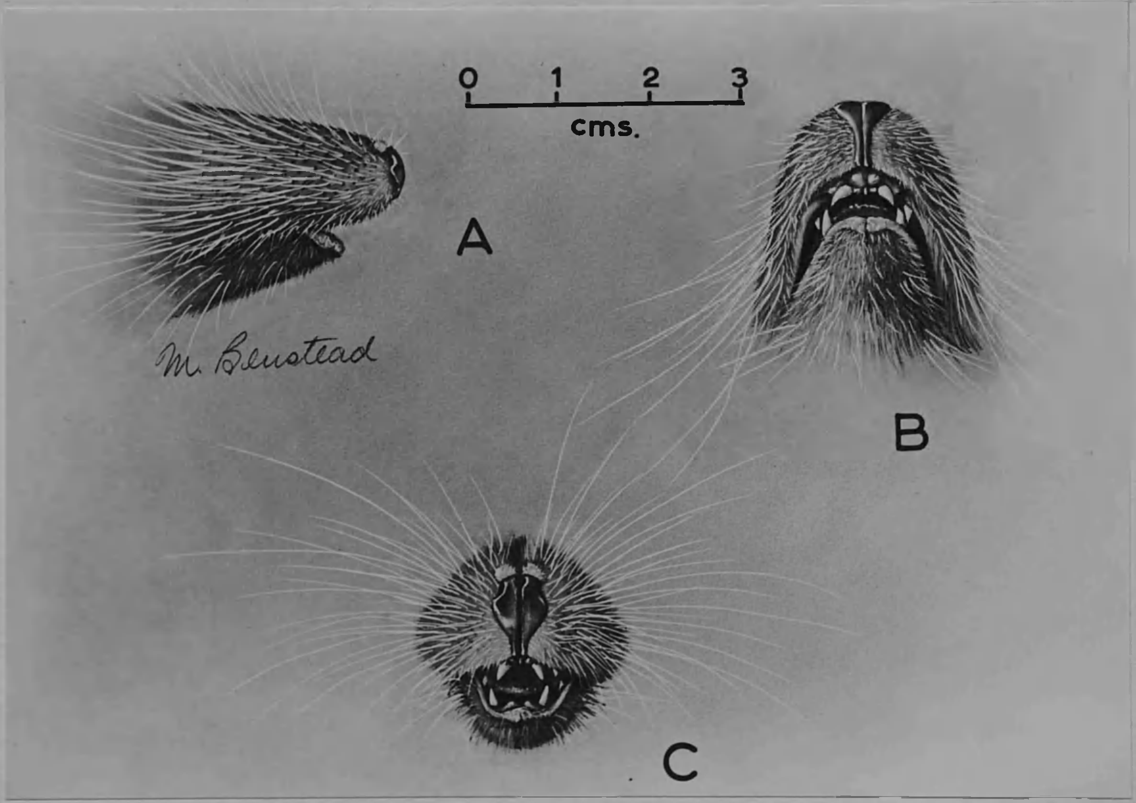


Fig. 5. Limnogale

philtrum extending from the rhinarium down the muzzle and then across the shallow labial sulcus between the lip and the alveolar process. It thus forms a superior labial frenum before ending by passing between the divergent central incisor teeth to the incisive papilla. The bulging mass of the upper lip on either side of the philtrum is covered by hair-bearing skin while there is considerable development of the mystacial vibrissae over all the anterior part of the muzzle. The nares open upwards just cranial to the rhinarium.

Potomogale

Only illustrations of Potomogale were available (Dobson,1882) but to judge by these the snout is similar to that of Limnogale although the rhinarial philtrum is apparently absent.

European Hedgehog

(Erinaceus europeus)

Three fresh dead specimens of Hedgehog were examined. The snout protrudes in front of the upper incisor teeth more than in the Tree Shrews and Limnogale. The rhinarium is a relatively large structure and is increased in size by convolution of the lateral narial borders (Fig. 6). There is a shallow groove starting in the infranarial region and extending

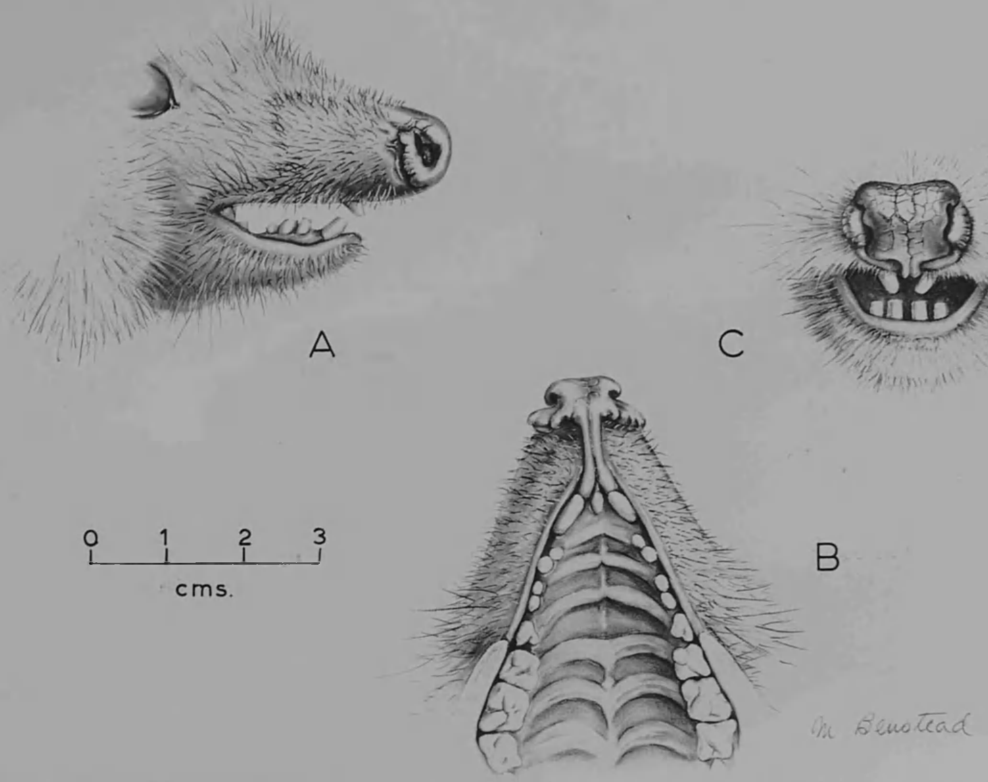


Fig. 6. European Hedgehog (Erinaceus europ.)

along the narrow, well-defined philtrum. At its oral end the philtrum divides completely, with each half passing into the alveolar process of the central incisor on that side. The incisive papilla lies midway between the two ridges of the divided philtrum. There is only a shallow sulcus on the lateral aspects of the lip and this is lost entirely where the philtrum is attached. The upper central incisors are conical in shape and are much larger than the remaining incisors. As in almost all the Insectivores the canine teeth are much reduced in size.

When the skin and mucous membrane are dissected off the underside of the snout, the Orbicularis oris muscle is seen to form the bulk of the upper lip (Fig. 7). Anteriorly, the muscle passes forwards to the lateral aspects of the central snout cartilage but its fibres stop short of the area covered by the philtrum. Tendons of the Zygomaticus major and minor muscles leave the anterior border of the Orbicularis oris muscle to pass forwards to the alar cartilage. A small muscle arises from the alveolar process of the central incisor and passes laterally into the Orbicularis oris muscle. This is probably the Depressor septi

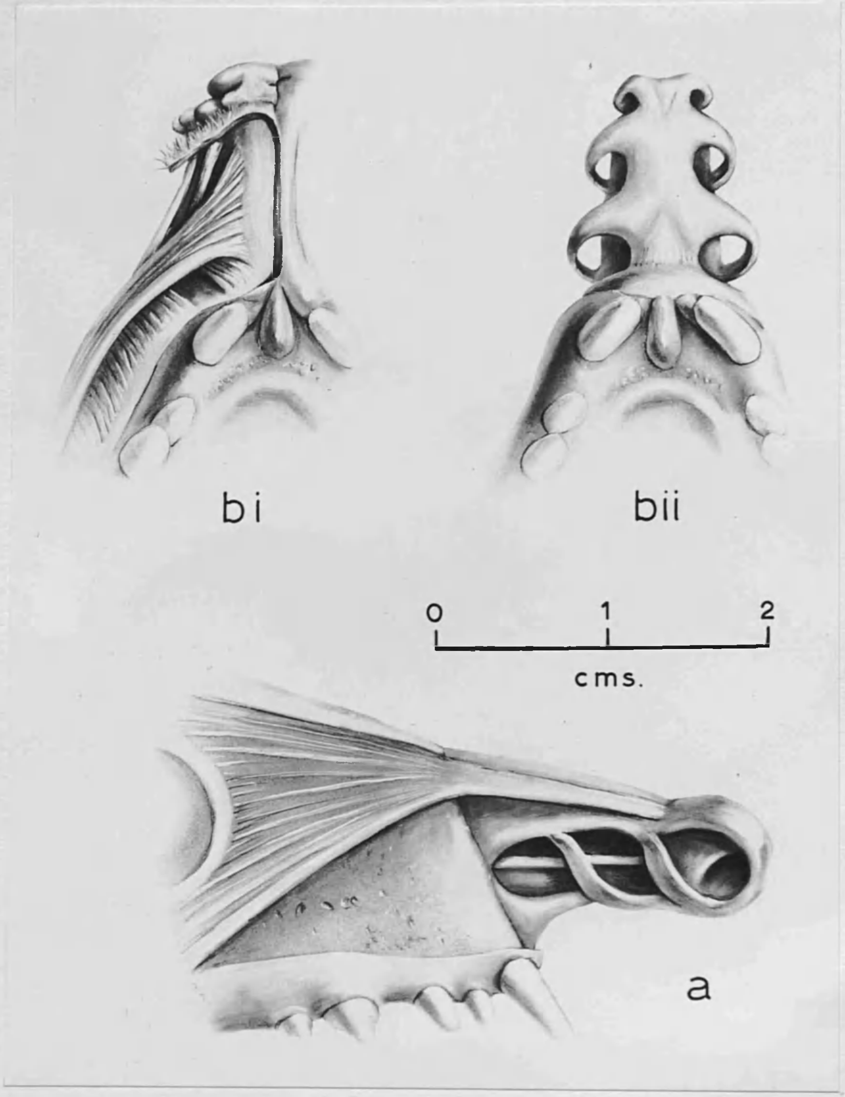


Fig. 7. Hedgehog. Superficial tissues removed to show distribution of the musculature and the central cartilaginous framework of the snout.

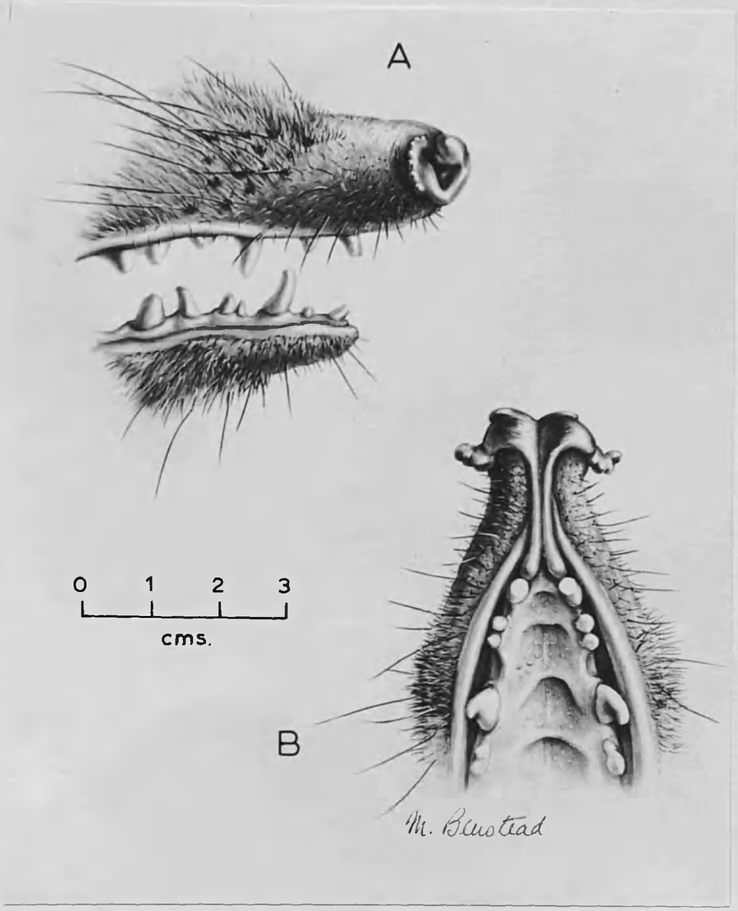


Fig. 8. Gymnura

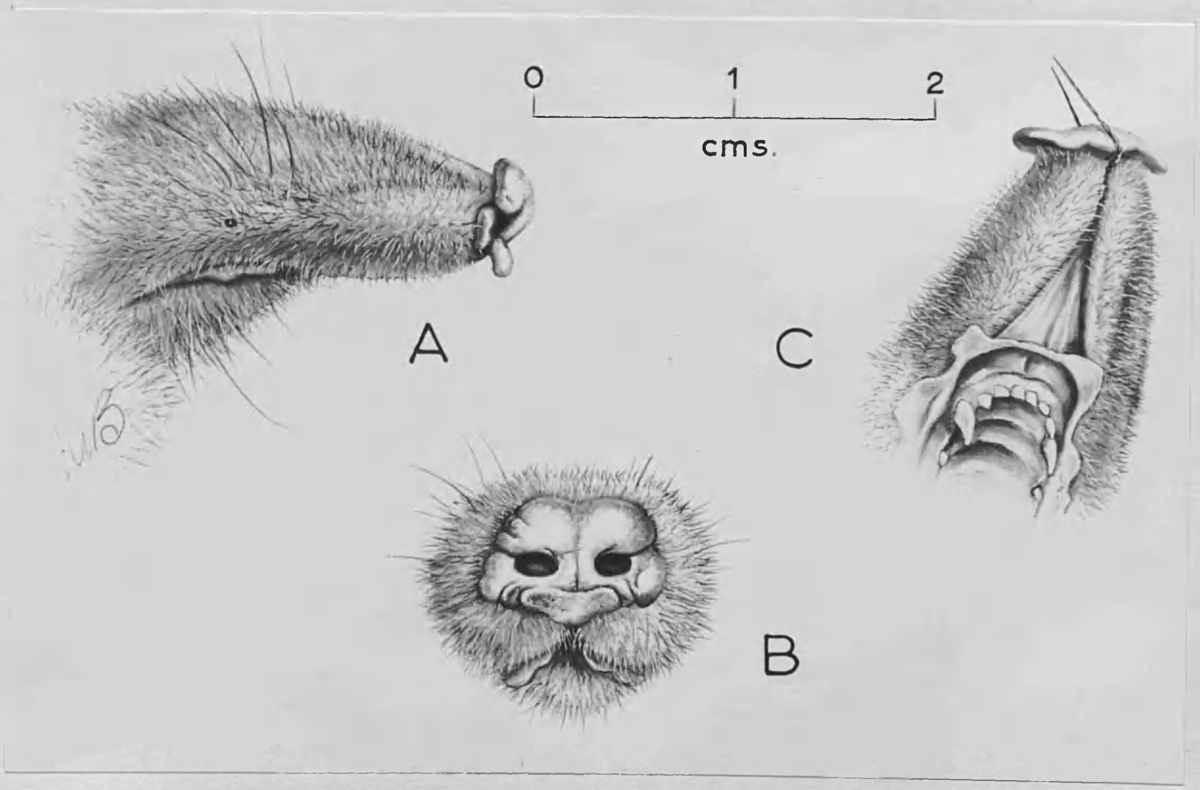


Fig. 9. European Mole (Talpa europ.)

muscle of the related Myogale (Dobson, 1882). The nasal cartilage is firmly attached to the bony part of the snout and is capable of only limited movement.

Gymnura

One dried specimen of Gymnura was available (Fig. 8). It bears a strong resemblance, as regards the snout, to the closely related Hedgehog although the lateral convolutions of the rhinarium are more pronounced.

European Mole

(Talpa europeus)

Three fresh specimens of European Mole were examined (Fig. 9). The snout is longer than that of the Hedgehog but is more massive than that of the Common Shrew (Fig. 10). The rhinarium is limited to a disc-like area reminiscent of that in the Pig but the hairy lip does not fuse in the midline underneath the snout as does that of the Pig. When the lip is reflected, a shallow groove, devoid of hair, is revealed separating the hair-bearing portions of the lip anteriorly. The two halves of the lip diverge as they approach the teeth and a triangular area of naked mucosa is formed bounded by the teeth and the margins of the lip. Within this triangle there is a fringe of mucous membrane forming what seems to be an inner lip. Anterior to the fringe are two slightly raised ridges of mucosa stretching anteriorly. The teeth are quite unlike those of the other Insectivores, with small conical incisors of equal size and large canines. This pattern is more akin to the carnivorous arrangement and in fact the Mole is partly carnivorous. It also differs from the other Insectivores in having almost no vibrissae and only rudimentary visual apparatus.

Common Shrew

(*Sorex vulgaris*)

Six fresh dead specimens of Common Shrew and one of the Water Shrew (*Neomys*) were examined, together with dried specimens of several other species. The Common Shrew can be taken as the type specimen. The rhinarium is situated at the tip of a long, flexible snout which is well supplied with vibrissae (Fig. 10). The extent of the rhinarial skin is less than in the Hedgehog but extends laterally to a greater degree than in the Mole.

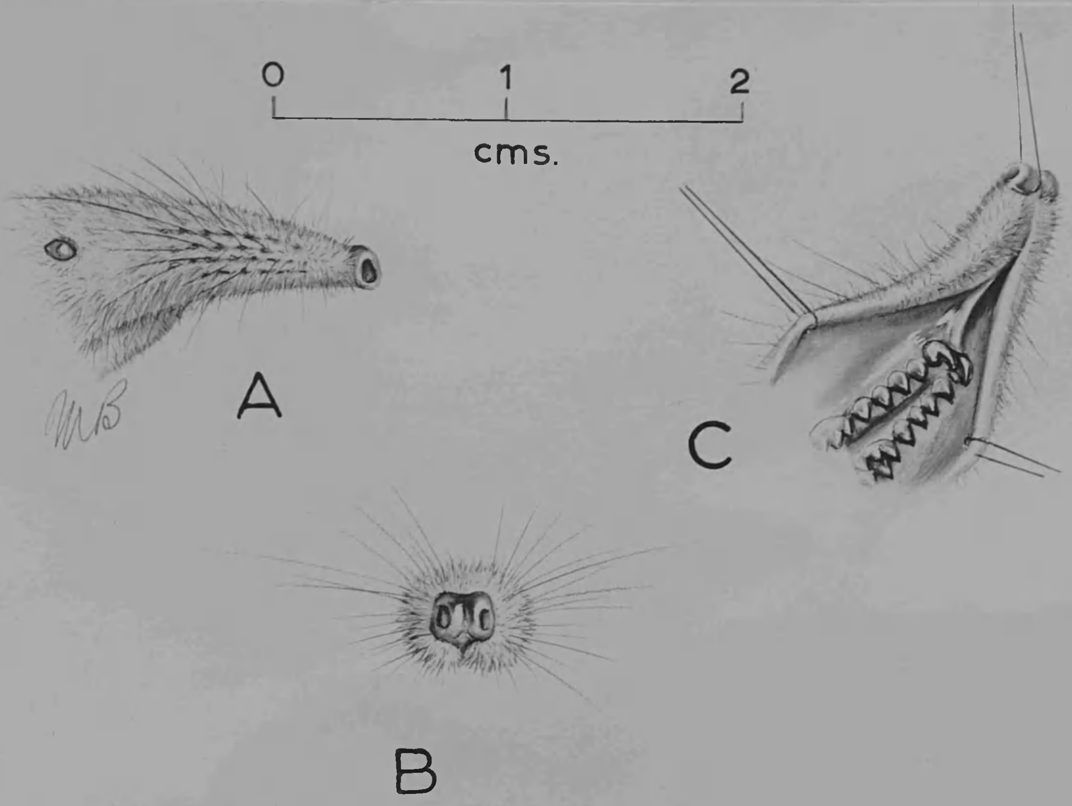


Fig. 10. Common Shrew (Sorex vulgaris)

Fig. 11. Common Shrew. Transverse section through part of the superior labial frenum showing its relationship to the lip and central incisors. x32.

As in the Mole, the hair-bearing skin extends onto the underside of the snout and the two halves of the lip are separated by a shallow groove. When the snout is reflected upwards, however, the inner aspect of the lip is quite different. The central incisors are large, hook-shaped teeth with two cusps, arranged antero-posteriorly. Arising from the alveolar process between the central incisors, which are almost contacting each other, there is a superior labial frenum. It passes upwards and forwards to end just behind the junction of the hairy skin of the lip. It is a thin, translucent sheet of membrane, in fresh specimens, and appears to act as a ligament limiting upward displacement of the snout.

In order to examine the fragile superior labial frenum, two specimens were fixed, sectioned transversely parallel to the palatal surface and stained (Fig. 11). The frenum contains a loose mass of collagenous fibrous tissue running antero-posteriorly, with fibroblasts scattered through this mass. Elastic or muscle tissue was not found within the frenum in either specimen. The musculature of the lip is well defined and forms a band of muscle which crosses the midline with only a slight interruption of the fibres in the midline.

Tenrec

(Centetes ecaudatus)

Only dried specimens were available. The elongation of the snout together with the distribution of hairy skin and rhinarium resemble the appearance of the Common Shrew.

Macroscelididae

Only dried specimens were available. The Macroscelididae have a relatively enormous proboscis, hence the name "Elephant Shrews" is given to some species. Unfortunately it was not possible to determine the relationship of the tissues on the underside of the snout due to damaging of the skins. According to Osman Hill (1948) the distribution of the rhinarium is not unlike that of the Hedgehog with a long, grooved philtrum present on the underside of the proboscis.

MYRMECOPHAGOUS SPECIES

Myrmecophagous species all show extreme specialisation of the jaws including a considerable reduction in the number of teeth present and defects in the structure of the teeth, such as hypoplastic enamel. The incisors are particularly affected and are usually absent or much reduced in number. Several species have a rhinarium but in most species this has been replaced by hair-bearing skin. Dried or mounted specimens were the only material available.

Aard-Vark

(*Orycteropus*)

The Aard-Vark shows elongation of both the upper and lower jaws and has the long extensile tongue characteristic of the myrmecophagous species (Fig. 12). The rhinarium has been completely replaced by skin which is covered with short, thick tufts of hair.

Great Ant Eater

(*Myrmecophaga jubata*)

The Great Ant Eater possesses the most extreme specialisation of the myrmecophagous feeding mechanisms. Both the upper and lower jaws have become greatly elongated to give a narrow tube-like appearance.

Fig. 12. Aard-Vark (Orycteropus). Mounted specimen, Royal Scottish Museum.

Fig. 13. Pangolin (Manis) Mounted specimen, Royal Scottish Museum.

The presence or absence of rhinarial skin at the anterior end of this extension is not known. The tongue is capable of being protruded to a relatively enormous length.

Pangolin

(*Manis*)

Elongation of the snout is not a marked feature of the Pangolins (Fig. 13), but, despite the apparent absence of rhinarial tissue on the mounted specimen shown, Osman Hill (1948) states that there is a rim of rhinarial skin on both the upper and lower lips. The remaining skin of the snout is hairless but is of a tough, thick type.

CARNIVOROUS SPECIES

Carnivorous species are almost all found in one Order, the Carnivores, and there is relatively little variation of the snout and lips. Consideration of the Carnivores is therefore limited to a detailed examination of a few species and brief comments on several others. The more readily available Carnivores are discussed first.

Domestic Cat

(*Felis domesticus*)

Three fresh dead specimens were examined and dissected. There is strong similarity of the snout features of all the Cat family and the Domestic Cat may be regarded as a type specimen. There is much less rhinarial skin than in the other terrestrial Carnivores. It is present around the nostrils and in a narrow philtrum in the shape of a "T" (Fig. 14). The sagittal midline groove extends from the internarial region down to notch the border of the lip. The Cat has a well developed vibrissal system.

Within the mouth the dentition shows complete adaptation to the carnivorous pattern. Anteriorly the labial sulcus is shallow but the entire upper lip and the

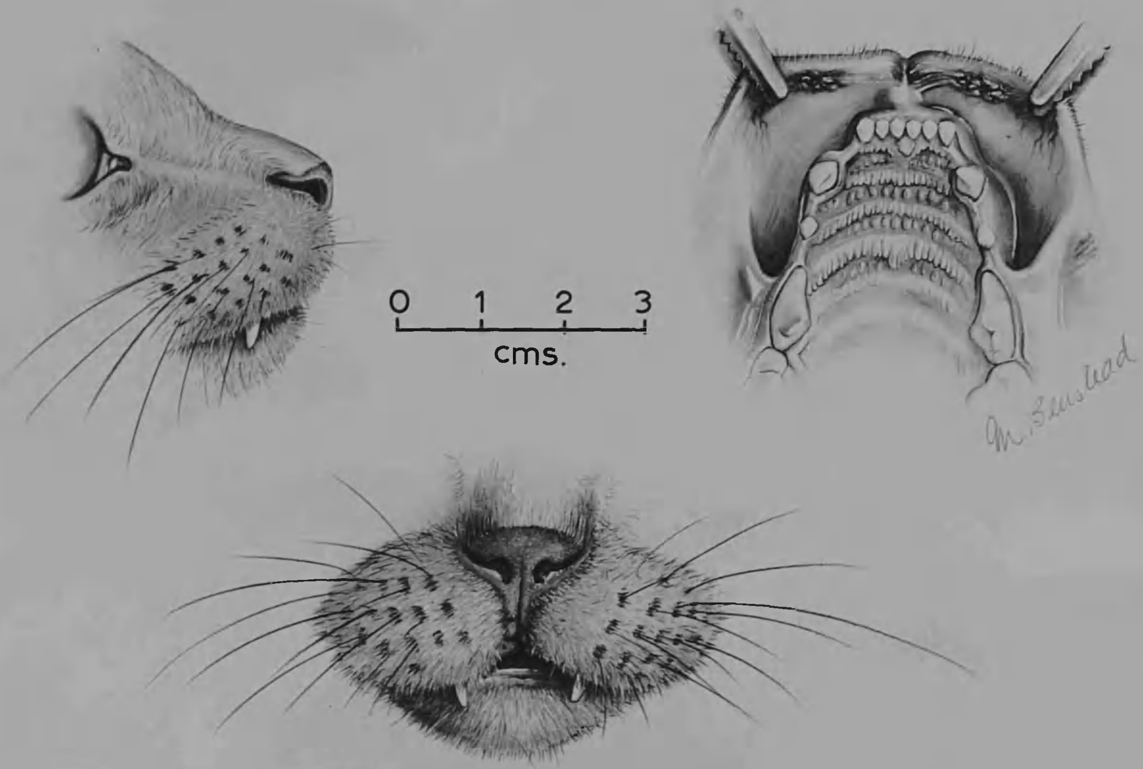


Fig. 14. Domestic Cat (Felis dom.)

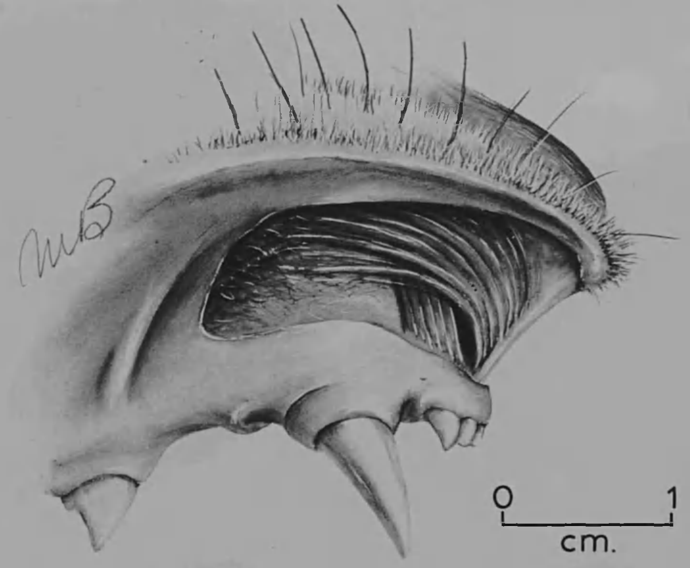


Fig. 15. Cat, showing distribution of musculature on the inner aspect of the lip.

nares are flexible, mobile structures. There is no bulging or ridging of the sulcus suggestive of a frenum.

When the mucosa over the roots of the anterior teeth is incised and reflected upwards as far as the lip margin (Fig. 15) it is found that a fibrous ligament extends from the alveolar process upwards and outwards to the edge of the lip. Arising from this ligament is a paired muscle which curves upwards and laterally to mingle with the Orbicularis oris muscle and then the vibrissal musculature. This muscle is analagous to the Incisivus superioris muscle of the higher Primates. The central portion of the lip deep to the philtrum is almost devoid of muscle. Deep to the Incisivus superioris muscle is a smaller muscle extending upwards to the underside of the snout. This is analagous to the Depressor septi nasi muscle of the higher Primates.

On the lateral aspects of the upper lip the bulky vibrissal musculature (M. Maxillo-naso-labialis and M. Naso-labialis) forms the main substance and, together with the vibrissal insertions,accounts for the characteristic bulging of the upper lip. By partial contraction of these muscles the Cat can erect the vibrissae. Further contraction raises the lip as in snarling.

Domestic Dog

(*Canis domesticus*)

Two distinct types of snout are found in Dogs. Most breeds of domestic Dog have a long snout but a few have a receding snout. Four specimens of a long-snouted breed (Greyhound) and one specimen of a recessive-snouted type (Bulldog) were examined.

Greyhound

There is an extensive rhinarium occupying the anterior portion of the snout (Fig. 16). It protrudes slightly in front of the upper incisor teeth. The upper lip extends across between the rhinarium and the oral mucosa as a narrow hair-covered strip interrupted only by the midline sagittal groove. When put under lateral tension this groove is seen to be a shallow one, devoid of hair. The mystacial vibrissae are much reduced in number compared to the Cat and the two halves of the upper lip are thin, flabby structures easily reflected upwards to expose the teeth. When this is done (Fig. 17), a superior labial frenum can be seen extending from high

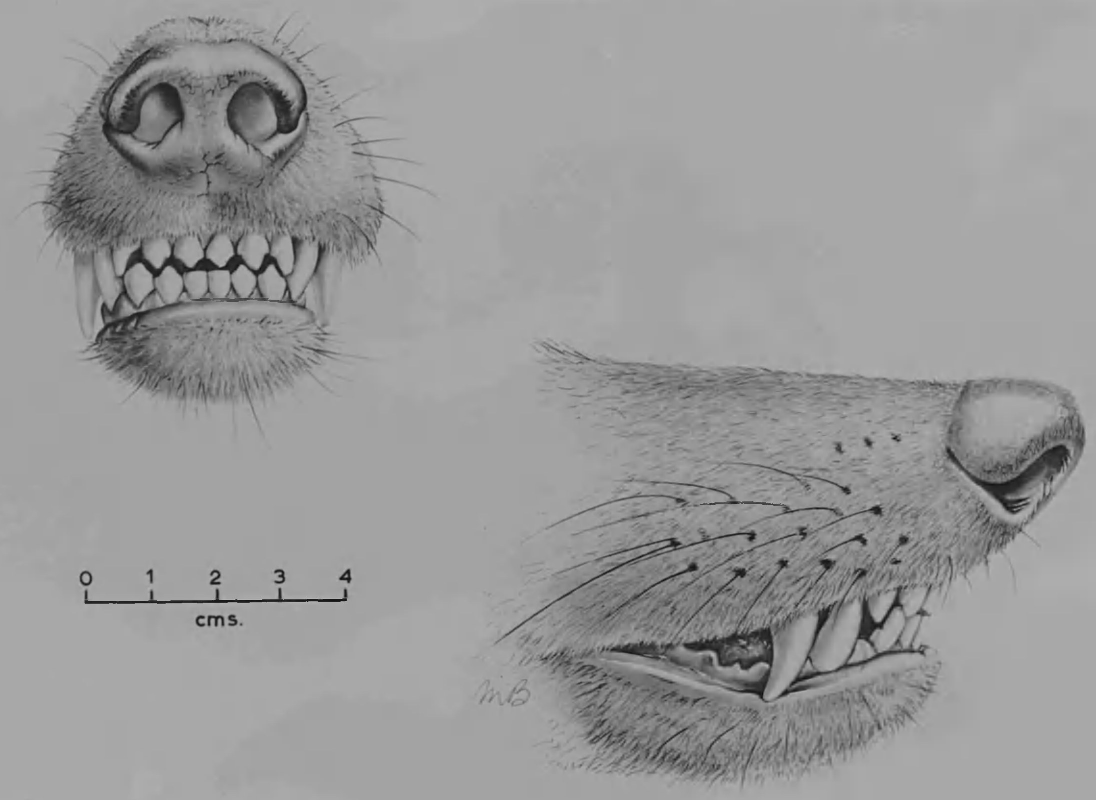


Fig. 16. Dog (Canis dom.) Greyhound.

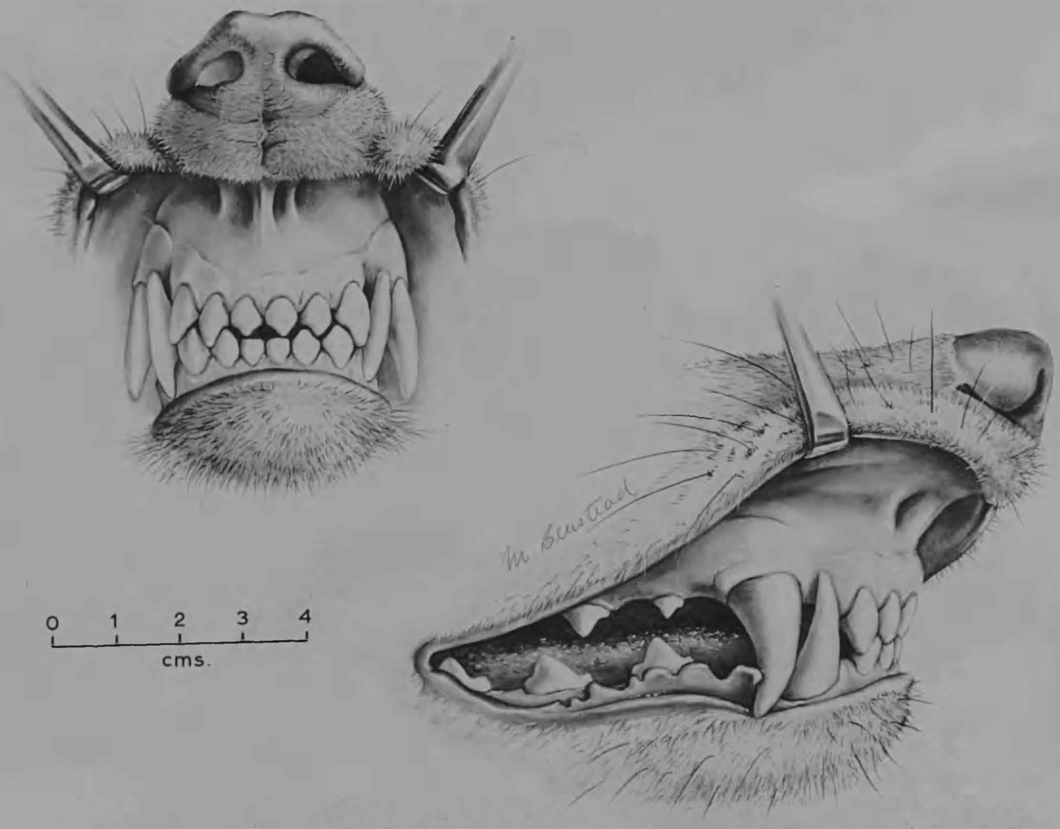


Fig. 17. Greyhound. Upper lip reflected.

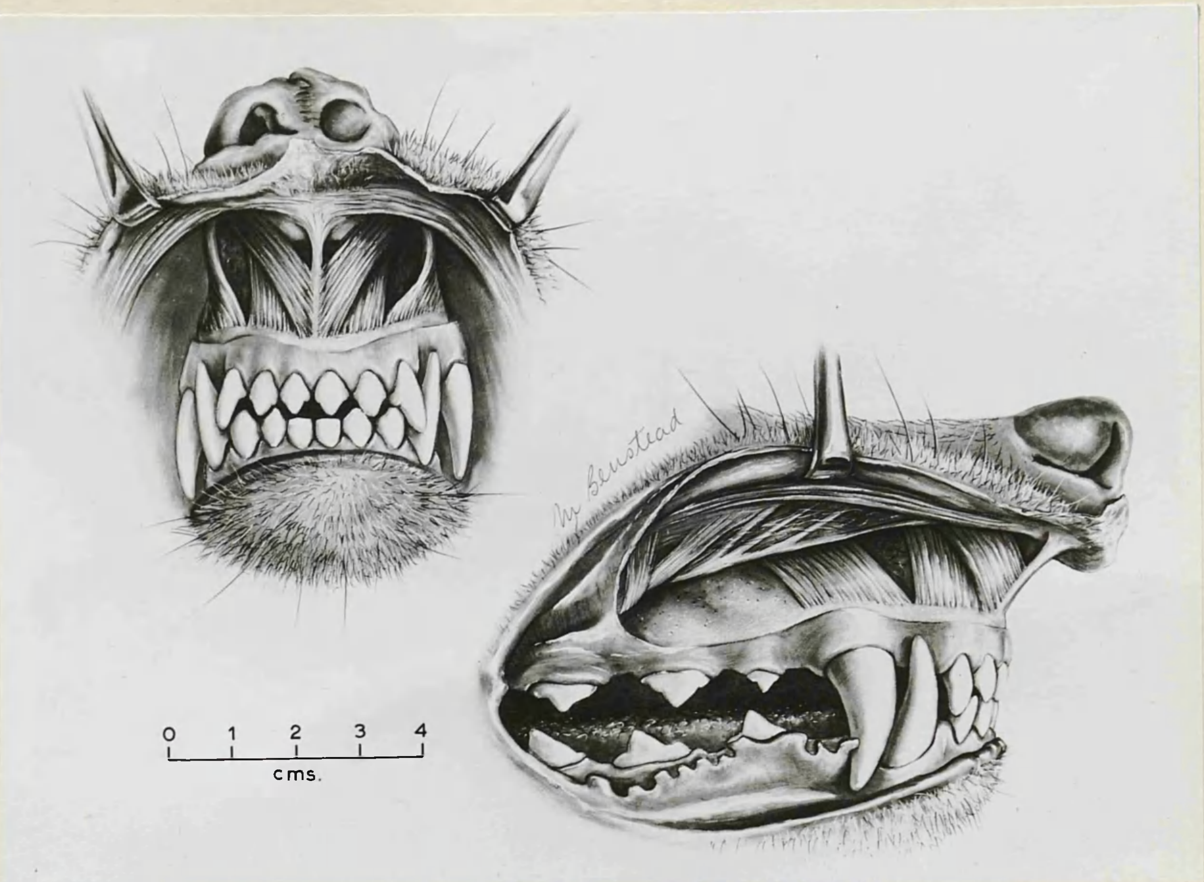


Fig. 18. Greyhound, showing distribution of the infranarial musculature.

Fig. 19. Bulldog, showing inner aspect of the lip.

up on the alveolar process above the incisors upwards and outwards to the inner aspect of the lip where the reflection of the mucosa onto the floor of the sulcus begins. Along the anterior border of the frenum there is a narrow raised portion and on each side there is a secondary, smaller fold of mucosa.

After the mucosa is incised and reflected off the alveolar process (Fig. 18), the frenum is seen to be a muscular structure except for the anterior raised edge which is composed of a fibrous ligament extending from the premaxilla to the underside of the nasal cartilage. Arising from this ligament and also from the bony rim of the pyriform fossa is the Incisivus superioris muscle which extends upwards and outwards, with the superficial fibres crossing the floor of the sulcus to intermingle with the Orbicularis oris muscle. The deeper fibres become attached to the alae of the nasal cartilage and appear to be analagous to the Nasalis muscle of the Strepsirhine Primates (Lightoller, 1934). Deep to the Incisivus superioris and Nasalis muscles is another muscle arising from the rim of the pyriform fossa to pass to the underside of the central body of nasal cartilage. This resembles the Depressor septi nasi muscle of the Primates. Its distal edge is lateral to the Incisivus superioris muscle and forms the secondary fold observed on the side of the frenum.

The Orbicularis oris muscle forms a small group of fibres extending across the midline of the lip but it is widely fanned out across the cheek where the fibres intermingle with the rib-like tendons of the vibrissal musculature. The infranarial musculature of the Dog does not appear to be described in standard textbooks of anatomy (Sisson & Grossman, 1961).

Bulldog

The most striking feature of the specimen examined was the lack of mobility of the snout and its position relative to the lower jaw. The rhinarium is well behind the upper incisor teeth and is set back almost within the pyriform fossa. Inside the mouth (Fig. 19) there is almost complete absence of a superior labial frenum, with only a tiny fold of mucosa marking the midline. There are irregularities of the upper incisors, a feature common to this breed (Aitchison, 1963).

Kinkajou

(Potos)

One fresh dead specimen and one live specimen were examined. Superficially the Kinkajou bears a

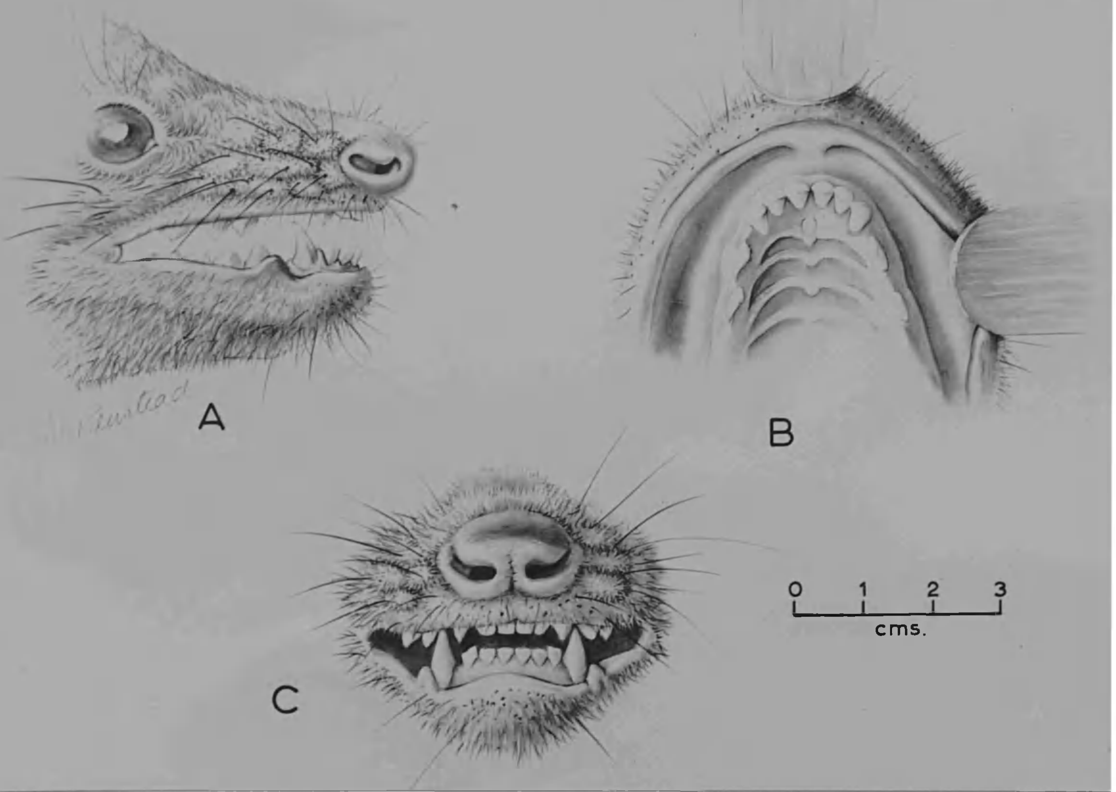


Fig. 20. Kinkajou (*Potos*)

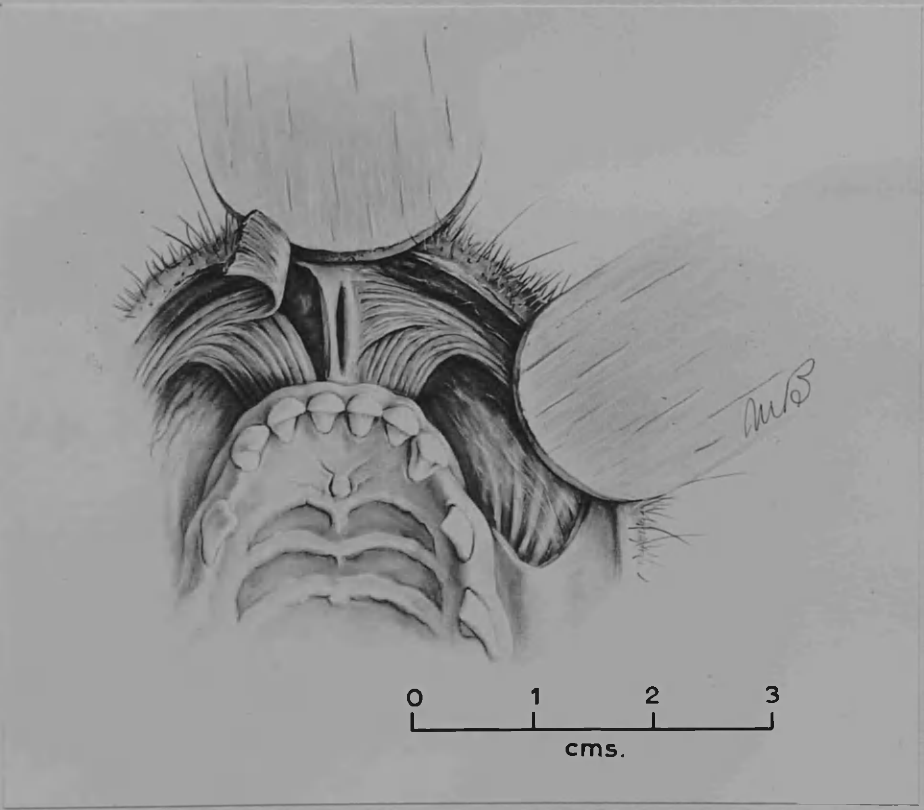


Fig. 21. Kinkajou, showing musculature on the inner aspect of the lip.

certain resemblance to the Dog but lacks the prominence of the rhinarium and mobility of the snout cartilage of the long-snouted breeds (Fig. 20). It has only a few vibrissae and a very narrow, hair-covered upper lip between the rhinarium and the oral mucosa. There is also a shallow midline sagittal groove down the lip.

Within the mouth, there is a shallow labial sulcus with a slight bulge on the inner aspect of the lip at the midline. On dissection (Fig. 21) it was found that there is a double strand of fibrous tissue passing between the alveolar process and the edge of the lip and this strand causes the bulging of the labial sulcus. The Incisivus superioris muscle arises partly from the alveolar process and partly from the central fibrous strands although this last group of fibres could be considered as part of the Orbicularis oris.

Coatimundi

(*Nasua*)

Two fresh specimens were examined and dissected. The Coati is an aberrant Carnivore with excessive elongation of the cartilaginous portion of the snout (Fig. 22). This flexible extension carries a very large rhinarium with the narial openings and anterior

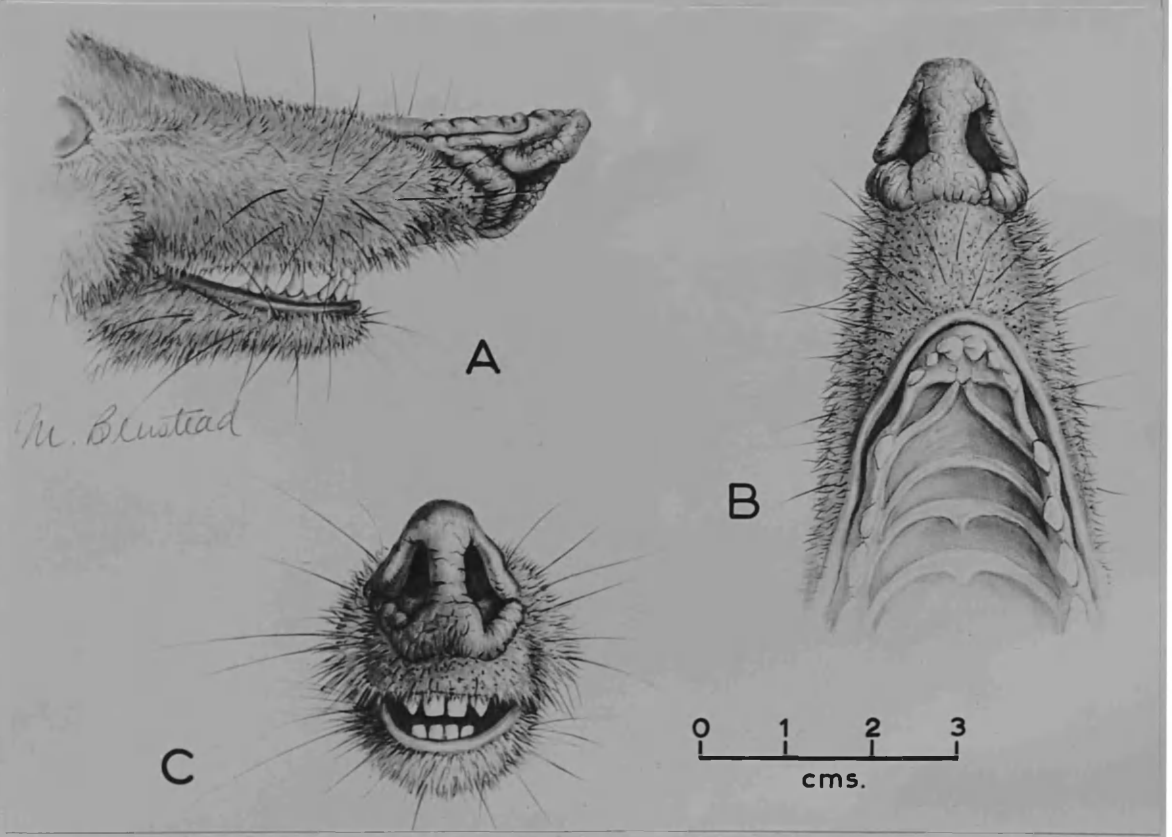


Fig. 22. Coatimundi (Nasua). Young specimen with permanent upper canine teeth not yet erupted.

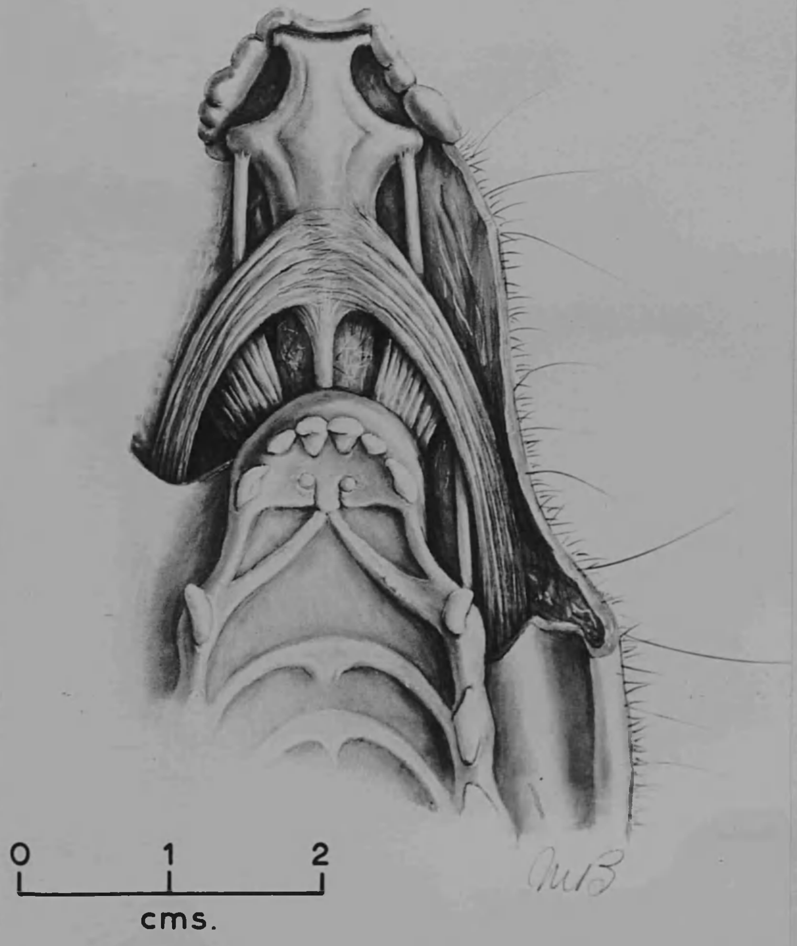


Fig. 23. Coatimundi, showing dissection of the underside of the snout.

rhinarial surface facing obliquely downwards. On the underside of the snout the hairy lip extends over the whole surface without any midline groove or philtrum. Vibrissae are only present in a few scattered groups. The dentition is of interest since the carnivorous central incisors have been replaced by teeth more spatulate in shape. The two young specimens examined both had large, unerupted, upper canine teeth and the molars had a quadrate shape more typical of insectivorous molars. The diet of the Coati includes not only flesh but also insects and fruit.

There is almost no labial sulcus in the Coati and no evidence of a frenum. When the hairy skin on the underside of the snout is reflected back (Fig. 23) the distribution of the Orbicularis oris muscle is reminiscent of that in the Hedgehog although fibres decussate across the midline in the Coati. The cartilaginous extension supporting the snout is also reminiscent of that in the Hedgehog.

Other Species

Several carnivorous species show specialisation related to an amphibious or aquatic existence. The

Otter (Lutra) has a deep spatulate muzzle with a much reduced rhinarium situated near the upper aspect of the muzzle. There is no philtrum or sagittal groove present. The Pinnepedia have little or no rhinarial skin and have slit-like valvular nostrils on top of a hair-covered muzzle. A sagittal groove is present, however; and the vibrissae are even more hypertrophied than in the Otter. The Badger (Meles) and Racoon (Procyon) also lack a central groove although both have a large rhinarium.

The remaining Carnivores appear to bear a fairly close resemblance to one or other of the species described. The great majority have a prominent rhinarium resembling that of the Dog together with a similar type of hair-covered upper lip. There appears to be a variable depth of labial sulcus as far as can be ascertained from available material. Vibrissae are usually present, being much reduced only in the Bears. One variation observed in the Sloth Bear (Melursus) by Pocock (1914b) appears to be unique among the Carnivores and consists of an enlarged mobile rhinarium, which forms the central part of the upper lip, and a protruding, mobile lower lip. The Sloth Bear has a specialised diet of insects and honey.

HERBIVOROUS SPECIES

The members of several Orders are included in the herbivores. These Orders are the Artiodactyla, Perissodactyla, Sirenia, Rodentia and Lagomorpha.

Artiodactyla and Perissodactyla

Variations of the snout and upper lip in these two Orders may be grouped into two divisions. In the first group, upper incisors have been lost and are replaced by a hard pad of fibrous connective tissue covered by mucosa. There is almost no sulcus between the anterior border of this chewing pad and the edge of the upper lip. The lip itself is firmly attached to the underlying bone and is not mobile to any extent. In the second group, a wide variety of feeding mechanisms have been evolved. In some species both the upper and lower lips play an important part while in others it is the snout itself which is predominant.

Ruminants

Artiodactyles showing the first type of arrangement form a fairly closely related series, the ruminants (Tragulidae, Bovidae and Cervidae). In the species to be described, examination of live or fresh dead specimens has been made wherever possible but use has been made of mounted specimens for photographic purposes. The principal variation observed in the snout structures of the ruminants is the amount of rhinarium present. Accordingly, the common variations are, for convenience, divided into four classes and only a brief description is given of a type species for each class.

In the first group, the rhinarium is very broad and extends orally to form the central part of the lip without lateral contraction. The portion at the edge of the lip is therefore almost as broad as the transnarial portion. The Musk Deer (Moschus moschiferous) is typical (Fig. 24) and also the Chevrotains (Tragulidae). All the species with this pattern of rhinarium have upper canine teeth and lack horns or antlers. They are also the species showing the lowest level of general development among the ruminants.

In the second group there has been some lateral encroachment of hair-bearing skin on the rhinarium, thus producing a broad philtrum. The lip portion of the rhinarium is therefore more narrow than the transnarial portion. The Swamp Deer (Cervis duvauceli) has this arrangement (Fig. 25) as do many

Fig. 24. Musk Deer (Moschus moschiferous). Mounted specimen, Royal Scottish Museum.

Fig. 25. Swamp Deer (Cervis duvauceli). Mounted specimen, Royal Scottish Museum.

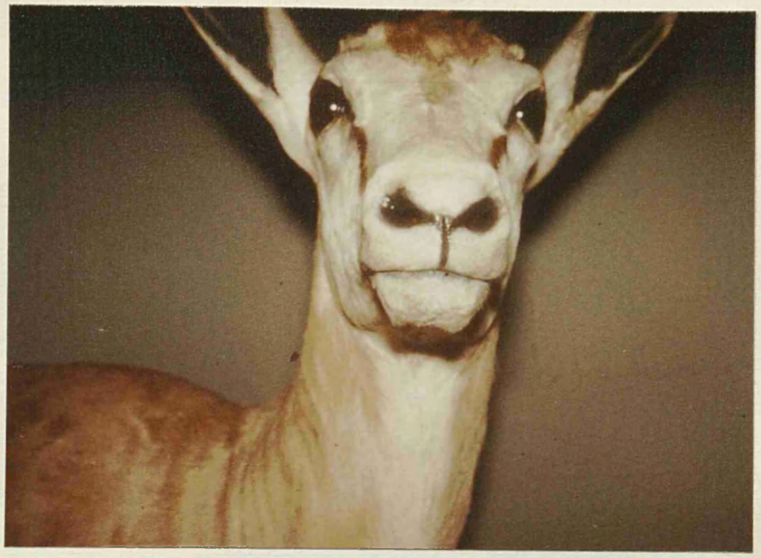


Fig. 26. Springbuck (Antidorcas marsupialis). Mounted specimen, Royal Scottish Museum.

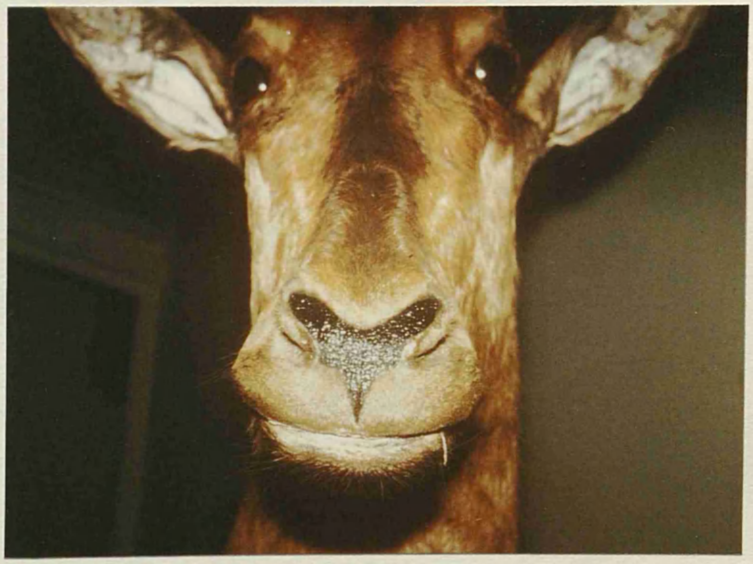


Fig. 27. Hartebeest (Bubalis cama). Mounted specimen, Royal Scottish Museum.

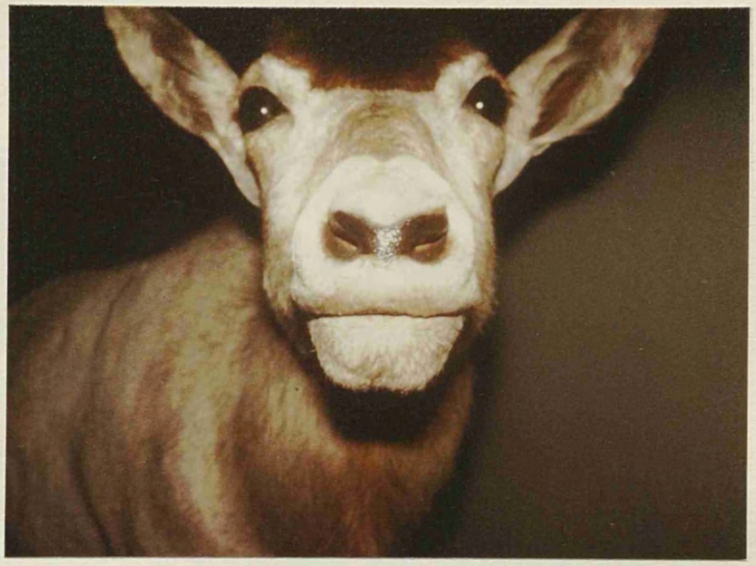


Fig. 28. Addax (Addax nasomaculatus). Mounted specimen, Royal Scottish Museum.

Fig. 29. Camel (Camelus bactrianus). Mounted specimen, Royal Scottish Museum.

of the Cervidae. The Ox (*Bos*) is also included in this group.

In the third group, the rhinarial philtrum is reduced to a narrow sagittal strip and the rhinarial skin around and between the nares is also diminished to give a "T" shaped distribution as in the Springbuck (*Antidorcas marsupialis*) (Fig. 26). Almost all the Gazelles (Gazellae) and all the Sheep (Ovidae) show this arrangement. Variations may occur, e.g. Hartebeest (*Bubalis cama*), (Fig. 27) where the area around the nares is lost, leaving a central zone only.

In the fourth and final group, the rhinarial skin is reduced to a small patch between the nares as in the Addax (*Addax nasomaculatus*) (Fig. 28) or forms such a slight labial extension of the oral mucosa, as in the Reindeer(*Rangifer*), that it is virtually absent, thus giving a complete hair-covered snout and upper lip.

Another variation found in the ruminants is the amount of protrusion of the upper jaw in front of the lower jaw. This protrusion may be a massive one as in the North American Mosse (*Wapiti*) but most of ruminants have an arrangement similar to the Ox where the lower jaw extends almost as far forwards as the upper jaw and the snout has a broad flat anterior surface, enabling the lower incisor teeth to be used in cropping herbage at ground level. The lower lip appears to play little part in the feeding process and the tongue is the chief means of drawing food into the mouth (Hafez, 1962).

Other Variations in the Jaws of Artiodactyles and Perissodactyles

Other variations of the jaws in these Orders are roughly those where the lips are important functional organs and those where the snout is predominant, becoming of increased importance in the location and seizure of food.

Development of the Lips

Horse

(*Equus*)

The most familiar example of a species showing development of the lips as important functional organs is the Horse. The nares are proximal to the most anterior part of the muzzle so that the upper and lower lips are the first part of the head to come into contact with an object under investigation. Tactile sensitivity of the lips in the Horse is therefore highly developed and the lips themselves are capable of a wide range of movement including protrusion. In association with this increased lip activity there are relatively deep labial sulci separating the lips from the alveolar process supporting the teeth. Despite a comment by Sisson and Grossmann (1961) that frena are present in the Horse, no evidence to support this could be found in six live specimens examined. Externally the rhinarium has disappeared entirely and the snout is covered by skin with fine short hairs scattered over it.

Okapi and Giraffe

(Okapia and Giraffa)

The Okapi also shows hypertrophy of the lips but still has a narrow rim of rhinarial skin around the nares which, as in the Horse, are placed proximal to the lips. This process is carried a stage further in the Giraffe where the rhinarial skin has been lost entirely, the nares are well behind the lips and the lips themselves are relatively very large, resembling saucer-like projections. They are also highly mobile prehensile organs.

Llama and Camel

(Lama and Camelus)

As in the Giraffe the nostrils are proximally placed (Fig. 29) and in these species are also reduced to slit-like openings. The lips are again very mobile and this capacity for movement is enhanced by the upper lip being partly divided in the midline.

During the prehension of food the two halves can be brought together to aid in this process.

Development of the Snout

Tapir and Elephant

(*Tapirus* and *Elephas*)

Rhinarial skin is present around the external nares on the short proboscis of the Tapir. According to Osman Hill (1948), on the underside of the proboscis there is a centrally grooved philtrum which widens gradually as it extends towards the mouth. In the Elephant, however, the rhinarial tissue is restricted to a narrow rim around each nostril and the underside of the proboscis is completely covered in hairy skin. Boyd (1933) states that there is still a rudimentary upper lip in the Elephant despite hypertrophy of the snout. The lower lip has become adapted so that it can approximate the two halves and seize food passed back by the proboscis.

Pig

(*Sus*)

In the Pig the rhinarium is confined to a disc-like area on the tip of the snout (Fig. 30). The rhinarial

Fig. 30. Pig (Sus dom.)

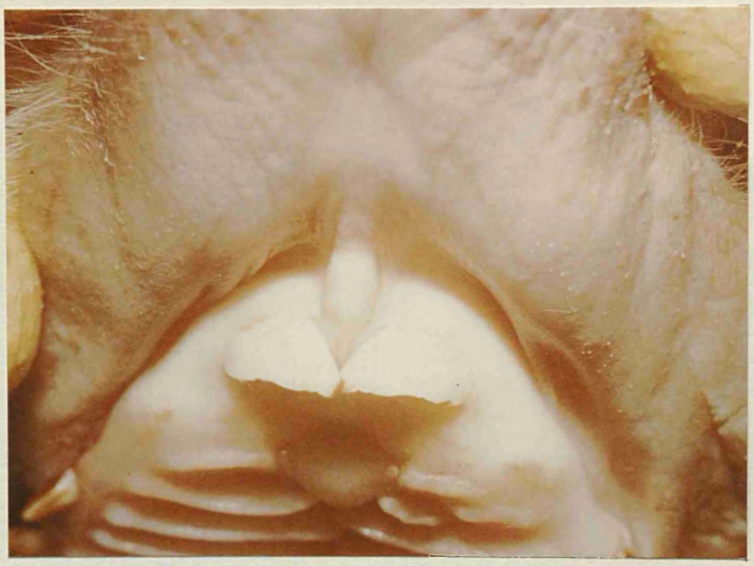


Fig. 31. Pig. Upper lip reflected to show superior labial frenum.

skin is attached fairly firmly to the underlying Os rostri but the upper lip is a loose, flexible structure easily lifted to show the teeth. The central part of the lip narrows down to a thin strip separating the rhinarium from the oral mucosa but it is covered in fine hairs. When the lip is reflected upwards (Fig. 31) it shows the central incisor teeth and, extending between them, a large superior labial frenum which is soft and flexible.

Dissection established that the Orbicularis oris muscle occupies the lateral edges of the lip but towards the central portion it becomes mingled with a mass of loose fibrous and fatty tissue and appears to decussate with the opposing fibres across the midline. Two of the frena which were relatively the same size in all four specimens examined, were fixed and sectioned. This showed that it is composed of a dense mass of fibrous tissue running antero-posteriorly (Fig. 32) with small mucous glands scattered throughout this mass. A few elastic fibres can be found towards the deeper, more central, part of the frenum. No muscular tissue could be identified.

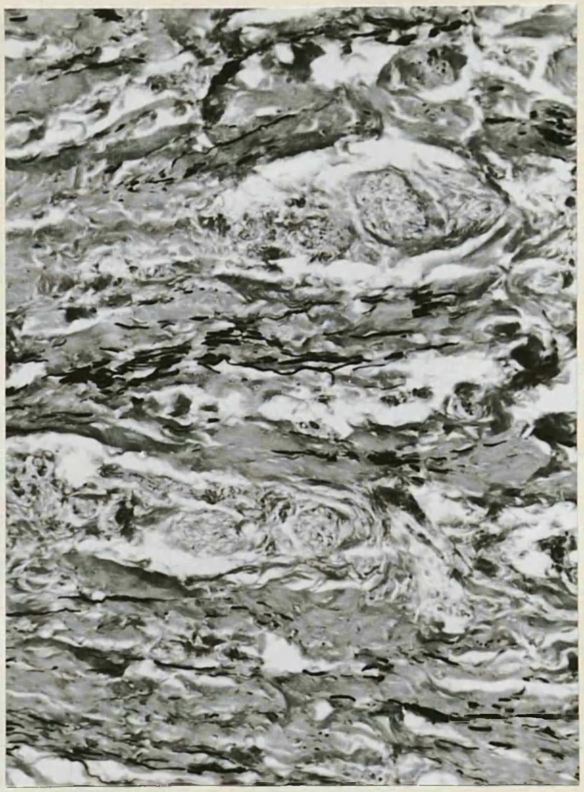


Fig. 32. Pig. Transverse section through frenum showing elastic fibres. Verhoeff's elastic tissue stain, x80.

Fig. 33. Rat (Rattus)

Other Herbivorous Species

Sirenia

The American Manatee (Manatus amer.) has been described by Murie (1880). The muzzle is blunt and rounded, forming a massive bulging snout which completely overhangs the lower jaw. This mass is covered with fine hairs except on the anterior surface on the upper lip where there are many short vibrissae. The Manatee has lost the rhinarium entirely and almost all the teeth as well. It is unusual in having an upper lip which is the sole means of gathering food. The upper lip consists of two highly mobile halves which can be brought together to seize the water weeds forming its diet. The lip then carries them into the mouth.

Rodents

Despite the large number of species in this Order there is only a limited range of variation of the snout and upper lip (Pocock, 1926). The Rat (Rattus) is therefore described as a type species for the Order.

Rat

The rhinarium is not so extensive as in, for example, the Dog and there is only a very shallow central sagittal groove of the lip (Fig. 33). The hair-covered lip extends mesially to separate the rhinarium from the mouth but it is bound down to the alveolar process with a consequent absence of labial sulcus anteriorly. There are numerous long vibrissae over the anterior surface of the lip. The lip edges curve upwards as they approach the midline thus exposing the large central incisor teeth. Dissection of two specimens established that the Orbicularis oris does not decussate across the midline but is attached to the thick fibrous raphe underlying the philtrum. The vibrissal musculature is a prominent feature of the lateral aspects of the lip.

Lagomorphs

The Lagomorphs all appear to have a lip arrangement similar to that in the Rabbit (Oryctolagus). Superficially (Fig. 34), there is almost no rhinarial skin visible and only on close insepction is it possible to see a slight rim at the mesial aspect of each nostril. The upper lip is well supplied with long vibrissae.

When the upper lip is stretched laterally (Fig. 35) the two halves of the lip can be readily separated.

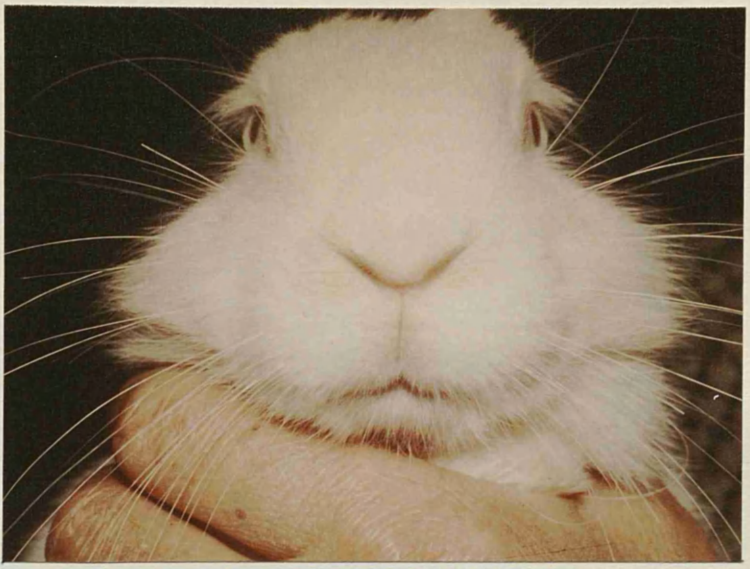


Fig. 34. Rabbit (Oryctolagus)

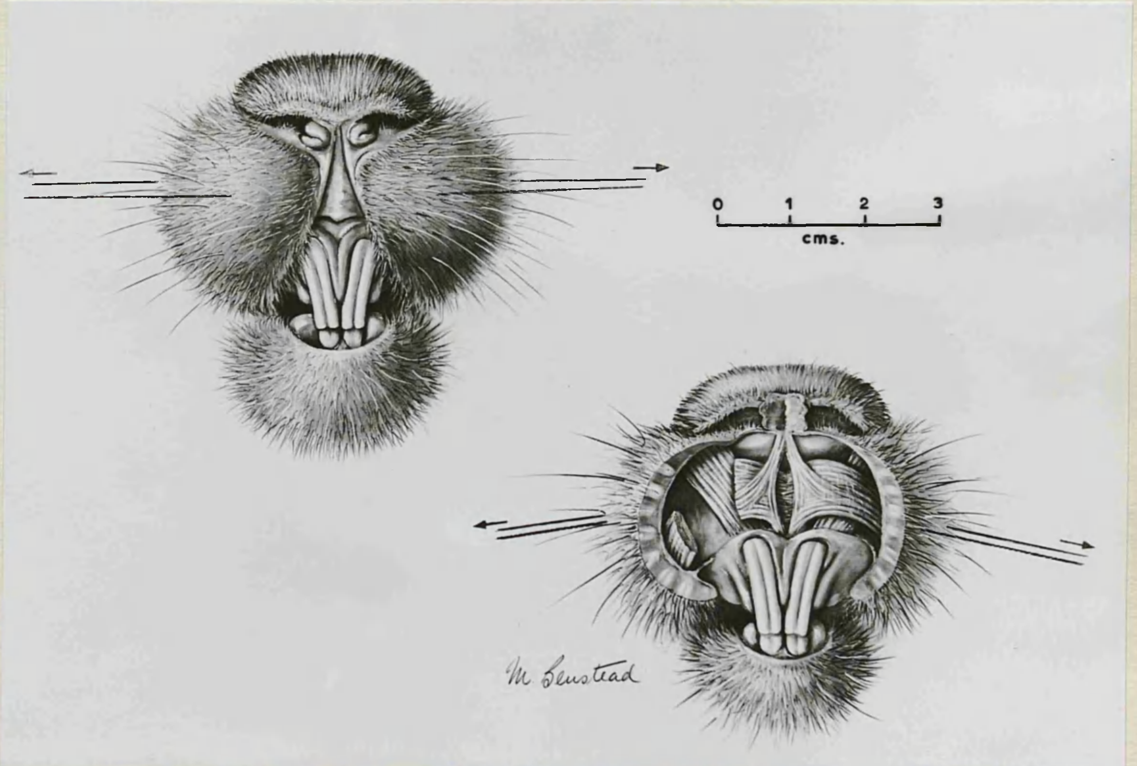


Fig. 35. Rabbit, showing split upper lip and the distribution of the underlying musculature.

Deep to the lip there is a layer of mucosa covering the alveolar process above the teeth. This sheet is reflected off the alveolar process and onto the inner aspect of the lip just above the distal edge of the central incisor. The central portion of mucous membrane is only loosely attached and can be readily moved. On each side of the septum there is a small mass composed of folds of rhinarial skin, first described by Osman Hill (1948). The free mesial borders of the lip have a fold of mucous membrane running from the upper aspect of the free edge to each side of the nasal septum.

When the superficial tissues are dissected off (Fig. 35) it is found that this fold of membrane covers a strand of muscle which extends up to the septum. This strand is part of the terminal portion of the Quadratus labii superioris muscle (Young, 1957). A deeper part of the muscle continues horizontally across the midline to decussate with the fibres of the other side. The insertions of the vibrissae form the bulk of the lateral bulges of the upper lip and are activated by the Orbicularis oris and Quadratus labii superioris muscles.

OMNIVOROUS SPECIES

Omnivorous species are found almost entirely in one Order, the Primates. Some of the lower Primates are insectivorous rather than omnivorous but it is convenient to group them with the other Primates. The principal divisions of the Order (Osman Hill, 1953) are based on the relationship of the rhinarium and philtrum to the upper lip. In the Strepsirhine or lower Primates there is persistence of the philtrum, with the upper lip thus being interrupted in the midline and bound down to the alveolar process. In the Haplorhine or higher Primates there is no rhinarial skin and the upper lip forms an unbroken, hair-covered strip which can be reflected away from the alveolar process due to the presence of a deep labial sulcus.

Strepsirhine Primates

Osman Hill's (1953) theory of classification is followed (Fig. 36).

Demidoff's Galago

(*Hemigalago demidoffii*)

One fresh specimen was examined (Fig. 37). Demidoff's Galago differs slightly from most of the

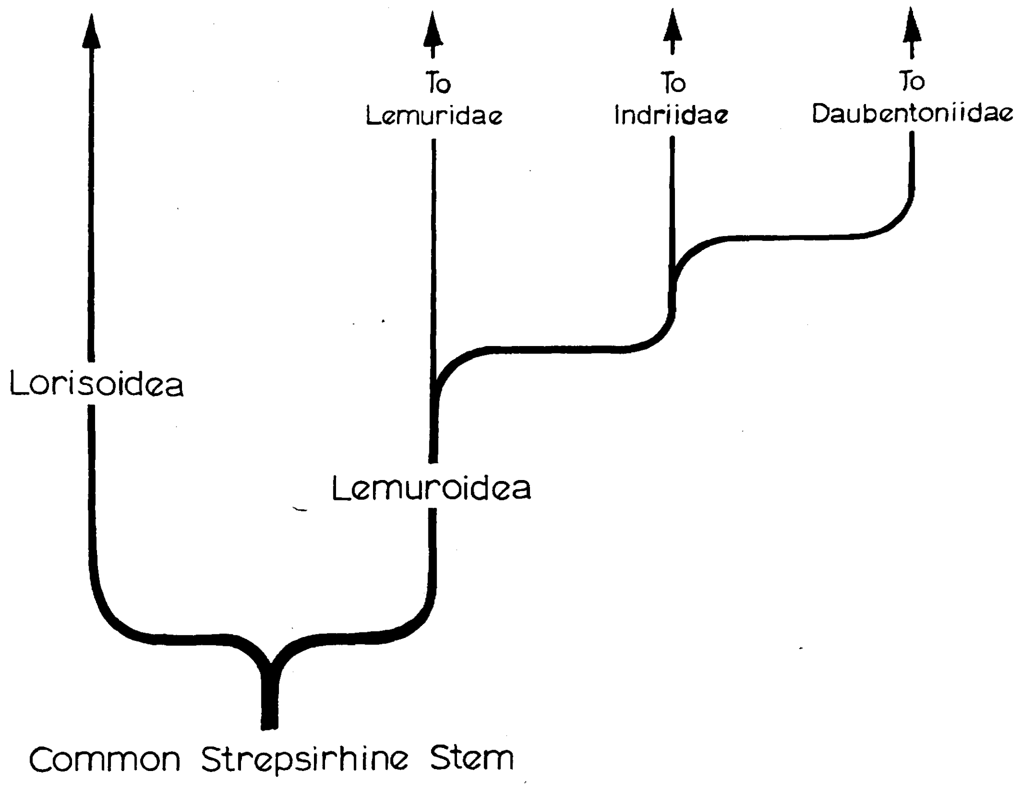


Fig. 36. Theory of classification of the **Strepsirhine** Primates. **Redrawn from W. C. Osman Hill's "Primates". Vol. 1, 1953.**

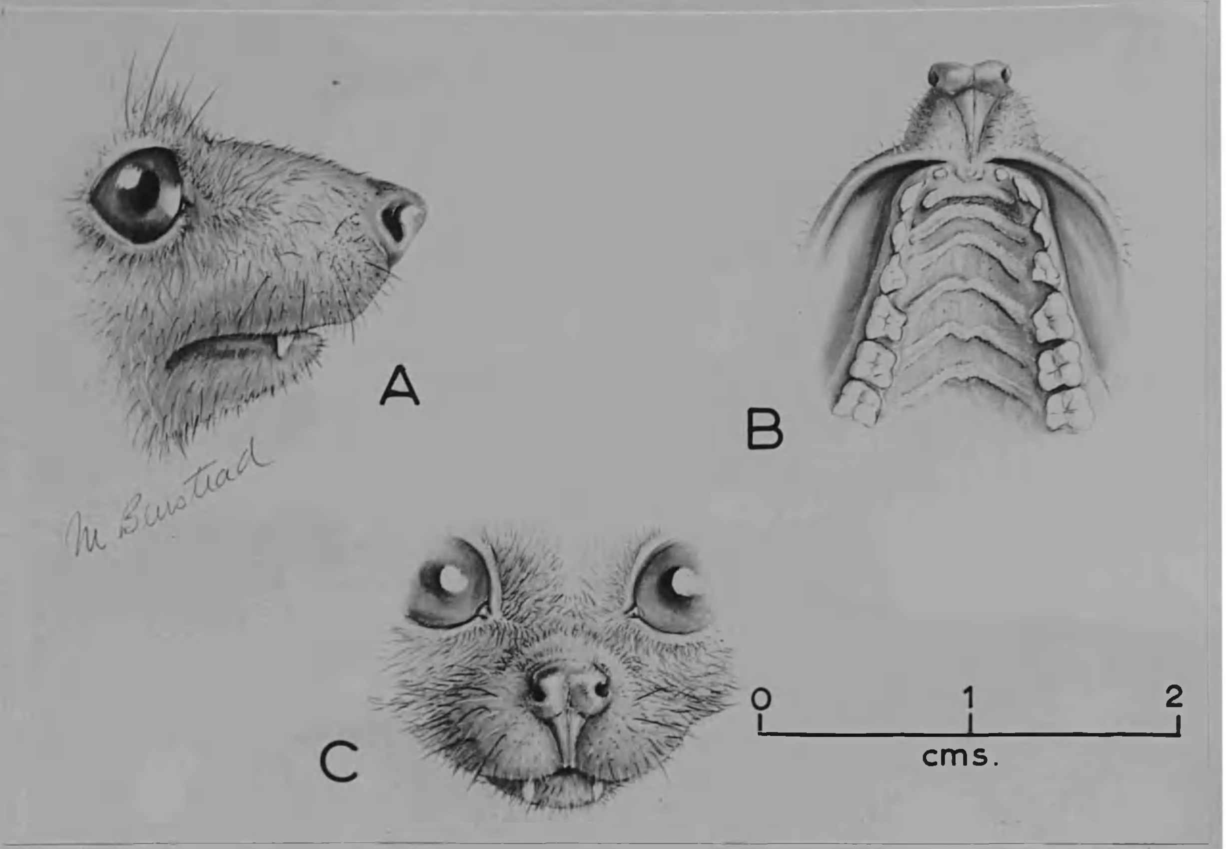


Fig. 37. Demidoff's Galago (Hemigalago demidoffii).

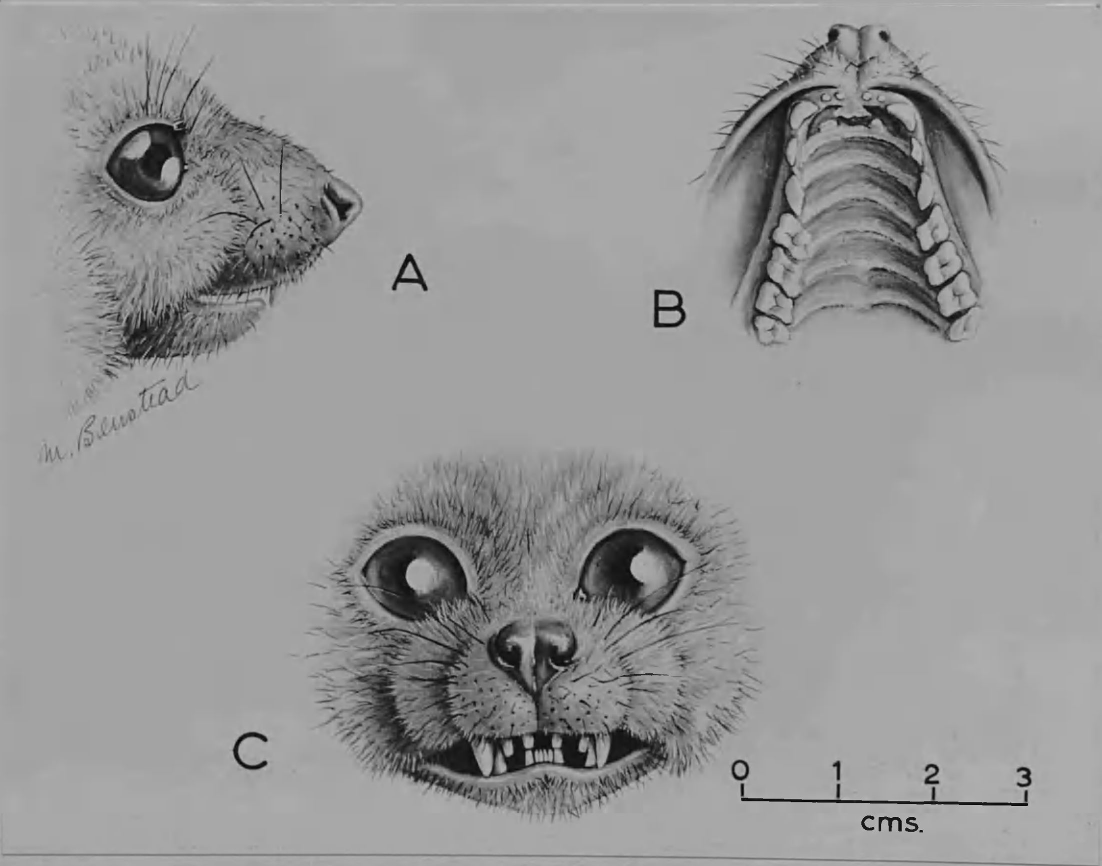


Fig. 38. Moholi Galago (Galago senegalensis moholi).

Fig. 39. Moholi Galago. Transverse section of upper lip. The superficial midline vertical groove is at the top of the field. The transverse muscle fibres form a narrow band with vertical fibres, superficial to this band, on either side of the midline. x32.

other Lorisoids in having a more prominent snout. There is a large rhinarium with an elongated philtrum which broadens gradually as it approaches the rhinarium. A sagittal groove extends along the philtrum. The upper lip is firmly tethered to the alveolar process with a consequent absence of labial sulcus in the midline. The philtrum ends at the small incisive papilla situated in the diastema between the small, conical, central incisor teeth. Sectioning of the lip in a transverse plane shows that there is a fibrous raphe underlying the philtrum with muscle fibres arising from either side of the raphe and extending distally.

Moholi Galago

(Galago senegalensis moholi)

One fresh dead and two live specimens were examined. In the Moholi Galago the philtrum is absent (Fig. 38) and the lip is divided only by a shallow midline groove which is a continuation of the internarial groove. The lip is firmly attached to the alveolar process with absence of a labial sulcus anteriorly.

When the specimen was sectioned transversely (Fig. 39) muscle fibres are found extending across the midline while some decussate with those from the other side. Superficial to these fibres, on either side of the midline are a few groups of vertically placed muscle fibres, cut transversely.

Slow Loris

(Nycticebus)

One fresh postmortem specimen was examined (Fig. 40). The large rhinarium extends orally as a wedge of tissue before narrowing into a true philtrum. The philtrum extends palatally as far as the incisive papilla but unlike previous species the lip can be reflected partially, due to the presence of a short superior labial frenum. This frenum is formed by the palatal extension of the philtrum and the sagittal groove continues into the frenum giving a double strand of tissue. The small central incisors are much closer together than in previous species.

Transverse sectioning shows that the frenum does not contain muscle fibres, only a loose mass of fibrous connective tissue, running antero-posteriorly. A section taken above the level of the frenum shows the central, hair-free, philtral region (Fig. 41), with a few scattered transverse muscle fibres, cut longitudinally, lying deep to it. Deep to these muscle strands, the

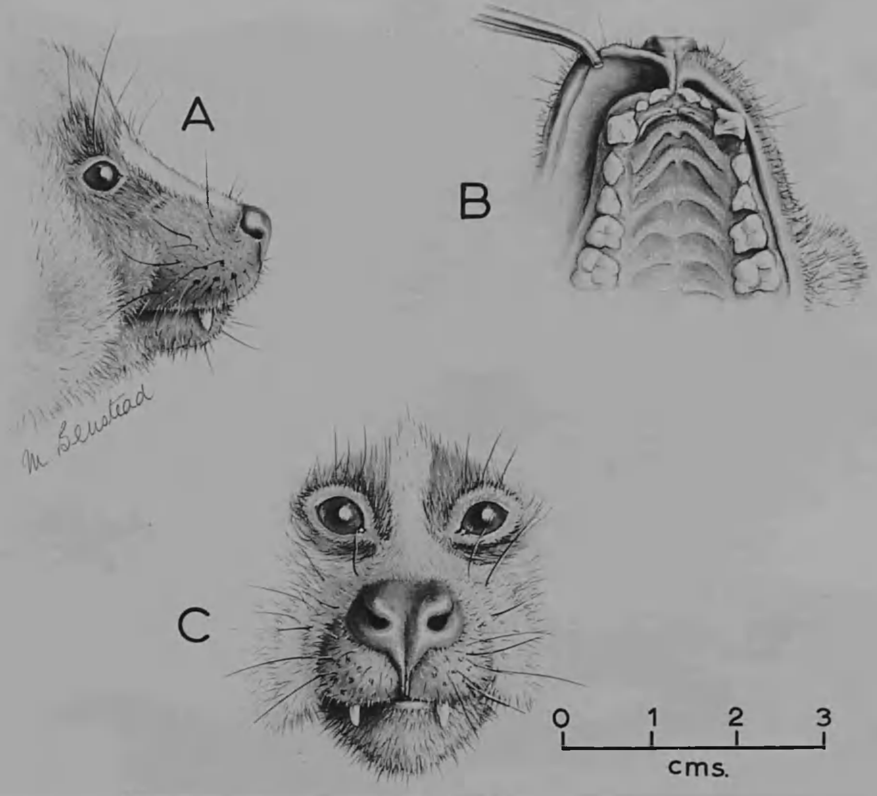


Fig. 40. Slow Loris (Nycticebus)

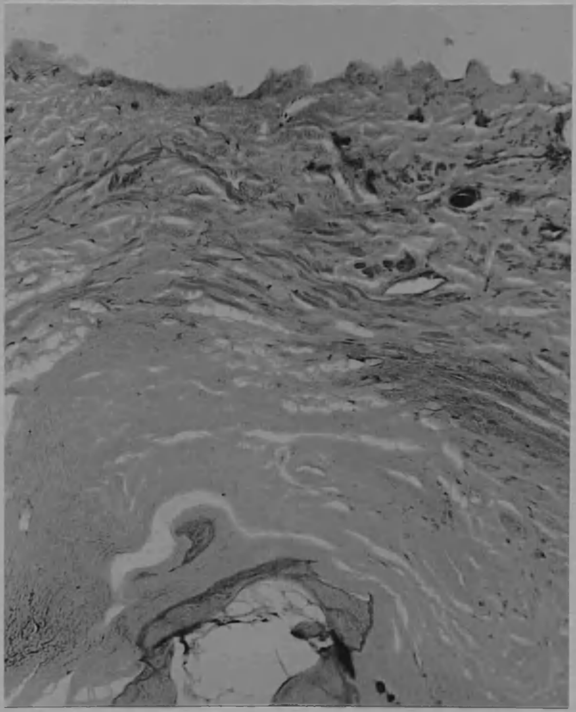


Fig. 41. Slow Loris. Transverse section of upper lip. Centre of lip is slightly to the left of the field. The central wedge of dense fibrous tissue extends superficially towards the surface of the lip and only a few transverse muscle fibres can be traced across the midline. x32.

central part of the lip is occupied mainly by a dense mass of fibrous tissue.

Lemurs

According to Osman Hill (1953), Mouse Lemurs (Cheirogaleinae) and Lemurs (Lemurinae) all have a well-developed, grooved philtrum which binds down the upper lip and there is apparently no superior labial frenum. The snout tends to be more protruded and in the Lemurs is not unlike that of a long-snouted Dog.

The Aye-Aye (Daubentonia) is quite different from the Lemurs in that it has large, rodent-like, central incisors. Osman Hill (1953) states that it has a narrow, much reduced rhinarium with a thin philtrum which ends as a short superior labial frenum passing between the central incisors. Some eversion of the lip is said to be possible.

Indris

(Propithecus diadema)

One wet-preserved foetal specimen was examined together with three dried specimens. The main variation between the foetal and the dried specimens was the absence of teeth in the foetus. In the adult animal the central incisors are large, spatulate teeth very nearly in contact at their mesio-incisal edges.

Superficially, although the Indris still has a rhinarium and philtrum, these are very much reduced in extent. The profile and general facial appearance resemble those of the Haplorhine Primates rather than the Lemurs and there is a greater degree of differentiation of the lip musculature. Consequently, a wider range of lip movement is possible (Osman Hill, 1953). A short superior labial frenum is said to be present.

Haplorhine Primates

Man should be placed with the Haplorhine or higher Primates but in view of the uniformity of the findings in the Haplorhines and the uniqueness of the human variations he is considered separately.

Tarsier

(Tarsius)

One wet-preserved specimen was examined. The Tarsier alone among the Haplorhines still has a narrow rim of rhinarial skin around the nares (Fig. 42). Apart from this region, however, hair-covered skin extends over all the snout and upper lip. The upper lip has no philtrum or groove to indicate the midline and there is no notching of the edge of the lip. There is a deep labial sulcus, but in the one specimen available there did not appear to be a superior labial frenum. Pocock (1918) and Osman Hill (1955) both state that a small frenum is found high up in the sulcus. This may have been lacking in the specimen examined due to distortion of the tissues after many years in preserving fluid. Lightoller (1934) states that the level of muscular development of the upper lip in the Tarsier is much the same as in the Lemurs.

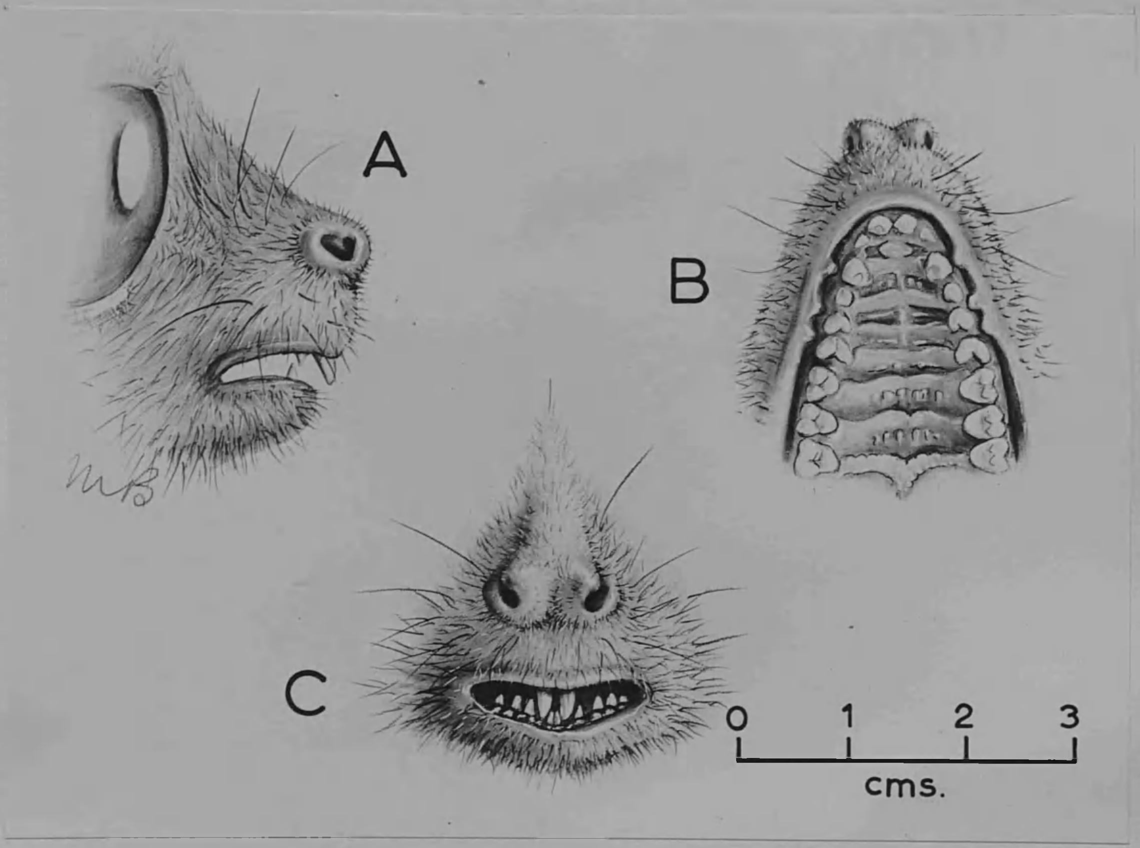


Fig. 42. Tarsier (Tarsius)

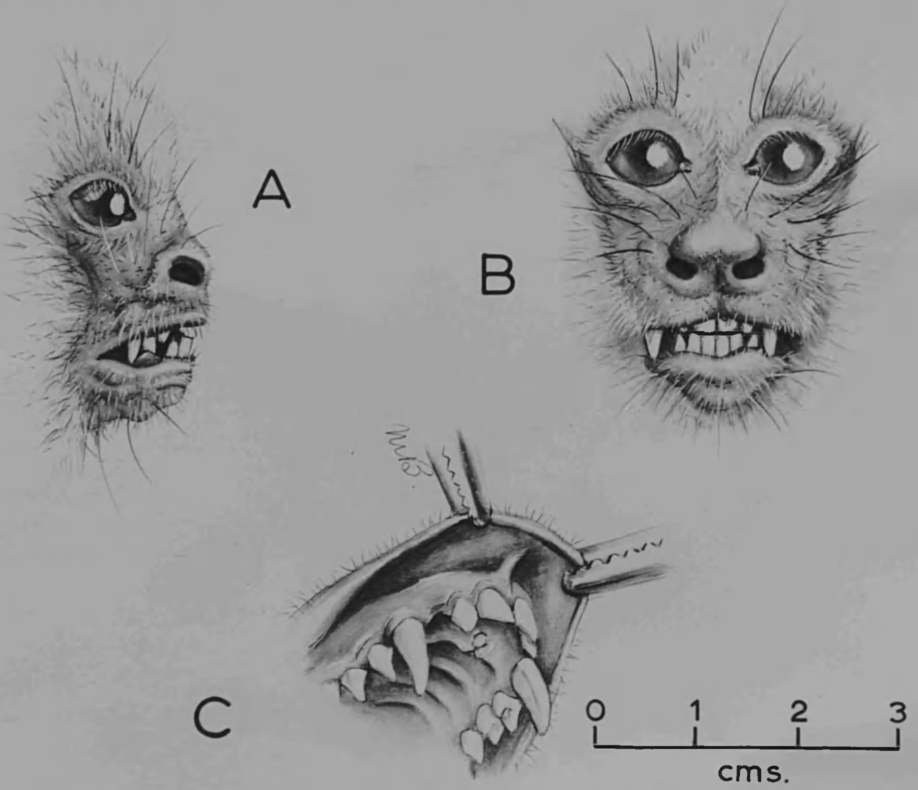


Fig. 43. Tufted Marmoset (*Hapale jacchus*)

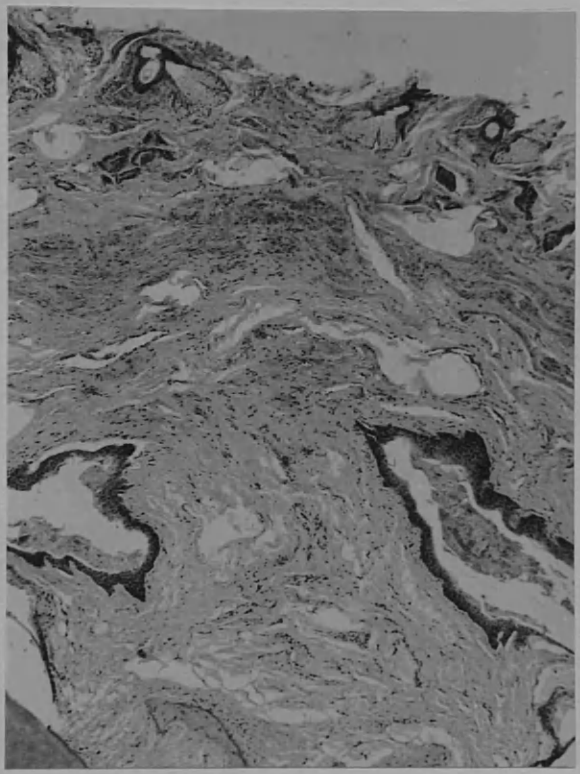


Fig. 44. Tufted Marmoset. Transverse section of upper lip. Superficial surface at the top of the field. The frenum occupies the lower, more central area. Transverse fibres of the Orbicularis oris muscle form a well-defined band crossing the midline without interruption. The fibres of the Incisivus superioris muscle within the frenum extend towards the Orbicularis oris fibres. x32.

Tufted Marmoset

(Hapale jacchus)

One fresh dead specimen was examined. The profile of the Tufted Marmoset is typically Haplorhine (Fig. 43). The nostrils are surrounded by an area of dark skin with only a scanty distribution of hairs but this is not moist rhinarial tissue. The upper lip is still a flat, thin structure with just a suggestion of a vertical indentation at the midline but no real groove.

When the upper lip is reflected (Fig. 43), a small superior labial frenum is visible arising from the alveolar process above the central incisors and passing outwards to the inner aspect of the lip. On sectioning in a transverse plane (Fig. 44) some muscular tissue can be identified within the frenum. This is probably the Incisivus superioris muscle (Lightoller, 1934). The Orbicularis oris muscle is still a relatively feeble structure.

Spot Nose Monkey

(Cercopithecus nictans)

One fresh dead specimen was examined (Fig. 45). The narial openings are reduced to slit-like apertures.

Superficially, there is a deep upper lip, giving a

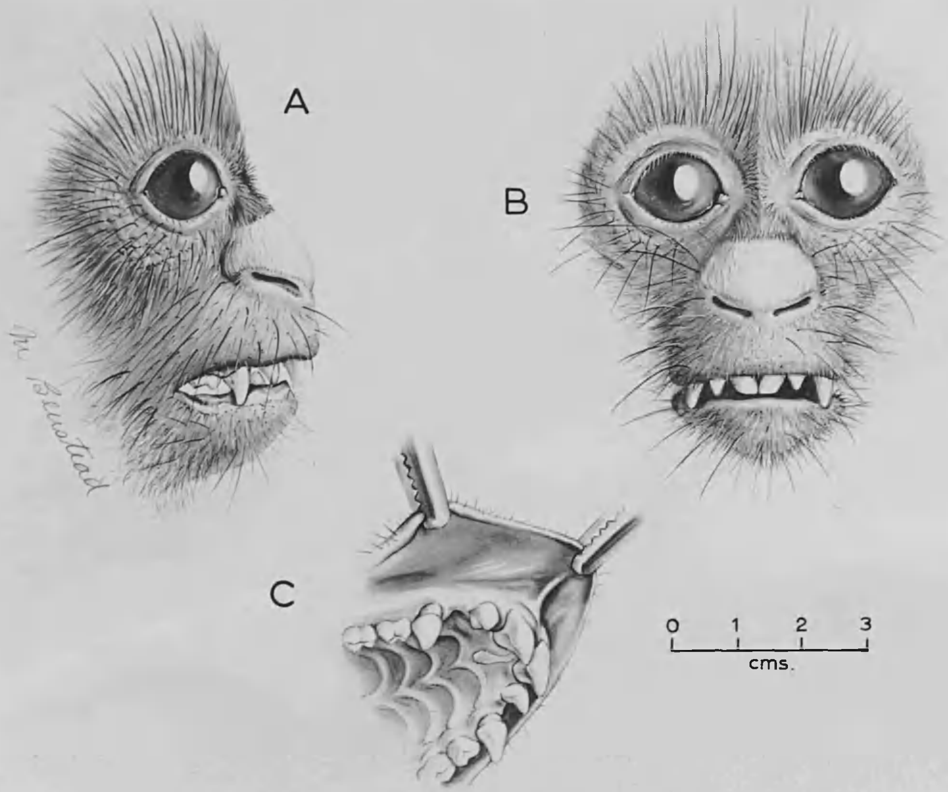


Fig. 45. Spot Nose Monkey (Cercopithecus nictans)

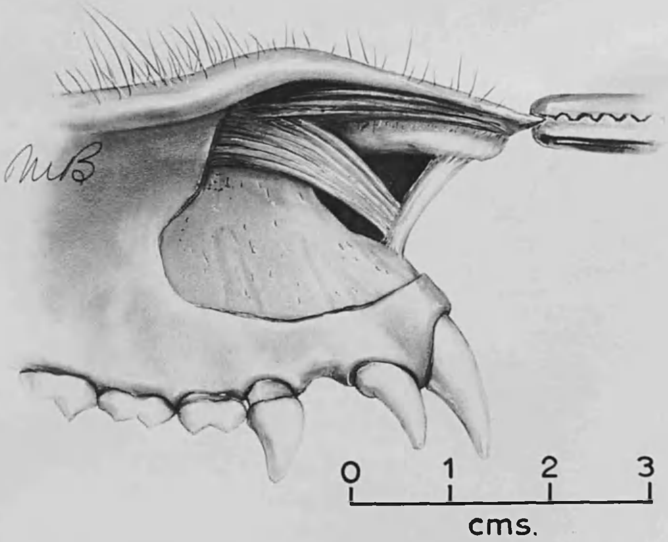


Fig. 46. Spot Nose Monkey, showing the attachment of the Incisivus superioris muscle to the fibrous portion of the superior labial frenum.

bulbous appearance to the mouth. There is complete absence of any central groove. Inside the mouth the incisors show only partial progression towards the typical Haplorhine distribution of four spatulate incisors grouped together in contact with each other. There is a small, thin, superior labial frenum and when the mucosa is removed (Fig. 46) the frenum is seen to be composed of a central fibrous ligament arising from the edge of the pyriform fossa and extending upwards and outwards to the lip. From this ligament arises the paired Incisivus superioris muscle which curves laterally to mingle with the Orbicularis oris. This latter muscle is much reduced in size where it crosses the central part of the lip.

Baboon

(Papio)

Two wet-preserved specimens of young animals were examined (Fig. 47). The Baboon has the most protruding snout among the Haplorhines, with the exception of the aberrant Proboscis Monkey (Nasalis). The anterior part of the snout is covered in tough, almost hairless skin of a darker colour than the rest of the muzzle.

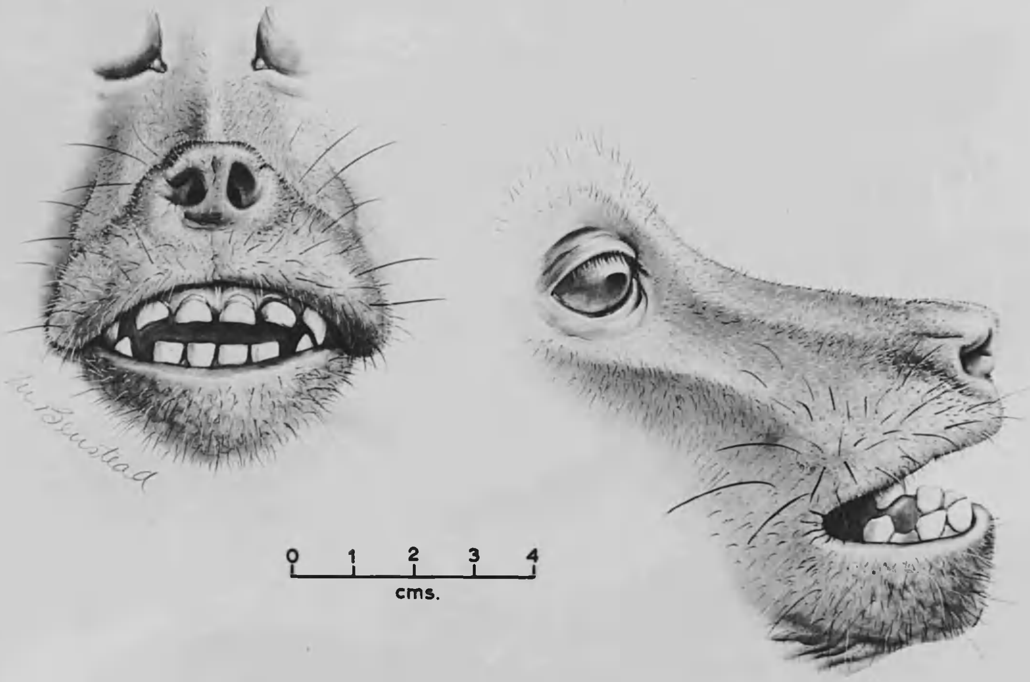


Fig. 47. Baboon (Papio). Young specimen, with deciduous dentition still present.

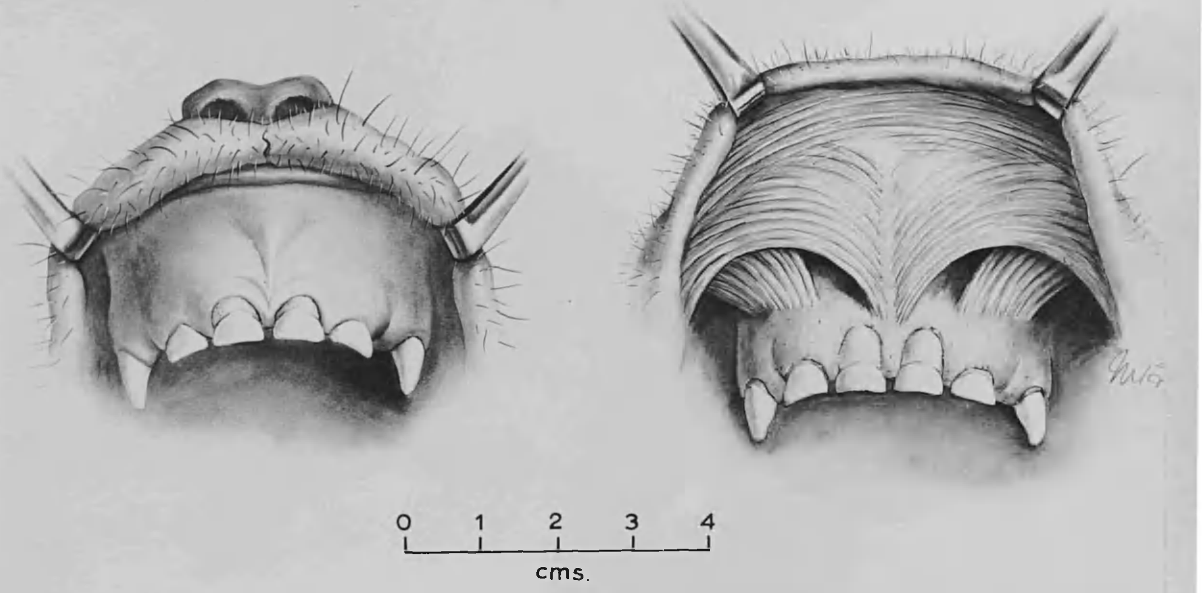


Fig. 48. Baboon, showing muscle attachments to the alveolar bone.

When the lip is reflected (Fig. 48) a flattened superior labial frenum is visible extending down the alveolar process as a wedge-shaped swelling. After the mucosa is reflected it is found that the most anterior portion of the frenum is formed by a fibrous raphe arising from the alveolar process and extending up to the anterior border of the nasal cartilage. The Incisivus superioris muscle takes origin from the raphe and partly also from the alveolar process. It then curves laterally to mingle with the Orbicularis oris. When the Incisivus superioris muscle is dissected away from its origin a few fibres are found passing up to the underside of the nasal cartilage. This is the Depressor septi nasi muscle (Lightoller, 1928). The Orbicularis oris is a relatively bulky structure occupying the greater part of the lip and forming a thick, continuous band around the periphery.

Other Haplorhine Species

Single specimens of Macaque (Macaca) and Grivet Monkey (Cercopithecus) were examined and dissected. The general distribution of muscles appears to conform closely to that of the Baboon. Intra-oral examination of the two live, young specimens of Chimpanzee (Pan) and Orang Utan (Pongo) suggests that they too may have a similar pattern. This is confirmed by Lightoller's (1928) descriptions of dissections. It would appear therefore that there is considerable similarity of the features of the upper lip in the Haplorhines and the main variation is in the level of muscular development achieved.

MAN

The detailed anatomy of most of the structures forming the human upper lip has been well documented (Lightoller, 1925; Cunningham, 1964; Gray, 1964) and the present investigation is limited to consideration of morphological variations found in Man alone among the Haplorhine Primates. These variations include a fibrous superior labial frenum, the so-called philtrum, with its two flanking vertical ridges, the vermilion border of the lip and the labial tubercle.

Superior Labial Frenum

In most adults the superior labial frenum consists of a small fold of mucosa high up in the labial sulcus. This is not the case in infants, however, (Fig. 49) in whom the frenum is relatively much more prominent. It frequently notches the crest of the alveolar ridge as it passes back to end at the incisive papilla. At its junction with the lip it becomes a broad, fanshaped structure.

During the eruption of first the deciduous and then the permanent incisor teeth there is vertical development of the alveolar process but not the frenum, so that it usually becomes less prominent. A space between the

<u>Fig. 49.</u> Human infant, lip reflected to show large superior labial frenum.

<u>Fig. 50.</u> Human adult, showing persistence of a large thick frenum in association with a midline space between the central incisor teeth. An epithelial tag is clearly visible on the alveolar process where the frenum is attached.

upper central incisors is often found in association with the frenum up to the age of 12 - 13 years. With the eruption of the upper permanent canine teeth and continuing vertical development of the alveolar process the space closes in most instances and the frenum recedes still further up the alveolar process. However, this sequence of development is not always found. One variation is the persistence of a large thick frenum which may prevent the lip being reflected upwards (Fig. 50). The individual, in this instance, also has a bulbous tag of tissue where the free edge of the frenum enters the alveolar process. A similar but smaller tag is occasionally found on the free edge of the frenum where it enters the lip. Crowley (1956) has investigated these tags and states that they are composed of a core of vascular fibrous tissue of varying density plus a covering of normal stratified squamous epithelium. A few specimens show a duct-like structure suggestive of a rudimentary salivary gland. He estimates that they are found in approximately one out of every five adults. Another type of variation found occasionally is a frenum with a sagittal groove, thus giving a double-strand effect (Fig. 51).

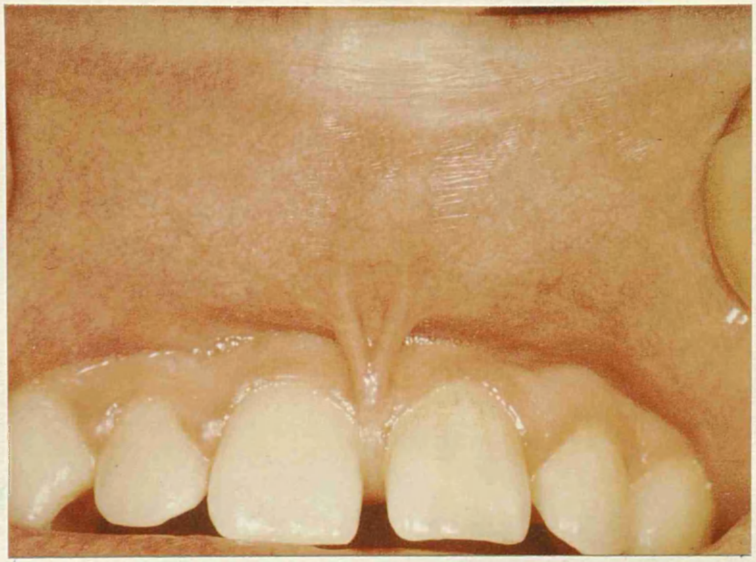


Fig. 51. Human adult, double-stranded frenum, attached low down on alveolar process.

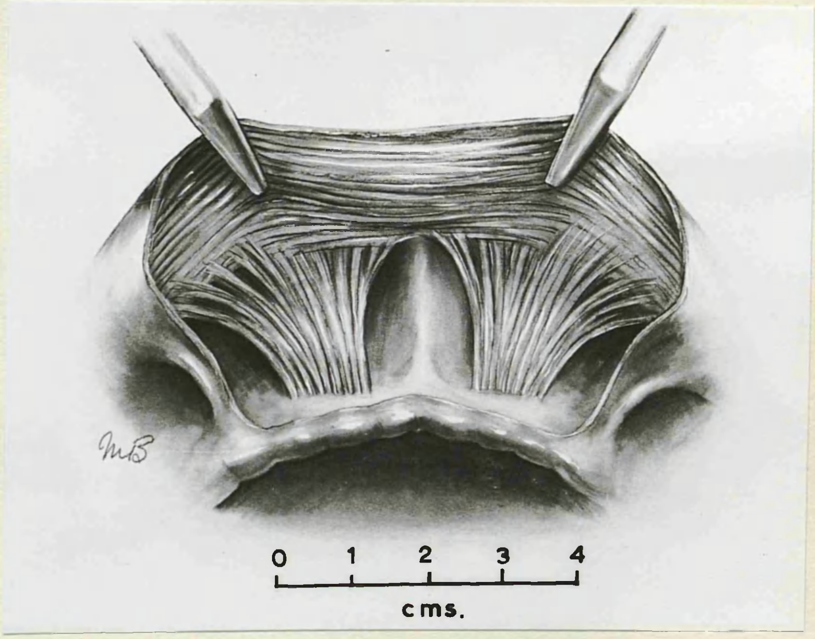


Fig. 52. Human adult, dissection to show the muscular distribution relative to the central bony ridge.

The mucous membrane was reflected off the alveolar process and inner aspect of the lip in three stillborn and three adult specimens. Although the small, vertically placed muscles attached to the bone were difficult to define in the infants they were clearly visible in the adults (Fig. 52). The central zone of the alveolar process is devoid of muscle although Virchow (1924) has described a single instance of an unpaired, centrally attached muscle - the Nasalis impar - in a Negro. The flat, thin sheet of fibres arising from the alveolar process on each side of the midline is composed of two muscles. The mesial fibres, which pass deep to the Orbicularis oris muscle, are part of the Nasalis muscle complex and form the Depressor septi nasi muscle (Gray, 1964). The distally attached fibres curve laterally to mingle with the Orbicularis oris. They form the Incisivus superioris muscle which is now considered to be part of the bony attachment of the Orbicularis oris (Gray, 1964).

Frena from the dissected specimens and from four other foetal specimens were next examined histologically (Fig. 53). The muscle of the lip does not invade the frenum. Between the muscle fibres and the frenum

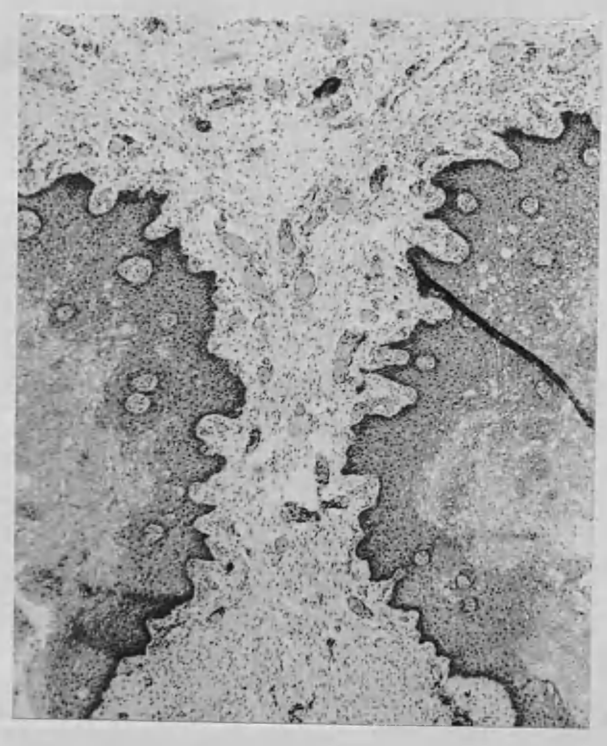


Fig. 53. Human adult. Transverse section through superior labial frenum. Superficial surface at the top of the field. No muscle fibres visible.

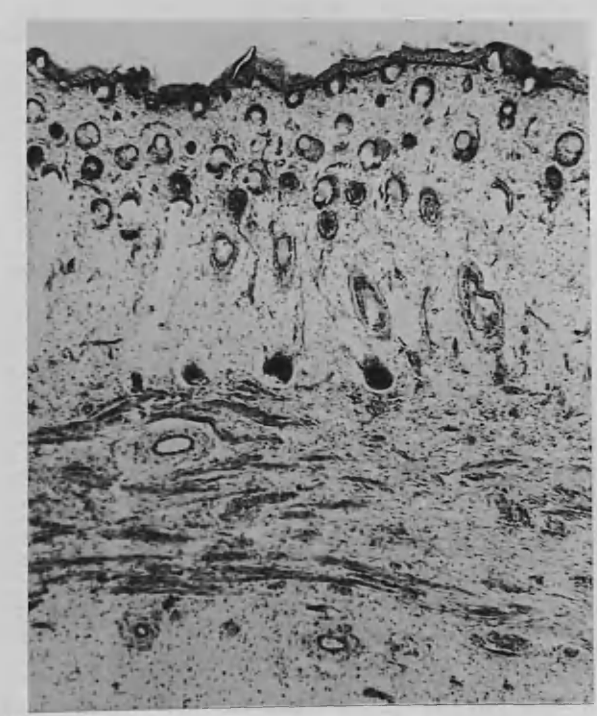


Fig. 54. Human foetus at 17 weeks. Transverse section of upper lip. The midline, with beginnings of a philtral groove, is slightly to the left. The central region deep to the philtrum is devoid of muscle in front of the well-defined transverse fibres of the Orbicularis oris muscle.

there is a zone of loose, vascular, connective tissue. Within the frenum, the fibrous tissue is oriented antero-posteriorly along its long axis. No elastic fibres could be found in any of the specimens when a specific stain was used.

Philtrum and Paramedian Eminences

The name "philtrum", as applied to the fine median sagittal groove on the human upper lip, is incorrect since there is no rhinarial tissue present and Boyd (1933) has suggested that the term "abortive philtrum" be used. However, as the name "philtrum" is widely applied to the human it is accepted in this investigation. The philtrum in most individuals is barely detectable and resembles a fine vertical scar in the centre of the upper lip. It is made less obvious by the presence of two, slightly divergent, vertical ridges lateral to the philtrum. These ridges, which end at the vermilion border, are called the paramedian eminences (Monie and Cacciatore, 1962).

Transverse sections of the upper lip of a foetus at the 17th week (Fig. 54) show that the paramedian eminences are present even at this early stage. The philtrum is just detectable as a slight groove in the midline. The fibres of the Orbicularis oris muscle are well defined. Superficial to these fibres but deep to the paramedian eminences are a few, vertically placed, muscle strands, cut transversely. The central zone immediately deep to the philtrum is almost devoid of these last fibres.

Monie and Cacciatore (1962) have studied the development of the philtrum and paramedian eminences. They have shown that the philtral groove deepens during the later prenatal phase and there is a condensation of the connective tissue deep to it. There is only slight development of the superficial vertical muscle fibres deep to the paramedian eminences during this time but in the adult they are much more obvious. Some fibres of the Orbicularis oris muscle are found in the late foetal and adult specimens crossing the midline without interruption and entering the paramedian eminence of the other side.

Vermilion Border and Labial Tubercle

The vermilion border of the lip is composed of modified mucous membrane very similar to the oral mucosa and, while Man alone among the Primates has such an extensive membraneous border of the lip, Duckworth (1910) has shown that several other species approach

Fig. 55. Human foetus at 17 weeks showing labial tubercle portion of the vermilion border.

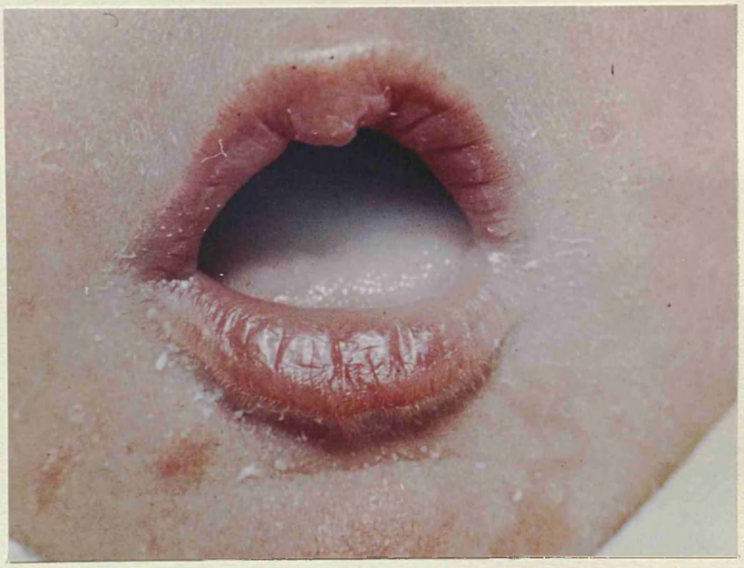


Fig. 56. Human infant 7 days after birth, showing thickened pad of epithelium on the labial tubercle.

the human in this respect. The "Cupid's bow" appearance of the upper lip is most marked in infants and there is a definite change in the morphology of the upper lip during the second year of postnatal life.

The part of the vermilion border known as the labial tubercle is already obvious in a foetus at the 17th week (Fig. 55), and forms a well-defined central swelling separated from the lateral portions of the lip by shallow antero-posterior grooves. In the suckling infant (Fig. 56), the tubercle may become enlarged due to the formation of a thick layer of stratified squamous epithelium. The thickened pad of skin and the grooves separating the tubercle from the rest of the vermilion border tend to disappear spontaneously when the suckling phase is over (Dannenberg, Leider and Bass, 1958) although a partially defined tubercle may persist in individuals with a full everted type of upper lip. It is this loss of the labial tubercle which produces the change in the shape of the lip in the infant during the second year.

The combination of vermilion border, philtrum and paramedian eminences give Man a shape of upper lip quite unlike the relatively flat upper lips of the rest of the

Haplorhine Primates. However, before discussing the implications of these distinctive features, it is necessary to consider the development of the upper lip in mammals generally and thus achieve a better understanding of the factors involved.

DISCUSSION

INSECTIVOROUS SPECIES

Feeding Mechanisms

The first problem is to try to establish what was the arrangement of the snout structures in the early, unspecialised, placental mammals. If this can be done, then it will be possible to determine the patterns of evolutionary changes which have taken place.

There is agreement that the early placental mammals were small, generalised, insectivorous creatures (Lull, 1948). Modern Insectivores bear the greatest resemblance to these early mammals but among present day species it is possible to distinguish obvious specialisations of the snout and thus to eliminate some species from the possibility of having retained the primitive arrangement. Two such groups are the Macroscelididae and the amphibians Limnogale and Potomogale. The proboscis of the Macroscelididae presents obvious advantages in the location of prey but is clearly an extreme development of a feature common to most of the Insectivores. Similarly, the adoption of an amphibious mode of life is accompanied by specialised adaptations suitable to this environment. Both Limnogale and Potomogale show a pattern of snout development which is found in other amphibious species such as the Otter and the Seals. The broad muzzle is covered with vibrissae highly specialised for detecting objects in the water and even changes in the water pressure (Huber, 1930). The nares are situated on top of the muzzle and the rhinarium is much reduced in extent since its tactile function has been largely taken over by the vibrissae.

If there has been a persistence of the primitive snout pattern it must therefore be sought among the other Insectivores, although they too may show specialisations and it is possible that none of the existing species may show the early mammalian arrangement.

The remaining Insectivores show two main types of snout. In most species it takes the form of a cartilage-supported extension in front of the upper incisor teeth, with the rhinarium situated at the tip of the snout and a variable amount of philtrum linking the rhinarial mucosa to the oral mucosa. The other form of snout is found only in the Tree Shrews in whom the rhinarium is situated directly above the upper incisors. It extends orally, without obvious lateral contraction, to form a large part of the upper lip.

It seems reasonable to conclude that the early mammals either possessed an elongated, cartilage-supported snout or a shorter, mainly bone-supported structure. Since the majority of existing Insectivores have the protruding type of snout it seems at first sight that this is more likely to be the primitive arrangement. There is at least one argument in favour of this view. The Tree Shrews are so near the Primates in some respects that several authorities (Simpson, 1945; Le Gros Clark, 1959) place them with the Primates rather than with the Insectivores. Wood Jones (1929) has pointed out that one of the features of Primate development is the tendency to regression of the snout beneath the skull instead of being in front of it. Tree Shrews would seem to have advanced some distance along this path. However, an important distinction is that it is the bony structures of the snout to which Wood Jones is referring and in fact the protrusion of the bony nasal complex in the Tree Shrews is no less, relatively, than in other Insectivores such as the Hedgehog. The elongation of the snout in the Hedgehog is due to the cartilaginous extension.

As regards the olfactory part of the brain, Le Gros Clark (1924b) states that there is some regression in Tupaia compared to other Insectivores and the visual part of the brain in Tupaia shows an advance on that of the other Insectivores. The Tree Shrews, therefore, may have lost some degree of olfactory sensitivity, although Negus (1956) points out that they still have a very efficient olfactory apparatus. An alternative possibility to be kept in mind is that the other surviving Insectivores show a high degree of specialisation of the olfactory mechanisms and that only the Tree Shrews have retained the primitive level of olfactory sensitivity.

Systematic studies of several features of the snout have been undertaken by previous workers. These studies have established what was probably the pattern of the rhinarial markings, facial vibrissae and facial musculature in the early mammals.

Osman Hill (1948) considers that the rhinarium is an important tactile mechanism and that the pattern of markings on the rhinarium - the rhinoglyphics - can be used as an aid in classification. He has shown that the simplest variation is found in the Opossum (Didelphys) among marsupial mammals and the Tree Shrews among placental mammals. However, all the other Insectivores have relatively simple rhinoglyphic markings.

Pocock (1914a) has established that a definite ground plan of the facial vibrissae exists. Where vibrissae are reduced or absent the species tends to be a higher derivitive type. Among existing mammals which still retain a full complement of all the groups of facial vibrissae are the Opossum and the Tree Shrews.

Huber (1930), after investigating many species of mammals, has concluded that there is also a basic ground plan for the facial musculature. This plan is common to marsupial and placental mammals. Le Gros Clark (1924a) has established that the musculature in Tupaia varies from that in the other Insectivores but both from Huber's text and from his diagram of a theoretical early mammalian head (Fig. 57), it appears Huber takes the view that an elongated, flexible snout was not a feature of the early mammals. He also considers that the musculature of the upper lip was very feeble in the central portion and was bound down to the underlying bone in the midline. When the appearance of the Tree Shrews

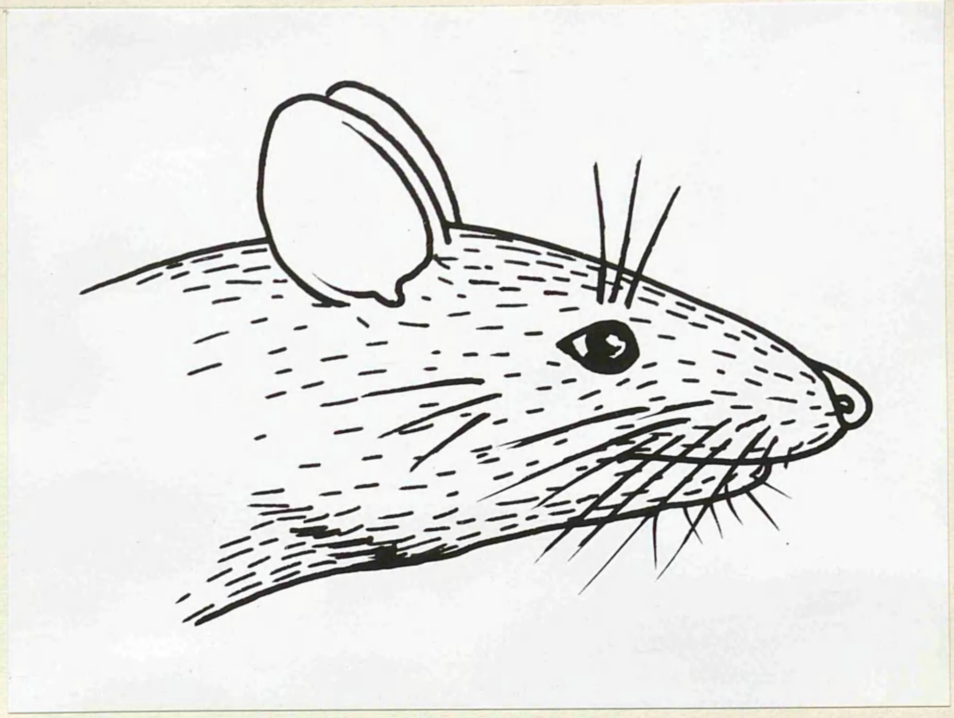


Fig. 57. Diagram of theoretical primitive mammalian head, redrawn from E. Huber's "Evolution of the Facial Musculature", Quart. Rev. Biol. (1930) V: 113 and 389.

Fig. 58. Opossum (Didelphys). Mounted specimen, Royal Scottish Museum.

and the Opossum (Fig. 58) is considered it can be seen that, while the Tree Shrew certainly bears more resemblance to Huber's concept than do the other Insectivores, the Opossum head is even more akin to the theoretical mammalian head.

Tree Shrews and Opossum

The evidence provided by the different anatomical structures suggests that, although the Tree Shrews show definite specialisations, it is at least possible that they may be nearer than the other Insectivores to the primitive pattern by not having an elongated, mobile snout. The Opossum shows many generalised features and is considered to be the most primitive of the marsupial mammals. Simpson (1935) states that it has probably changed very little since the Cretaceous period. The Opossum is similar to the Tree Shrews in not having an elongated snout and also in its general resemblance to Huber's theoretical mammal. It is argued therefore that, while the Tree Shrews' specialisations raise some doubts as to the primitiveness of their particular snout pattern, the appearance of the Opossum is strong support for the view that the Tree Shrews alone among the Insectivores have retained something like the basic mammalian arrangement.

If this hypothesis is accepted then the variations found in the existing Insectivores can be satisfactorily explained. Le Gros Clark (1959) considers that in adopting a terrestrial existence most of the Insectivores have developed considerable specialisation, as the price paid for survival. Olfaction and tactile sensation become of increased importance to nocturnal, terrestrial species and the development of an elongated, mobile snout is of assistance in this process. The amphibious species have followed a different evolutionary path and have developed a deep muzzle covered by vibrissae which replace the rhinarial tactile apparatus.

Snout specialisations of the existing Insectivores may be due principally to a change in their environment since their diet has remained insectivorous in most instances. The adoption of an amphibious, terrestrial or fossorial way of life induces specialisations while the partly arboreal, diurnal existence of the Tree Shrews has permitted the retention of a more generalised sensory dependence. Hence the Tree Shrews may resemble the early mammals, as regards the snout, more closely than do the other Insectivores while the Opossum may be even nearer the primitive pattern.

Upper Lip

It is suggested that the primitive mammalian upper lip had a broad central portion of rhinarial mucosa extending down to the oral mucosa with only a limited contraction to form a broad philtrum. There would therefore have been no labial sulcus in the midline. As the cartilaginous portion of the snout becomes more elongated a stage is reached, as in the Hedgehog, where the rhinarium is some distance away from the oral mucosa and there is only a strip of rhinarial tissue persisting as a narrow philtrum. The hair-bearing skin extends mesially to separate the rhinarial mucosa from the mouth. In some species, e.g. the Soricidae, the hair-bearing skin of the lip forms an almost unbroken strip, possibly to give greater flexibility of the snout by elimination of the inelastic rhinarial tissue. Muscle accompanies the hairy skin in its mesial migration.

The same process is seen in the amphibious species. In _Limnogale_ the rhinarium has moved up the deep muzzle leaving only a thin philtrum separating the two halves of the lip. In _Potomogale_ even the philtrum appears to be lost giving an unbroken, hairy, upper lip. It is argued therefore that Boyd's (1933) hypothesis concerning development of the mammalian upper lip is supported by the findings of the present study concerning the Insectivores.

Superior Labial Frenum

A superior labial frenum was found in several species of Insectivore. In *Limnogale* the frenum appears to be the extension of the philtrum as it goes palatally to pass between the divergent central incisor teeth. This supports the view of Bolk (1921) and Boyd (1933) that the superior labial frenum is part of the philtrum. In the Common Shrew, however, the problem is whether the frenum also represents the vestiges of the now overlaid philtrum or whether it could be a primary structure developed to assist in limiting movement of the flexible snout. It seems reasonable to conclude that the superior labial frenum in the Common Shrew is probably a remnant of the rhinarial extension to the mouth.

MYRMECOPHAGOUS SPECIES

Discussion on this group is limited by lack of information on certain aspects such as the presence or absence of a labial sulcus. Nevertheless, despite the extreme specialisation of the jaws found in some of the species, it is possible to deduce some of the evolutionary factors which may be involved.

Simpson (1945) considers that the myrmecophagous species arose from proto-Insectivores. Their diet is still basically insectivorous although adapted to a very limited range of insects, mainly of the termite variety. A snout bearing a large rhinarium would seem to be vulnerable to possible damage by the insects and the feeding mechanisms may be partly a protective development. In the case of the Aard-Vark the nares are protected by thick tufts of hair on the upper lip and snout. Although the Pangolins still have rhinarial skin present the method of picking up the termites by a long extensile tongue may solve the problem of not bringing the snout into contact with the food source.

The Great Ant Eater shows the most extreme degree of specialisation. The lower jaw is capable of very little movement and the sticky elongated tongue carries the insects up into the tube-like mouth where they are passed back into the oesophagous without being broken up by molar teeth.

CARNIVOROUS SPECIES

Feeding Mechanisms

Carnivores show a limited range of variation of the lip and snout structures particularly among the terrestrial species. Only the Coatimundi shows any striking difference in snout pattern and to some extent in the dentition with its spatulate central incisors and four-cusped molars capable of a grinding action. The Coatimundi in fact has a partially insectivorous diet which accounts for the aberrant secondary development of a mobile snout. Unlike the Hedgehog there is no philtrum or midline sagittal groove but the Orbicularis oris muscle distribution is reminiscent of that in the Insectivores. The muscle extends across the midline but, as in the Hedgehog, it is concerned in movement of the snout.

Most of the Carnivores have an acute sense of smell and the most highly developed olfactory mechanism among mammals is found in the Dog (Negus, 1956). The rhinarium is usually large and most species have a well developed vibrissal system. Flesh is torn off the prey and swallowed without mastication therefore the upper lip is involved very little in the actual feeding process and serves predominantly to carry the vibrissae. The amphibious Carnivores show typical adaptation to their environment with reduction or loss of the rhinarial tissue. The Cat family, although still possessing a keen sense of smell, hunt more by sight than do most of the Carnivores.

Upper Lip

The Carnivores show an almost uniform level of separation of the rhinarium from the oral mucosa and in having a narrow hair-covered upper lip, usually with a shallow, midline, sagittal groove, devoid of hair but not forming a true philtrum. In the Coatimundi, Badger and Racoon the central groove has been lost completely. The lip musculature is usually concerned with vibrissal movement and is otherwise poorly developed.

Superior Labial Frenum

Most species lack a clearly defined labial sulcus, e.g. Cats, and even where a sulcus is present there may be no evidence of a superior labial frenum e.g. Coatimundi. It is only in the Dog that a true frenum is found and this is composed of muscle and not connective tissue. Development of this structure appears to be associated with hypertrophy of the olfactory apparatus. Study of live specimens suggests that only a very limited movement of the central part of the nares is possible and that the rhinarium is not usually brought into contact with an object under investigation. The animal gives a series of short sniffs, drawing air inwards to the extensive olfactory mucosa. The musculature in the infranarial region may assist in this process by partly closing the airway,thus helping to retain the odour. It is probable that the rhinarial skin serves to moisten the air and thus aid olfaction (Negus, 1956). The absence of a superior labial frenum in the Bulldog is almost certainly associated with the recessive position of the rhinarium and the firm attachment of the snout to the underlying bony structures.

HERBIVOROUS SPECIES

Feeding Mechanisms

The type of food available to the herbivores is much more varied than that of carnivores and therefore there is much greater variation of feeding mechanisms. One factor influencing the structure of the jaws is whether the animal is a grazer or a browser. In the grazers, e.g. the domestic Ox, the lower incisors are brought into contact with herbage on the ground and they assist in tearing and cutting the vegetation. To achieve this the upper jaw must be relatively square at its anterior aspect and the lower jaw must protrude as much as the upper jaw. In the browsers, e.g. the North American Moose, the food is composed of leaves of bushes or young trees and an overhanging upper jaw is not a disadvantage.

Another factor is the environment of a species. Where a species inhabits an area with mixed vegetation it tends to be selective and in this process the rhinarium is of importance (Hafez, 1962). If, however, food has to be sought in a rocky environment e.g. the Sheep, the upper lip may require the protection of hair-bearing skin and the animal will crop as closely as possible. Where conditions are climatically unfavourable, a large moist rhinarium may be a disadvantage as in arid desert conditions e.g. the Gazelles, or in regions with prolonged snow e.g. the Reindeer.

The ruminants Tragulidae, Cervidae and Bovidae form a relatively unified group as regards snout and lip pattern. It is among the other herbivores that the greatest variations of the lips and snout are found. In a few species the lips take on a much greater share of functional activity and act both as a source of tactile sensation and as the principal means of drawing herbage into the mouth. The nares are situated well behind the lips in these instances. The Horse, Llama and Camel are examples of this process. The Okapi is interesting in that it retains a rim of rhinarial tissue around the nares, whereas in the Giraffe this has been completely lost. A midline split of the upper lip permits greater activity of the two separate portions. This process is partly seen in the Camel but it reaches an extreme degree of specialisation in the two lip pads of the Manatee by means of which the animal browses on underwater vegetation.

The split upper lip of the Lagomorphs shows complete separation of the two halves, at least superficially.

This split, however, does not seem to be concerned with food gathering but has a double function. The rhinarium is much reduced in the Lagomorphs and the mystacial vibrissae are particularly prominent. The mobile muscular upper lip activates these vibrissae which extend on to the anterior surface of the lip. Furthermore, the lip also plays a part in preventing dust entering the airway while the animal is underground. It acts by constantly applying a downward pull to the paired membranes on the inner aspect of the lip surface. These membranes, with their underlying muscles, assist in the repeated twitching of the nostrils characteristic of the Lagomorphs.

Among species showing excessive development of the snout, the Tapir is a browsing animal and its short proboscis serves as a tactile organ. In the Elephant, however, the highly mobile proboscis is both a tactile organ and a food gathering mechanism. The snout in the Pig is also a highly specialised organ capable of being thrust with considerable force into the earth in the search for roots and grubs. In all these animals the upper lip can still be identified but the lip musculature has become modified to assist in the snout action.

In the rodents, it is the central incisor teeth which are the chief food gathering mechanisms. The upper lip, although almost completely separating the much reduced rhinarium from the oral mucosa, is still primarily a vehicle for the vibrissae which are a prominent feature. The lip is bound down in the midline to the underlying bone.

Upper Lip

Encroachment of the lateral hair-bearing skin on the centrally placed rhinarium is clearly seen in the ruminants. It is of interest that the large rhinarium tends to be found in the more primitive species such as the Chevrotains and Musk Deer. The Ox is exceptional in retaining such a large rhinarial area. Only a few species e.g. Reindeer have a complete, hair-bearing upper lip. Most of the ruminants show a philtrum of varying width.

Despite the tremendous contrasts in the snout structures of the other herbivorous species, various stages of encroachment of hairy lip on rhinarial skin can be identified. The Tapir still has a narrow philtrum of rhinarial skin on the underside of its proboscis but in the Elephant the encroachment is complete and the proboscis is completely covered in hair-bearing skin except for a narrow rim of rhinarial tissue around the nares. The Pig also has a continuous hairy upper lip although this is modified by the enlargement of the snout.

By and large, where there is a considerable degree of specialisation of the feeding apparatus e.g. Pig, Horse, Giraffe, a hair-bearing upper lip, even although modifed, forms a continuous strip separating the nares from the mouth.

Superior Labial Frenum

A superior labial frenum is found in only two of the herbivorous mammals. In the Pig it is a thick fibrous mass which appears to tether the loose layer of fat and muscle on the underside of the snout. Histological examination of the frenum tends to confirm the view that it is simply a restraining, ligamentous type of structure.

In the Lagomorphs it seems likely that the fibrous paired ligament running from the inner surface of each portion of lip to the septum represents a persistence of the rhinarial philtrum which has become modified for the specialised function of assisting in movement of the nostrils.

OMNIVOROUS SPECIES

Strepsirhine (Lower) Primates

Feeding Mechanisms

There is relatively little variation of the snout and lip structures among Strepsirhine Primates (Lorises, Lemurs, Indris and Aye-Aye) when compared to those of herbivorous species. All the Strepsirhines have a rhinarium and an upper lip which shows a varying amount of central philtrum or groove. Most species are partly insectivorous but may include leaves, fruit, eggs or even small birds in their diet (Osman Hill, 1953). Although the upper canine teeth are enlarged there is a tendency to reduction in size and number of upper incisors. A central diastema between the teeth is common. Only the Aye-Aye, with rodent-like incisors suitable for gnawing trees to obtain grubs and the Indris, which has spatulate central incisors and a frugivorous diet, show any striking dental variations. The anterior limbs are used to assist in eating by seizing food and carrying it to the mouth. Most active species possess vibrissae but these are much reduced in the slow-moving Lorises.

Upper Lip

The upper lip in the Strepsirhines is a feeble structure not capable of movement beyond a raising of the lip to expose the canines. It is bound down firmly in the midline. The exception seems to be the Indris in whom an increased level of muscular development is achieved together with a definite increase in the range of possible movement (Osman Hill, 1953).

Le Gros Clark (1924a, 1959) argues that the Tree Shrews should be placed with the Strepsirhine Primates rather than the Insectivores. Although this has not been done in the present investigation the undoubted close relationship of the Tree Shrews to the Strepsirhines suggests that the different types of lip arrangement observed in the Strepsirhine Primates may be looked on as a progressive enclosure of the large rhinarium of the Tree Shrews by the lateral hair-bearing portions of the lip. In Demidoff's Galago and the Lemurs there is still a narrow philtrum. In the Slow Loris the rhinarium, at its lower border, forms a wedge of tissue before narrowing into a philtrum proper. In the Moholi Galago the philtrum is lost entirely, leaving only a shallow sagittal groove beneath which muscle fibres cross the midline. Although this last stage is among the most advanced to be found in the Strepsirhine Primates the

Moholi Galago does not have any labial sulcus in the central region of the upper lip and movement is limited. It is only in the Indris that any notable advance in this direction occurs and the Indris has partial separation of the upper lip from the alveolar process. It therefore has the nearest approach among the Strepsirhines to a Haplorhine type of snout and upper lip.

Superior Labial Frenum

Of the species examined, only the Slow Loris has a superior labial frenum. This is formed by a very short grooved extension of the philtrum as it extends palatally to end at the incisive papilla. The frenum is composed of fibrous connective tissue running in an antero-posterior direction and does not contain muscle fibres. As was mentioned earlier, the Indris and Aye-Aye are also said to have a superior labial frenum.

HAPLORHINE PRIMATES

Feeding Mechanisms

There is considerable uniformity of lip and snout structures in Haplorhine Primates. The rhinarium, except for a vestigial strip in the Tarsier, is completely replaced and vibrissae are much reduced or absent. The nares are situated proximal to the lips in most species except the Baboon. The development of a protruding snout is therefore exceptional. The Proboscis Monkey (Nasalis) has a unique variation of sexual rather than functional importance.

The sense of smell becomes of steadily decreasing importance in the higher Primates compared to the Strepsirhine Primates and the Tarsier. At the same time, the lips in the higher Primates become of greater functional importance. This increased activity is partly associated with use of the lips in mastication e.g. the Chimpanzee. They are also of importance in tactile sensation, despite increased use of the hands for this purpose. The third functional development of the lips is one unique to the higher Primates. This is the extensive use of movements of the face as a means of communication. Whereas in the Lemurs only slight movements of the eyes or ears are possible, a much wider range is achieved by some of the Haplorhine Primates. The lower Haplorhines, e.g. Marmoset, are restricted to up and down "chattering" movements of the lips and jaws. In the more advanced species many different lip movements, including eversion of the lips, are possible. Three which are particularly common are pouting, exposure of the teeth and rhythmic up and down movements of the lips (Zuckerman, 1933). The Pithecoids are also capable of smacking the lips together during grooming or sexual activities.

Much of this increased lip activity is achieved by the development of the lip muscles such as Orbicularis oris (Lightoller, 1928) but also by the vibrissal musculature which becomes modified to assist in facial movements following loss of the vibrissae (Huber, 1930).

The incisor teeth, except in the Tarsier, are of the spatulate type and in adult specimens are always grouped close together without a central diastema but with lateral spaces between the second incisors and the canine teeth to accommodate the lower canine teeth in occlusion.

Upper Lip

All the Haplorhines have a similar lip pattern in that the lip is a continuous strip, of varying depth, not interrupted by a philtrum or groove. A deep labial sulcus is found in all species. This is correlated with increased use of the lips.

The Haplorhine Primates have presumably descended from a series of early Primates who showed some of the stages of lip formation observed in the present day Strepsirhines. Even the Tarsier, which is much the most primitive of the Haplorhines, has an intact upper lip. This suggests that, in the Haplorhine stem, lip development must have been very early.

Superior Labial Frenum

It has been shown that the superior labial frenum in the Haplorhines is essentially a muscular structure. The development of a centrally attached group of muscles is associated with the wide range of lip movements which can be achieved by the more advanced Haplorhines, in particular eversion of the upper lip. There is some variation in relative size of the frenum in the Haplorhines. In the lower species it is a thin strand of tissue due to the poor development of the muscles but in the Baboon and other more advanced species it is a flatter, more broadly attached, structure. This reflects the increased size and importance of the underlying musculature.

CONCLUSIONS CONCERNING FEEDING MECHANISMS IN THE PLACENTAL MAMMALS

It is convenient,before discussing the variations found in Man,to summarise the main changes which have occurred in the snout and lip structures in placental mammals. It is argued that the primitive mammalian snout may have been something like that of the Opossum or the Tree Shrews and the early mammals may have had a generalised dependence on all the sensory receptor mechanisms of the head.

In most of the insectivorous species there has been a forward movement of the rhinarium on an elongation of the cartilaginous portion of the snout. This gives an extended, mobile, tactile organ which is particularly useful in a nocturnal, terrestrial existence. The dentition remains relatively primitive but some tendency to a carnivorous type can be found in a few species which have a more generalised diet. The amphibious Insectivores have evolved a deep, spatulate muzzle, covered with long vibrissae, typical of amphibians in other orders.

In myrmecophagous species the elongation of both the upper and lower jaws and the development of a specialised, prehensile tongue are extreme specialisations of an aberrant group and are associated with the limited nature of the diet.

Carnivorous species have retained a simple structural pattern and a relatively generalised dependence on the various receptor mechanisms of the head. There are certain specialisations, e.g. olfactory development in the Dog, but extreme variations are the exception.

Among the herbivores, the ruminants all have a roughly similar arrangement with variation being confined mainly to size of the rhinarium. In contrast to the relatively simple pattern observed in the ruminants many of the other herbivores show great variations of the feeding mechanisms. These variations can be divided into three main groups. In the first, the snout becomes the predominant factor and serves both as a tactile organ and a food gathering mechanism, e.g. Elephant. In the second, the lips have taken over these functions with a consequent regression of the snout, e.g. Horse. In the third group, the central incisor teeth predominate in food gathering and the rhinarium and vibrissae are the principle tactile receptors, e.g. Rat.

Omnivorous species do not show wide variation of feeding mechanisms although a gradually increasing dependence on the limbs in assisting the feeding process is evident. Within the lower Primates, a range of variation of the snout and lip from something like that of the Tree Shrews to that of a Haplorhine Primate can be found. Higher Primates all employ the lips as important feeding mechanisms, particularly the advanced Primates, who have also developed the lips as a means of communication.

Rhinarium

The rhinarium is an important tactile sensory mechanism closely associated with the oral mucosa in many lower mammals. It probably also has a secondary olfactory function in bringing odours into solution and thus aiding in the recognition of the odour. Where it is partly or wholly replaced there is a transference of its main function to another sensory mechanism,in some instances the vibrissae, in some the lips and in others the limbs. As a general rule, where there is considerable specialisation of the snout structures, the rhinarium tends to be reduced or absent.

Upper Lip

A basic pattern of phylogenic lip development in mammals has been suggested by Boyd (1933). He has described a steadily progressive encroachment of hair-bearing skin from the lateral aspects of the upper lip onto the centrally placed rhinarium. The rhinarial philtrum undergoes a progressive lateral contraction until it eventually disappears, to be replaced by a completely hair-covered upper lip. This hypothesis is supported by the evidence of the present investigation. Within the insectivorous species, almost the whole range of phylogenic development can be traced and, in other groups, some or all of the stages can be identified. Even in those species showing considerable specialisation of the snout and lips the hypothesis remains valid, although considerable modifications may have occurred.

The upper lip is a rudimentary structure in most lower mammals but in a few instances it has become adapted to take over the functions of the rhinarium and vibrissae and to assist to a large extent in feeding. In the more advanced Primates an additional function of communication by means of facial expressions has also been developed. As a general rule, there does not appear to be muscle underlying the rhinarium or philtrum and lip musculature tends to be confined to beneath hair-bearing skin only. The extent of upper lip activity in mammals is related to the level of complexity of the musculature and the degree of separation of the upper lip from the alveolar process.

Superior Labial Frenum

Only a few lower mammals possess a superior labial frenum. In the Common Shrew it is a fibrous, ligamentous structure, probably serving as a means of limiting snout movement. In the Pig it performs a similar type of function in tethering the mass of loose fibrous tissue and skin on the underside of the snout while in the Lagomorphs it may assist in maintaining a free airway. In lower Primates possessing a frenum it is an extension of the rhinarial philtrum and its presence allows some movement of the upper lip. In the Dog and the Haplorhine Primates, however, the frenum is a muscular structure associated, in the Dog, with the highly developed olfactory apparatus and, in the higher Primates, with greatly increased capacity for movement of the upper lip.

The superior labial frenum is found only where there is considerable reduction or loss of the rhinarial philtrum. It seems probable that where the frenum is fibrous in nature it is derived from the remains of the philtrum. The muscular frena observed appear to be examples of convergence.

MAN

DISCUSSION

The human upper lip differs from that of a typical Haplorhine Primate in having a superior labial frenum composed of fibrous tissue only, a sagittal midline groove flanked by two paramedian eminences, and a vermilion border. Since Man is also a Haplorhine Primate the reasons for these differences are most probably related to the contrasting behaviour of the upper lip in the human and the apes.

Superior Labial Frenum

Functionally, it seems unlikely that the human superior labial frenum is of importance, although Tait (1929) has suggested that it may tether the upper lip and thus minimise trauma to the lip during birth. This theory seems improbably since normal delivery is head first but it does recognise the fact that the frenum is much more prominent in the infant. Another possible explanation may be associated with suckling. Gunther (1956) has described an infant feeding problem known as "fighting at the breast". During suckling the upper lip is displaced upwards by the breast tissue until the lip covers the nostrils and cuts off the airway. The infant stops suckling in order to breathe and gives the appearance of actively resisting attempts to feed it. The frenum, although not mentioned by Gunther as a factor, may play a part in limiting this upward displacement of the lip in suckling.

It has long been established that there can be considerable variation in the size of frenum in the adult and in its level of attachment to the alveolar process. This variation in size can be found whether the diastema between the central incisors has closed completely or not. This fact, together with the relatively frequent presence of irregularities in formation, such as the epithelial tags on the free edge of the frenum, supports Crowley's (1956) view that the human frenum is undergoing a process of degeneration. Le Gros Clark (1959) has pointed out that marked variation in a structure and anomalies in its formation are often found where regression is taking place.

The question arises therefore as to what the frenum represents. It is considered, on the evidence of this investigation, that the frenum forms the vestiges of the rhinarial philtrum, thus supporting the view of Bolk (1921). The human frenum is thus akin to the muscle-free superior labial frenum observed in the Slow Loris.

The explanation of the double-stranded frenum occasionally found in the human may be the persistence of a sagittal groove as in the Slow Loris.

The reason for the development of a muscular superior labial frenum in Haplorhine Primates other than Man is possibly associated with their habit of using the labial as well as the buccal sulcus as a temporary food store during mastication. The relative size of the Incisivus superioris muscle in advanced Haplorhines such as the Chimpanzee indicates that it is of importance in movement of the upper lip, unlike the feeble slips of the human Incisivus superioris and Depressor septi muscles.

Philtrum and Paramedian Eminences

The human philtrum has been shown to develop only after embryonic lip formation is complete and it is therefore not a line of fusion of the median fronto-nasal processes (Monie and Cacciatiore, 1962). It is an open question whether the human philtrum represents a persistence of the sagittal midline groove found in many lower mammals or whether it is simply a vertical fold associated with the capacity of the human upper lip to contract laterally. The condensation of connective tissue deep to the philtrum perhaps favours the former view.

The paramedian eminences are among the most distinctive features of the human upper lip compared to that of a Haplorhine Primate such as the Chimpanzee. In the adult human there are two groups of muscle fibres associated with these ridges, a series of vertically placed fibres beneath each eminence and also transverse fibres of the Orbicularis oris muscle which cross the midline and end in the ridge of the opposite side. Neither of these groups of fibres are nearly so well developed in the infant. This suggests that the development of paramedian eminences in Man is associated with the increased complexity of lip movements in facial expressions and in the production of speech sounds, rather than with infant suckling movements. The approximation of the two ridges towards each other is clearly seen during production of the "p", "b" and "o" sounds (Lightoller, 1925). It is considered therefore that the paramedian eminences are the result of increased differentiation of the human lip musculature and the much more complex patterns of behaviour achieved by Man, compared to other Haplorhine Primates.

Vermilion Border and Labial Tubercle

One argument, put forward by Lightoller (1925) and supported by Huber (1930), is that development of a vermilion border of the lip in Man is related to the transference to the hands of part of the activities of the lips in the advanced Primates. Since the hands have taken over the function of food gathering, the lips are no longer required to be powerful prehensile organs, such as are found in the Chimpanzee, and become modified. In this process of modification the Orbicularis oris muscle becomes differentiated into a pars marginalis and pars peripheralis, while the muscles retracting the lips become more predominant. This results in the edges of the lips being dragged outwards to expose the oral mucous membrane and this mucosa becomes slightly modified to form the vermilion border of the lips.

This development may well be the chief factor in the evolution of the vermilion border but another functional factor may also be involved. It is clear that, although the hands are the principal source of tactile sensitivity in the adult, the lips are still very important tactile receptor mechanisms in the infant (Gesell and Amatruda, 1945). Since this is so, the presence of an area of thin, highly sensitive mucous membrane around the lips is advantageous and the vermilion border of the lips almost certainly helps to supply tactile information to the brain.

The labial tubercle, which is such a characteristic of the upper lip vermilion border in the human infant, appears to be part of the suckling mechanism. Presumably its contribution is to give greater mechanical advantage to the lip in bringing pressure to bear on the breast tissue. The thickened pad of epithelium often seen on the labial tubercle is probably a response to the increased friction involved in suckling.

CONCLUSIONS CONCERNING THE HUMAN UPPER LIP

The features of the upper lip which appear to be unique to Man among the Haplorhine Primates are an entirely fibrous superior labial frenum, a vertical midline groove and two vertical ridges, and a vermilion border. It is considered that the human superior labial frenum may represent the vestiges of the rhinarial philtrum of the lower mammals and that the frenum is undergoing a degenerative process. This degeneration explains the marked variation in size of the adult human frenum and anomalies in its structure.

The development of the two paramedian eminences is considered to be a response to the greater complexity of lip movement achieved by Man and to the needs of speech. The eminences are of importance in lateral contraction of the upper lip and in the production of certain sounds. The human philtrum may be a vertical fold associated with the movement of the paramedian eminences or it may represent the vertical groove seen in many lower mammals.

The vermilion border of the lip is probably evolved following a diminution of the need for the lips to be prehensile organs. The lips become dragged outwards and the oral mucous membrane becomes exposed. It is also possible that the development of the vermilion border gives Man a much greater area of sensitive mucous membrane which acts as a tactile receptor mechanism.

GENERAL SUMMARY AND CONCLUSIONS

Initially, an investigation was made concerning the presence or absence of a superior labial frenum in several species of lower mammals in order to understand its possible significance in the human. It was evident, however, that the superior labial frenum cannot be studied in isolation from surrounding structures. Finally, therefore, a systematic survey has been made of the morphology and functions of the upper lip and its related structures in placental mammals.

Specimens examined included live, newly dead, wet-preserved, mounted and dried material. Species are divided, on the basis of their dietary habits, into insectivorous, myrmecophagous, carnivorous, herbivorous and omnivorous groups. This arrangement has been chosen because the structures being investigated are primarily concerned in feeding.

Each dietary grouping is considered in turn and various species are described. Material is illustrated by the use of photographs, half-tone drawings and photo-micrographs. A gross dissection technique is used in most instances, but some small specimens have been fixed and sectioned.

With regard to the feeding mechanisms of the placental mammals it is argued that the early primitive mammals had a snout and upper lip structure resembling that of the present day Opossum and, to a lesser extent, the Tree Shrews.

Existing terrestrial insectivorous species, such as the Common Shrew, have tended to develop a specialised elongation of the cartilaginous portion of the snout. The amphibious, insectivorous species, such as Limnogale, have evolved a deep, broad muzzle covered with highly specialised vibrissae.

Carnivorous species have generally retained a simple structural pattern of the snout and extreme specialisation is found in only a few species such as the Coatimundi or the Seals.

Herbivorous species present much the greatest range of variation of the snout and upper lip structures. In the ruminants a relatively simple pattern has persisted. In some species, e.g. Pig, the snout becomes hypertrophied to form the main tactile organ and food gathering mechanism. In some, e.g. Horse, the lips have taken over these functions and the snout has undergone regression. In the last group, e.g. Rat, the central incisor teeth predominate in food gathering and the primitive tactile receptor mechanisms of rhinarium and vibrissae are retained.

Omnivorous species do not show such a wide range of variation and the lower or Strepsirhine Primates have mostly not developed a snout and lip pattern much in advance of that of the Tree Shrews. The higher or Haplorhine species, however, have evolved an upper lip which has become a mobile structure, reaching an advanced level of muscular complexity in some instances. This is related to their use of the lips in feeding and as a means of communication.

When the findings are considered, the rhinarium in lower mammals is seen to be primarily a tactile receptor mechanism and where it is partly or wholly replaced this function may be transferred to another sensory mechanism such as the lips or the limbs.

There also appears to be a basic pattern of lip development in placental mammals. The simplest arrangement is seen in the Opossum and Tree Shrews where the rhinarium extends orally to form the central part of the upper lip. The musculature of the lateral portions of the lip is feeble. Subsequent lip development involves the encroachment, on the central rhinarium, of the lateral hair-covered parts of the lip until the final stages are represented by species having a continuous, hair-covered lip and absence of the rhinarium. Only a few species, such as the Horse and the Haplorhine Primates, have achieved this level of development. Accompanying this process is the separation of the upper lip from its attachment at the midline to the alveolar process, thus permitting greater movement of the lip. Despite the very great differences in development of the snout and upper lip it is possible to support this hypothesis of lip development throughout the whole range of placental mammals. Those species showing the developmental pattern most clearly are the Insectivores, the Ruminants and the Strepsirhine Primates.

The superior labial frenum in lower mammals is rarely present and where it does occur it appears to serve differing functions in different species. In the Common Shrew and Pig it is a fibrous structure probably helping to stabilise the mobile portion of the snout. In the Dog it is a muscular structure acting on the mobile, cartilaginous snout probably as an aid in the highly developed olfactory mechanism. In the Haplorhine Primates it is also muscular and in this instance appears to assist in the movements of the upper lip.

The human upper lip differs from that of other Haplorhine Primates in having a fibrous superior labial frenum, a vertical midline groove, paramedian eminences and a vermilion border. It is considered that the human superior labial frenum is a vestigial structure derived from the rhinarial philtrum and that it does not appear to have any functional significance. The midline groove, or so-called philtrum and the paramedian eminences, are probably developed as a response to the increased refinement and complexity of the oral musculature and the specialised use of the human lips in speech.

The development of a vermilion border of the lip in Man may be related to the retractors of the lips becoming more predominant than the contractors and hence some of the oral mucosa is exposed. However, there may be another functional factor involved and the exposure of the oral mucous membrane may be to provide a highly sensitive tactile surface in addition to the other tactile receptor mechanisms of the human.

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