A study of the ontogeny of the molar dentition of some Microcheiroptera with special reference to the development of occlusal relations

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P.M. Aldridge B.Sc.

The Royal Holloway College
Englefield Green Surrey
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ABSTRACT

The functioning of the molar teeth depends upon a correct relationship between the cusps of the two jaws. This is perhaps less evident in man owing to the flatness of the molar crowns; accordingly, an animal with pointed, interlocking cusps was studied - the insectivous bat <u>Hipposideros</u> <u>beatus</u>. The purpose of the work was to find the growth processes involved to ensure a correct mutual positioning of the erupted teeth in an animal where normal occlusion is essential. So that with a knowledge of normal occlusion, factors causing malocclusion may be better understood.

Graphic and wax-plate reconstructions were made of the teeth and jaws in a series of <u>H. beatus</u> embryos. The methods of reconstructing this difficult material are described in Chapter II.

In Chapter III the adult dentition and the occlusal relations of the teeth are described. The latter aided by a slow-motion cinematograph study of the chewing action in a British bat.

Chapter IV is concerned with the growth and calcification of the tooth germs.

Chapter V is concerned with the movements of the tooth germs during ontogeny.

In both these chapters the growth of the upper toothrow is compared with the growth of the lower toothrow.

It is found that the intrinsic growth of the tooth germs is such, that at all stages, models of teeth, that will later occlude, will fit if put together. However the teeth do not occupy their correct positions relative to each other until eruption. To attain these positions complicated growth movements take place. These movements, and a possible explanation for them are described.

Eruption appears to be the terminal phase of these growth movements.

The results of the investigation are discussed in Chapter VI.

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CONTENTS

CHAPTER I

INTRODUCTION

The functioning of the teeth depends upon a correct relationship between the cusps of the two jaws. This is perhaps less evident in man owing to the obtuseness of the molar cusps. However in animals such as bats, with high cusped, deeply interlocking teeth, the attainment of normal occlusion is essential; should malocclusion occur, the animal would not survive.

The purpose of the present work is to establish whether the interrelations between the molar cusps in normal occlusion have a basis in ontogeny, and if so, to elucidate the growth processes involved in ensuring a correct mutual positioning of the teeth. Thus with a knowledge of the factors causing normal occlusion, causes for malocclusion may be better understood.

Much work has been done on the early development of individual teeth, on mechanisms of eruption, and on functional occlusion in adult dentitions, but little work has been done on the development of whole dentitions from an occlusal point of view.

Work on the early development of teeth is reviewed in most of the current text books of histology and embryology.

Sellman (1946) established that oral endoderm, neural crest and oral ectoderm make up the material necessary for tooth formation.

Glasstone (1936, 1938) has worked on cuspal development and has shown that young molar tooth germs of rabbit grown in vitro and in vivo have remarkable powers of self organisation. This has also been shown by Gerstner and Butcher (1958) for rat incisor, and Sellman (1946) for urodele teeth. Glasstone in her paper, showed that even in transplants made at the cap stage, a recognisable cuspal pattern developed.

Beust (1928) working on growth and calcification of the cheek teeth in the pig showed that the anterior cusps of the teeth calcify first. The order of calcification of the cusps in mouse molars, and deciduous cheek teeth of the cat, has been worked out by Gaunt (1955, 1959), and in man by Kraus (1961).

On tooth movement, Orban (1928) was the first to notice that the base of the tooth remains relatively constant whilst the crown grows away from it.

On eruption, Sicher (1942) and Gillet (1955) demonstrate the growth of the tooth pulp acting as an important factor in eruption.

Sicher and Weinmann, in joint and separate papers (1941, 1942, 1944), and Grüneberg (1940), have shown the importance of bone deposition in guiding the eruption and also the development of teeth. Grüneberg has shown that a gray lethal gene in mice, prevents bone resorption, and this prevents normal growth of the teeth.

Much work has been done on malocclusion caused by disturbances of bone, notably by Hellman (1933, 1920, 1942). He has also worked on normal occlusion in the adult dentitions of a wide variety of mammals (1920), each time relating form and position to functional occlusion.

Becht (1953), has used slow-motion filming methods to elucidate chewing action, and has written accounts of chewing, the structure of the mandibular joint, and the masticatory musculature in a number of Carnivora, Rodentia and Ungulata. He has also reviewed the work on functional occlusion before 1953. Since that date Butler and Mills have written comprehensive comparitive accounts of molar occlusion, Mills (~~1954~~, 1955, 1961) working on chewing action in Primates and Insectivora, and Butler (1952) on molar occlusion in the Perissodactyla.

Little work has been done on the development of normal occlusal relations. Gaunt (1959) mentions that in the cat the spacing of the buds, when they first arise on the dental lamina, resembles the spacing of the primary cusps (paracone and protoconid) of the completed dentition. He goes on to show that with subsequent growth of the jaws, growth of the dental lamina is such that the spacing remains relatively constant. However in the cat the upper and lower jaws do not lie directly one above the other throughout development, but come to do so only as the teeth erupt.

In the following study, the development of the cheek teeth in the insectivorous bat *Hipposider~~u~~os beatus* is described with special emphasis on the development of occlusal relations. The fully erupted adult dentition is described first, then the growth and calcification of the individual teeth. Lastly the developmental movement of the teeth, and a possible explanation of the mechanisms involved therein are described. The discussion constitutes Chapter VI.

Nomenclature and Terminology

The following abbreviations are used:

The teeth are identified by capital letters denoting the series to which they belong. Thus, I = Incisor; C = Canine; PM = Premolars; M = Molar. The position of the teeth in the series is indicated by a terminal super-, or sub-, script number, the position of the number denoting whether the tooth is in the upper or lower jaw. Thus, M^2 is the second upper molar. The superscript or subscript number can be used to indicate the homology of the tooth with the full insectivorous dentition. However it has been found more convenient in this study to ignore such homologies, and to use the figure to denote the position of the tooth in the toothrow in question. Thus, in H. beatus the two upper premolars represent the second and fourth premolars of the primitive condition, but in Chapter III they will be referred to as PM^1 and PM^2.

The term dilambdodont is used in the sense implied by Butler (1937), that is, dilambdodont means having two outer V shaped cusps as in Figure A.

The length of tooth row is measured from the anterior base of the canine to the posterior base of the third molar.

Length of mandible is abbreviated as Mn-length and is measured from the symphysis to the posterior border of the condyle, and is obtained from plan-view reconstructions.

Length of maxilla is again measured from plan-view reconstructions and is the distance between the anterior border and a point just medial to the zygomatic process.

Plan-view reconstruction refers to a dorsal-view or rather to a projection in the horizontal plane of the head.

Side-view reconstructions refer ideally to side-view or projections in the sagittal plane of the head. However, according to how the head has been sectioned, a "side-view reconstruction" may in fact constitute a slightly oblique view of the head.

In Chapter IV the terms 'occlusal', 'anterior' and 'posterior' refer to those surfaces of the teeth, as they will be in the erupted dentition, and so takes no account of the growth movements of the teeth; this is further explained in Chapter IV.

Occlusal surface refers to the ventral surface of the upper teeth and the dorsal surface of the lower teeth, or rather those surfaces that will be ventral or dorsal when the teeth have erupted.

Cusp terminology - after Osborn. See Fig. A.

Criterian of age. In studies of this kind where the embryonic age is not known, head-length is usually taken as an indication of the stage of development reached. However in the present study, mandibular-length proves to be a more reliable guide, since in two cases a pair of embryos with the same head-length (measured after fixation) exhibit different stages in tooth development (stages 3 & 3a, 6 & 6a) whereas no such anomolies are observed when mandibular-lengths are taken as the criterian.

A Commissure (Chapter III) is a ridge joining two cusps.

Drift or translatory movement (Chapter V) refers to a bodily movement of the tooth germ through the tissues.

CHAPTER II

MATERIALS & METHODS

1. Graphic and wax model reconstructions (page 7) were made from prepared serial sections of 13 embryos of Hipposideros beatus (fixed in Bouin, decalcified in dil. nitric acid. Stained in Masson's trichrome stain).

The series ranged from Mn-length 0.580 cm to 0.973 cm, listed in Table A.

2. The Cheiropteran collection in the British Museum, (dried skulls and preserved specimens).

3. Dried skulls and specimens of Hipposideros cyclops and H. tridens preserved in 70% alcohol.

4. Adult and young of the British pipistrelle bat Vespertillio pipistrellus collected at Saxmundham in Suffolk, by suspending mist nets, at dusk, in their line of flight.

5. Adults of the British greater horseshoe bat Rhinolophus ferum equinum insulans collected in February and April, 1961, from the Tor Bryan Caves, South Devon. The bats were collected from the cave walls when asleep.

A slow motion cinematograph study made of the chewing action in these bats is described in Chapter III, as are other Methods for determing occlusal relations of the teeth.

Graphic Reconstruction

The main problem in reconstruction from histological sections is the establishment of reference points in the material. Once established, these reference points, which must occur in each section, can be superimposed on to a base line drawn on graph paper, from this base line the structures to be reconstructed can be marked off.

It is essential that the reference points or lines follow definite known courses through the original block.

First the classical method for graphical reconstruction will be described (A) and then modified methods of reconstruction that can be used on difficult material will be described (B). A new modification that can be used on material already cut and sectioned will be described (C).

A. The classical method of graphical reconstruction when the sections are cut exactly transversely to the main axis of the material so that the midline can be used as a reference point is:

> A base line YY (see Figure 1) is marked along the Y axis of a graph sheet. Along this base line the sections are marked off to scale according to the thickness of the section and the magnification of the projector. The sections are then projected in series onto the paper, the midline of the material is orientated along YY, and the structures are marked off along the XX axis. e.g. structures on section 28 are marked off along XX 28.

B. In difficult material where no obvious axis or guide line is present, or only one which curves in the plane of sectioning, a method of using artificial reference points must be devised.

This is done by others in a number of ways e.g.

1) by embedding the material alongside a plate of stained tissue or elder pith. Sections are then cut at right angles to this plate; and its face seen in each section provides a base to which the position of organs can be referred (cited in Pantin 1948). Burston and Thurley (1957) describe a complicated technique of accurately placing strips of nerve tissue instead of elder pith in the wax block.
2) Heard (1931) uses a photographic method for orientating serial sections.
3) Pusey (1939) uses the side of the wax block as a reference point. This method involves painting round the outside of the paraffin ribbons before the wax is removed, so that the sides of each section are clearly defined and can be used as accurate reference points.

However Pusey emphasises the following points:

1) the block must be cut accurately;
2) the block must be trimmed close to the material and along the same axis;
3) the cutting must be exactly at right angles to the block;

4) sections must be cut as thick as possible and not less than 13u. Below this the ribbon fails to expand to proper proportions and an error is introduced;
5) when using the microprojector all sides of the block must show at once.

C. In the present study difficulty in establishing guide lines arose on 2 points.

A) The heads were sectioned slightly obliquely so that the course of the midline through the block was not known.
B) In side-view reconstructions of the head no tissue was straight and so no suitable known reference line was present in the material.

In the following methods of reconstruction, a way of determining the angle of obliquity is given. For side-view reconstructions a modification of Pusey's method is described whereby the sections (which do not conform to the essential requirements stipulated by Pusey above) can be reconstructed with a fair degree of accuracy. It is a method that can be used or sections that are already stained and mounted.

First the angle of obliquity is dealt with, 1. This is important in both plan-view and side-view reconstructions. Then the method of side view reconstruction is described, 2.

1. Obliquity of cutting was resolved along 3 co-ordinates at right angles to each other. These could be represented by the edges of the original block, if one imagines the block to have been a rectangular prism. See Figure 2.

The head could be said to roll in the plane AB; pitch in the plane AC or yaw in the plane CB.

The angle of rolling was called R, the angle of pitch, P, and the angle of yaw Y. Angles R, P and Y were determined as follows: Angle of roll by measuring the angle between the midline of the material and the perpendicular to the base of the wax section. When the base of the section could not be determined, an alternative method was used involving the scratch lines in the section. Scratch lines could be found in most sections, and as these were perpendicular to the base of the wax section, the angle between any scratch line and the midline of the material was equal to angle R.

When greater than 0° angle R caused distortion due to an oblique viewpoint in side-view reconstructions of the head, but not in plan-view reconstructions.

Angle of Pitch

To find the angle of Pitch, small scale, side-view reconstructions of gross structures in the material were made. In the present study, the out-line of the head, lower jaw, the eye, and the base of the internasal septum were reconstructed. From the lower jaw the long axis of the head could be determined, the angle between it and the Y axis equalled the angle of pitch, and was measurable. This is shown in Figure 2 IV.

Angle P introduced an error in plan-view reconstruction, when this angle was large, as in stage 7 (Mn-length 0.71 cm) a foreshortening of the structures resulted. In measuring mandibular lengths from plan-view reconstructions, it was essential to know angle P. (Mandibular lengths in the present study were checked from measurements of side-view reconstructions).

Angle of Yaw

The angle of yaw was determined by plotting a plan-view reconstruction of structures on both sides of the head which were equal distances from the mandibular symphysis. Unless the angle of yaw was neglible, the reconstruction appeared lop-sided, due to the structure on one side of the jaw having been sectioned earlier than the same structure on the other.

To demonstrate the method of finding the angle of yaw, the following example will be taken:

Figure 3 shows PM^{2}_{L} and PM^{2}_{R} on opposite sides of the head. It is assumed that they are at equal distances from the mandibular symphysis i.e. they are directly opposite each other in the head. Therefore the line M_1 M_1 will be at right angles to the true midline of the head shown by line NN. Therefore the angle between NN and the base line YY = the angle of yaw.

This is checked by repeating the above using teeth M^{2}_{L} and M^{2}_{R}, or by using any other paired structures at equal distances from the front of the snout, and from the midline.

In the plan-view reconstructions made, the angle of yaw was corrected. However for side-view reconstructions foreshortening due to the angle of yaw was not corrected, for when it was below 5°, the effect of foreshortening was found to be geometrically insignificant.

Methods for correcting angles R P and Y in the embryos of H. beatus

a. In plan-view reconstructions

Angle of Pitch

Figure 4 shows a tooth cut obliquely.

GM = long axis of tooth

A, B, C, D etc. = microtome sections

GN = apparent length of tooth

Angle P = angle of pitch

$$\text{True length of structure} = \frac{\text{Apparent length}}{\cos P.}$$

$$\text{i.e. } GM = \frac{GN}{\cos P.}$$

Since GN and cos P are observed values, GM can be determined.

This method was used for checking Mn-lengths and tooth row lengths determined from side-view reconstructions.

The maximum difference found between the Mn-length measured from side-view reconstructions and from this method proved to be less than 1%.

This method did not correct parallax errors.

Angle of Yaw

The following example demonstrates correction for the angle of yaw. In stage 12 (Mn-length 0.937 cm), from a posterior view point, the angle of yaw was found to be 3.5° to the right of the midline. Thus the left hand teeth were more anteriorly placed in the block than the right, as shown in Figure 5a & b. To correct for this obliquity, the known course of the midline was used as a base line instead of the y axis of the graph sheet. i.e. a line 3.5° to the left of the Y axis, see Figure 5c. NN represents the course of the true midline of the head.

No error due to parallax was introduced.

b. In side view reconstructions

Angle of roll was corrected by keeping the midline of the embryonic head at right angles to the base line (see method below).

The angle of yaw was not corrected in the present study because the percentage error that it introduced was too small to be significant. However the angle of yaw did introduce an error due to parallax particularly in the later stages when the teeth were very unevenly shaped.

Parallax

Parallax could not be corrected in the reconstructions. However its effect could be compensated for by making both plan-view and side-view reconstructions and from subjective experience, aided by wax models of key stages.

Other Sources of error

The curvature of the lens in the microprojector, the uneven stretching of the material in each section, and uneven shrinkage of the material during fixation were all possible sources of error. Each of the above types of error became more apparent as the distance between the base line and the structures being reconstructed increased. Error due to curvature of the lens was reduced as much as possible by using the same area of the microprojector field for corresponding areas in each successive section. The maximum amount of error due to the microprojector was found to be 3.33%, i.e. 2 mm in 60 mm. Uneven stretching of the wax, or shrinkage of the material, could only be corrected by the method of "best fit" i.e. by taking the mean through the dotted outlines of the graphical reconstruction. For this a knowledge of the material was necessary. Graphs, corrected for angles of pitch, roll, and yaw showed very little "smoothing out" of the lines to be necessary. Each point was seldom more than 3 mm from its correct position in a magnification field of x 60, and usually much less.

2. Side-view graphical reconstructions

The following modification of Pusey's method was used. Here, it was necessary to determine a reference line so that sections could be superimposed. Due to the sections being less than 13u thick the stretching of the wax in successive sections was uneven. (see Pusey above). Due to this and to the other factors mentioned above, e.g. the error due to the projector lens, it was obviously advantageous to have the reference line as close as possible to the structures being investigated. Therefore a method of establishing a "natural" reference point in the material was devised. This was done as follows:

1) The position originally held by the edge of the wax block in each section was marked in. This was just visible under a binocular microscope as a thin film of stain, or as a straight, but discontinuous line of dust particles. These markings were usually not visible in the image projected by the microprojector. Therefore they were marked by small dots of Pelikan ink. The ink was applied with a mapping pen on to the cover slip immediately above the dust marks. These dots showed up well on the microprojector image, and therefore indicated the line that represented the edge of the wax block.

The Pelikan ink having a low surface tension, adhered to the glass easily, but it was difficult to make markings less than 50u in diameter, the average diameter of the dust particles being 5u. This, together with the difficulty of assessing the exact position of the block edge, and the fact that the latter was often curved, caused a high percentage error to be introduced. In the present study this error averaged ± 3 mm for every point made (when reconstructing with a magnification of x 10).

2) Therefore a primary graph was made of gross structures only. i.e. the outline of the head, and the course of the mandibular and maxillary nerves.

By smoothing out the irregularities in the reconstructions, the courses of the above structures through the wax block was determined.

3) These "primary" graphical reconstructions made at a magnification of x 10 were then enlarged to a magnification of x 20 or x 30, and were themselves used as base-lines, for a "final" reconstruction i.e. a reconstruction of the teeth.

The course of the mandibular nerve was taken as the main base-line. The method is demonstrated in Figure 6.

Wax model reconstruction

A modification of Born's method of wax model reconstruction was used. Early models were made with Ash's Grade V dental wax, and all subsequent models with Ash's silicone toughened wax. The latter proved better in so far as the plates of wax were easier to stick one on top of the other. The toughened and therefore less brittle wax allowed finer structures to be reconstructed. However it tended to warp to a greater degree than the grade V wax and so the models were less permanent. The wax sheets were uniform 18.7 cm x 9.5 cm, and averaged 1.2 mm thick.

The magnification on the microprojector was fixed at x 60. The thickness of each wax sheet therefore represented the thickness of 2 microtome sections (cut at 10u).

The irregular shapes of the teeth, particularly the high cusps, when cut obliquely caused difficulty in piling one section on top of another, therefore each cutout was extended to include an artificial guide line. This was done as follows:

The sections were projected in the normal way, but onto graph paper. The latter was orientated so that the midline of the head fell along a base line on the Y axis. The tooth (including the calcified areas of the crown and the exposed root opening) and the associated alveolar bone and nerve were then traced. This was done for alternate sections. See Figure 7.

The tracings were transferred onto each sheets of dental wax, and the outlines cut out. However the outline was made to include a strip of wax 5 mm wide and parallel to the baseline representing the midline of the head. See Figure 7. Bridges of wax were left between unconnected parts so that no small pieces were left out of the cutout. The areas of calcification and of root openings were painted in different colours. The wax sections were assembled in series, and the 5 mm strips of wax aligned in a straight row. This caused the other parts of the reconstruction to fall automatically into place. Then, by checking against side-view and plan-view reconstructions, small alterations were made. For example, in reconstructing the third lower molar a side-view reconstruction of the base of the mandible to the same scale, was made. See Figure 8. The model was then laid on its side and the wax plates of the model were placed to coincide with the outline of the mandible in the graphic reconstruction. In the same way the outline of the wax model in plan-view was made to coincide with plan-view reconstructions.

The differences in shrinkage and spreading of the embryonic section (see page 14) and the fact that the 5 mm guiding strip was some distance from the tooth (usually 6 cm @ x 60 = 1 mm) caused discrepancies to arise between one wax section and the next, when the guiding strips were lined up. This gave an error of up to 10%. Therefore it was necessary to smooth out these discrepancies by the method of "best fit", the latter based on plan-view and side-view reconstructions. In this way the amount of error could be reduced considerably. Very unevenly shaped teeth retained an error of approximately 4%, and on simple outlines less than 1%.

The wax plates were sealed together by running a hot scalpel blade between adjacent plates, and by pushing wires through strategic points of the model e.g. through the bases of the sections.

Once the wax plates were fixed permanently in position, the wax bridges and 5 mm guide strips could be carved away leaving only the model of the tooth.

Once the shape of a tooth was known other models could be made without using the wax guide strips.

Figures 9 and 10 shows photos of completed models.

CHAPTER III

A DESCRIPTION OF THE MORPHOLOGY AND OF THE OCCLUSAL RELATIONS OF THE FUNCTIONAL DENTITION OF HIPPOSIDEROS BEATUS

It is proposed to give a detailed description of the fully erupted molar dentition of H. beatus with special attention to the morphological differences between the molar teeth. This will be followed by an investigation to elucidate the occlusal relations of the molars.

As the occlusion in this species is affected to a certain extent by the morphology and position of the antemolars, the description is extended to include these.

Morphology

In the following description it is assumed that the mandible or skull is viewed with the teeth uppermost, therefore, in the case of the maxillary teeth, they are viewed with the skull upside down. Thus, when it is stated that one part of a tooth is higher than or above another, it means that the former is further from the gum margin than the latter. The advantage of this method is that the teeth are described as they are viewed, and this has been found to lead to less confusion than if they were described as they occur 'in situ' in the head.

The teeth of H. beatus are small and translucent.

Mn. toothrow = 6.3 mm; Mx. toothrow = 6.1 mm.

The molars are approximately 1.5 mm. in length.

Dental Formula: $2 \times \frac{1 . 1 . 2 . 3 .}{2 . 1 . 2 . 3 .} = 30$,

or to signify the origin from the primitive insectivorous dentition, it can be written:

$$2 \times \frac{020 \cdot 1 \cdot 0204 . 123 .}{023 \cdot 1 \cdot 0204 . 123 .} = 30 \text{ (Miller 1907)}$$

The antemolars in the upper jaw consist of one incisor, one canine, and two premolars, and in the lower jaw of two incisors, one canine, and two premolars. They are shown in Figure 11.

Incisors

The incisors are small and do not occlude with each other. They play a very limited part in mastication.

The upper incisor is a small lobate tooth situated centrally on the edge of the small flexible premaxilla. The cutting edge is bilobed, the anterior lobe being greatly enlarged so that the incisor curves towards the midline of the premaxilla. (Figure 11).

The lower incisors: I_2 resembles I_1, and is a small spade-like tooth. The length is greater than the height or width; the crown is well differentiated from the root. The cutting edge is trilobed, the lobes being more or less equal. I_2 is slightly larger than I_1, and is located partially behind it, so that the posterior lobe of I_1 overlaps by half the anterior lobe of I_2. (Figure II).

Canines

The canines are large and caniniform, the upper being larger than the lower.

The upper canine has by far the highest cusp in the dentition, and is situated at the extreme anterior border of the maxilla. The root extends to a position just dorsal of PM^2. The body of the tooth is curved so that the crown is in line with the rest of the toothrow. The tooth is flattened in a buccal-lingual direction to give a blade-like appearance. The anterior surface is smooth, except for a small ridge upon which the point of the lower canine rests when the jaws are closed. With age, this ridge is worn into a ledge. A ridge from the tip of the canine extends backwards, becoming flange-like at the base, and giving rise to a small posterior cusp. There is a lingual heel which receives the tip of PM_2 when the jaws are closed.

The lower canine is not curved. It is semi-conical with a rounded anterior surface and a flattened posterior surface. In cross section the tooth appears semi-circular. A cingulum extends around the base of the tooth and gives rise to a small cusp on the posteior lingual side. This small lingual cusp lies in close contact with PM_1.

Premolars

These are caniniform, but smaller than the canines.

Upper Premolars

PM^1 is much reduced. It is circular in outline, and in height reaches only to the level of the cingulum of PM^2. PM^1 is situated immediately behind the small posterior cusp of the upper canine, that is, in line with the buccal border of the toothrow.

$\underline{PM^2}$ is essentially similar to the upper canine (see Figure 11), except that the main cusp is not so high. But PM^2 also resembles the posterior half of a true molar (see Figure 12). It is in direct line with the molar teeth, and functions in a similar way.

A flange-like ridge from the main cusp extends diagonally in a posterior buccal direction to meet, and to form a continuous line with, the parastyle of M^1. A cingulum is present around the base of the tooth, which is small on the buccal side but enlarged on the lingual side, where it forms a heel and a small anterior cusp.

Lower Premolars

$\underline{PM_1}$ is a small single cusped tooth with two small crests extending from its tip, one to the anterior and the other to the posterior borders. A small cingulum is present along the buccal and lingual sides.

$\underline{PM_2}$ is similar to PM_1, but larger and more triangular in crown view, having three small ridges running one anteriorly, one posteriorly, and one buccally from its tip.

Molars

The molars are typically insectivorous dilambdodont teeth. The upper molars are tritubercular, and the lower molars are tuberculosectorial.

Upper Molars

Each upper molar is set obliquely in the jaw, since the shallow buccal region rests on an elevated buccal ridge of the maxilla, whilst the deeper lingual portion extends downwards towards the palate. As can be seen from Figure 12, the high buccal region is sharply demarcated from the lower lingual portion.

The First Upper Molar

$\underline{M}^1$: the width is approximately equal to the length; the lingual height is greater than the length (by about 7/5ths); and the buccal height is less than the length (by about 1/2).

In lingual view the anterior border is smoothly convex, and the posterior border is concave. The crown bears three main cusps corresponding to those of the primary tritubercular tooth. These are the paracone (anterior-buccal), the metacone (posterior-buccal), and the protocone (anterior-lingual). At the extreme buccal edge of the tooth are three small cusps, the buccal styles, namely the hook-shaped parastyle (anterior), the mesostyle (medial), and the metastyle (posterior). The paracone and metacone are joined to the parastyle, mesostyle, and metastyle by four commissures. These are numbered according to Figure A. Thus, commissure one is the most anterior, and connects the parastyle to the paracone.

The commissures are sometimes referred to collectively as the ectoloph. The commissures together with the cusps that they join form a conspicuous W pattern.

On the buccal side, the commissures slope gently to form two shallow valleys, one between the parastyle and mesostyle and the other between the mesostyle and metastyle. By contrast, the lingual sides of the commissures descend almost vertically to the protocone.

The protocone is placed at a lower level being approximately half-way down the lingual side of the crown. It is anteriorly situated, and is almost directly lingual to the paracone. In a freshly erupted tooth the protocone has a sharp cutting edge which slopes buccally to the valley between the parastyle and metastyle, but with age the protoconal edge is soon worn flat. The lingual edge of the protocone extends forward, as a small crest, past the base of the paracone to the parastyle. There is no hypocone (absence of hypocone is a generic feature of <u>Hipposideros</u>), but there is a low posterior heel. A cingulum extends around the base of the tooth just above gum level.

The Second Upper Molar

M^2 is similar to M^1, but is slightly larger and differs in proportions as follows:

1) the protocone of M^2 is more anteriorly placed, being only just posterior to a line connecting the paracones of M^2 on both right and left hand sides of the skull.
2) the paracone of M^2 is nearly equal to the metacone whereas in M^1 the paracone is considerably smaller than the metacone. In M^1 the commissures increase

markedly in length from 1 to 4. In M^2 the commissures are approximately all the same size, and the angle at the paracone is almost equal to the angle at the metacone.

3) the parastyle of M^2 is larger than the parastyle of M^1.

The Third Upper Molar

M^3 is smaller than M^2 or M^1. From an occlusal viewpoint it is triangular in outline. The width is greater than the height (by about 4/3rds.), whilst the lingual height is greater than the width (by about 7/6ths.), and the buccal height is much less than the width. The buccal border of M^3 slopes lingually, so that it lies at an angle of 30° to the buccal borders of M^1 and M^2. Also, the crown slopes downwards, so that the posterior buccal cusp is lower than the anterior buccal cusp.

It is generally believed (Miller 1907, Allen 1940, Winge 1941, Grassé 1955) that the third molar in the Cheiroptera has been derived from a form similar to the second molar by reduction in the posterior region of the tooth. Indeed, in many respects, M^3 resembles the anterior region only of M^2. The parastyle, paracone, mesostyle and protocone are all present, whilst the posterior metaconal region is small and the metastyle is absent. There is no posterior heel in M^3, and there is no lingual cingulum. M^3 differs from the anterior part only of M^2 in the following ways:

In M^3 the protocone is more anteriorly placed being directly lingual to the paracone, the lingual part of the tooth is smaller, and commissure 2 is shorter in M^3 than in M^2. There is also a difference in the angle between the first and second commissures in M^2 and M^3, being smaller in M^3.

Lower Molars

The lower molars are smaller than the upper molars in height, and more so in width. In many respects the crown view of a lower molar resembles a mirror image of the buccal portion only of an upper molar.

The three lower molars are much alike, each having six cusps.

The First Lower Molar

M_1: the length is about twice the width, whilst the buccal height (of protoconid) is approximately equal to the length, and the lingual height (of metaconid) is about 2/5ths. of the length.

The tooth can be divided into two parts - an anterior part corresponding to the trigonid of the primitive tritubercular tooth, and a posterior part, the heel or talonid. The trigonid supports three cusps arranged at the apices of a triangle - the buccal protoconid, the anterior paraconid, and the lingual metaconid. The talonid supports the remaining three cusps, and these are arranged so as to enclose a central talonid basin. The talonid cusps are the buccal hypoconid, the lingual entoconid, and the small posterior hypoconulid.

Unlike the buccal cusps of the upper molars, the six cusps are not approximately equal in height; the protoconid is tall compared with the others, and the hypoconid, particularly in worn teeth, is low. See Figure 13.

The cusps are joined by commissures which are numbered 1 to 5, after Miller (1907). Commissures 1 to 4 join the paraconid, protoconid, metaconid, hypoconid and hypoconulid, and form an M shaped pattern similar to the W pattern found in the upper molars, but in reverse. The pattern is not an exact reversal, because the third commissure does not reach the metaconid, but arises from the middle of the second commissure. The fifth commissure joins the metaconid to the entoconid. See Figure A.

The commissures form sharp cutting edges. The lingual sides of commissures 1 and 2 slope steeply to form the narrow trigonid valley, whilst commissures 3 and 4 slope lingually, and commissure 5 buccally, to form the talonid basin. The <u>buccal</u> sides of commissures 1 to 4 descend almost vertically, (<u>cf</u>. the vertical descent of the <u>lingual</u> side of the ectoloph of the upper molars).

Ridges from the tip of the paraconid and hypoconid extend down the steep buccal sides of the lower teeth. These ridges run parallel to each other and curve slightly in a posterior direction. See Figure 13.

There is a marked cingulum along the anterior, buccal, and posterior surfaces just above gum level.

The Second Lower Molar

In M_2 the paraconid is smaller and the metaconid is more anteriorly placed than in M_1. Also in M_2 the lingual border of the talonid slopes buccally, i.e. the talonid is set at an angle to the trigonid.

The Third Lower Molar

M_3 is essentially similar to M_2, except that again there is a difference in proportions. The whole of M_3 is smaller than M_2 or M_1. It is generally believed that the third lower molar was originally similar to the second lower molar, but that in the course of time reduction has taken place in the posterior region, as in the upper molar.

The following differences between M_3 and M_2 are evident:

1) in the anterior region, the paraconid of M_3 is lower than that of M_2; and the lingual length of the trigonid is shorter; and the metaconid is more anteriorly placed.

2) the talonid is set at an angle to the trigonid so that the posterior region curves buccally to a greater extent in M_3 than in M_2, and is much reduced in size;

3) the angle between commissures 2 and 3 (angle T Figure 34) is smaller in M_3 than in M_2.

The Occlusal Relations of the Teeth

Methods of determination

The functional occlusion, or chewing action of the teeth, was established primarily by examination of dried skull specimens of H. beatus, particularly from an investigation of the wear facets on the teeth. The latter were discerned by holding the specimens so that light was reflected directly from the worn surfaces.

The small size and translucency of the teeth made it necessary to examine them under a high power binocular microscope (x 10 eyepiece plus a x 2.5 objective), and with strong illumination from a 60 watt bulb close to the microscope.

Under a higher power, (x 10 eyepiece plus a x 5 objective), fine scratch marks were visible on the wear facets. These appeared to have been made by the coarser particles of food caught between the shearing surfaces, (Mills 1961). Most of the scratches were parallel to each other. Their direction indicated the direction of the shear.

This technique was first described by Butler, 1956.

As the bat ages, the wear facets become larger and eventually join up with each other. Thus, in older teeth, individual wear facets cannot be discerned (see Knud Anderson's excellent illustrations of progressive wear of the teeth of Rhinolophus rouxi 1917-18).

The specimens of H. beatus at the British Museum all had markedly worn teeth, so there was a possibility that small wear facets had become masked by joining up with others. Therefore, young specimens of a related species, H. caffer, (the teeth of which showed little wear), were examined. However, in these species the same number of wear facets were found present and in the same relative positions as in the specimens of H. beatus.

The direction of the scratch marks did not indicate whether they had been made in the closing or opening movement of the jaw. In the present study, I have attempted to solve this problem by making a slow motion film of the chewing action of the British Horse-shoe bat (where the dentition is similar to that of H. beatus), and by observing live specimens of these bats kept in captivity. Manual movement of the jaws of freshly killed specimens before rigor mortis had stiffened the muscles, provided a further guide to the occlusal relations of the teeth.

The slow motion film was made under laboratory conditions with a Bell and Howell slow motion camera and Kodak tri-X film.

Before commencing, the camera was focussed at a point three feet from the lens, and the boundaries of the focal field were marked out.

The experimental animals were taken from caves in S. Devon just a few hours before filming, so that their chewing action was not affected by secondary factors due to long term captivity.

During the experiment, the bat was held in the palm of the operator's left hand with the fingers and thumb enclosing the wings in a way that prevented the bat from attacking the operator or from fluttering its wings. Care was taken to hold the head of the bat within the focal field of the camera.

Cockroaches and mealworms were fed at intervals, both of which it ate voraciously.

As the bat chewed, a second person operated the camera.

The film was shot at 120 frames per second. Two hundred feet of film were taken.

After processing, the film was projected at speeds varying from 5 to 30 frames per second thus allowing 8 to 48 minutes viewing time. Therefore the action in the film was 4 to 24 times slower than in life.

The course of the mandibular symphysis during a single chewing stroke is shown in figure 14, this was established by projecting on to the screen one frame at a time and tracing the outline of lips, anterior teeth (where possible), and the midline division of the upper lip on successive frames.

These tracings were then superimposed in series using the midline division of the upper lip and the upper canines as reference points. The course of the mandible through several tracings could then be seen and drawn on to the top-most tracing. This latter was then used as the bottom one for superimposing more tracings. Figure 14 is a composite drawing made up in this way.

To avoid distortion, only shots filmed from a point directly anterior to the midline of the bat could be used.

Movements of the Jaw from Observations on a Slow Motion Film of Two Specimens of Rhinolophus, (Rhinolophus ferum-equinum insulans)

When food was presented to the bat, it was grasped and pierced by the canines, manoevred into the mouth, and, by movements of the tongue, lips, and jerking of the head, brought into contact with the cheek teeth. Once there, the food was sliced into smaller pieces more manageable for chewing. This was done by a series of orthal and sideways movements of the mandible, the teeth themselves hardly coming into contact with each other, but effectively cutting the food between them.

The effective chewing stroke came into play as soon as the food was in sufficiently small pieces.

The bat chewed first on one side of the jaw, and then on the other. The number of strokes on each side was not constant, varying in the film from one to twelve.

At all times the lips and tongue aided the manoevring of the food.

In a right hand chewing stroke the jaw action was as follows:

Starting from when the jaws were open, the mandible moved upwards and slightly inwards, until the teeth made contact. There was then a rapid upward movement, presumably as the teeth sheared against each other. This movement ceased abruptly, to be followed by a horizontal movement, in which the mandible moved towards and then past the centric position. During this movement the teeth on the other side of the jaw came into contact. The lateral movement was followed in turn by the recovery stroke, whereby the jaws opened and moved in an arc to the right. See Figure 14.

However, the smooth arc of the recovery stroke was not always followed, for the jaw sometimes made small lateral excursions, no doubt due to manoevring the food within the mouth.

It was interesting to note that in the younger of the two bats filmed, the lateral movement was less marked.

The film was shot at 120 frames per second; a completed chewing action averaged 44 frames, and therefore the bat made approximately three chewing cycles per second.

Possible Jaw Movements of a Freshly Killed Specimen of the British Horse-Shoe Bat, and of Dried Skull Specimens of H. beatus

In the horse-shoe bat the jaws were moved to simulate chewing. When this was done a considerable lateral movement of the mandible was possible, but only when the jaws were widely open. As the jaws closed, lateral displacement was restricted by the massive interlocking canines. The mandible could be moved in an arc similar to that shown in Figure 14. A limited forward movement (approx. 2 mm) of the mandible was possible.

The same movements could be made on the dried skull specimens. But the canines of H. beatus interlock to a greater degree than those of the horse-shoe bat, and therefore there can be even less lateral movement of the mandible when the jaws are closed. In a similar way to Rhinolophus the large canines cause the upper and lower teeth automatically to interdigitate as the jaws shut. The canines can therefore be said to act as guides to secure the correct occlusion of the toothrows.

The Temporomandibular Joint of H. beatus

The glenoid fossa lies on a level with the occlusal plane of the teeth. It is situated relatively far from the last molar, and lies almost directly transversely in the skull.

The floor of the cavity is flat and is wider than the mandibular condyle that fits into it. There is a marked post-glenoid flange which prevents backward movement of the mandible and acts as a support against which the mandibular condyle can hinge. There is also a small anterior flange.

The condyle is narrowly cylindrical in shape. The articular surface encloses the posterior side and extends on to the dorsal side.

Sections of late embryonic stages of H. beatus (Mn. length 0.90 to 0.97 cm.) showed a thin meniscus to be present. Unfortunately no adult specimens were available for sectioning. However, adult specimens of Hipposideros cyclops, and the related Hipposideros tridens were dissected, and these showed a meniscus to be present in the lateral part of the joint only, see Figure 15. In the lingual part, the joint surfaces were separated by a thin membrane only. The meniscus was bound on to the lateral half of the condyle, by a strong tendon which extended along the anterior border of the condyle.

All the specimens dissected had well worn teeth and so it is possible that advancing age had caused the meniscus to be worn away on the medial side. However, the presence of the thin membrane between the joint surfaces in this area would seem to discount this.

Juvenile and aged specimens of the British pipistelle bat were dissected and it was found that in both a marked meniscus was present extending across the entire joint surfaces from the lateral to the medial margins. Therefore in the pipistelle at least, age does not cause the meniscus to be worn. Correlated with the presence of a larger meniscus the shape of the condyle in the pipistelle was smooth and cylindrical, whereas in the adult Hipposideros cyclops dissected, the condyle was broader towards the medial margin, see Figure 15.

It is hoped to do further work on this point and to elucidate the reason for a partial meniscus in the large specimens of nose-leaf bats dissected.

The condyle in Hipposideros beatus is bound into the glenoid fossa by strong capsular fibres attached to the anterior and posterior flanges of the fossa and to the margins of the articular surfaces on the condylar head.

The capsule fibres together with strong ligaments surrounding the capsule, prevent dislocation of the jaw and severely limit the anterior movement of the mandible.

Jaw Action

Due to the fact that the glenoid fossa is wider than the mandibular condyle that fits into it, a small degree of rotation of the mandible can take place, but in H. beatus the tooth rows converge, and when the jaws are closed the interlocking canines restrict the horizontal movement in the anterior region. Therefore, to account for the wear facets found on the third molars, the jaw must translate laterally from the jaw joint, i.e. there is lateral movement of the condyle within the glenoid fossa. This is in agreement with observations made by Mills 1961.

In all dried skull specimens and dissections examined, there was room for a lateral movement of the cylindrical condyle within the fossa without dislocation of the jaw. (The movement necessary to translate the mandible in the lateral chewing stroke is in fact extremely small: being only the width of the talonids, which in H. beatus is 0.33 mm, and in the larger skull of the British Horseshoe bat less than 1.0 mm).

The fact that the jaw joint in H. beatus is not set exactly transversely in the skull, but is such that the lateral margin is slightly anterior to the medial margin, also suggests that the mandible translates as well as rotates, so that the posterior teeth transcribe a greater arc than the anterior teeth.

Conclusions on Occlusal Relations

By combining the above evidence, the chewing action of H. beatus is found to consist of three movements:

1) vertical shearing movement
2) lateral grinding movement
3) recovery stroke

1) Vertical Shearing Movement (when chewing on the right)

From a position with the jaws widely open and the mandible displaced buccally to the right, the mandible moves upwards until the lower molars make contact with the uppers. They are then in the extreme buccal position shown in Figure 16B. The protoconid and hypoconid of the lowers are in contact with the lingual sides of the parastyles and mesostyles of the uppers. From this position there is a vertical shearing stroke whereby the buccal surfaces of the M shaped commissures of the lower molars shear against the lingual surfaces of the W shaped commissures of the upper molars. Thus, from anterior to posterior, the occlusal action is as in Table I. This action causes the wear facets shown in Figure 19 and 18A.

During the stroke, the M shaped commissures of the lower molars keep in contact with the vertical W shaped commissures of the upper molars. But the outer ridges of the protoconid and hypoconid are not vertical, for they curve outwards away from the tip; see Figure 20.

Thus, as the basal part of the tooth follows the apical part between the cusps of the upper molars, this outward curvature causes a lingual movement of the lower teeth.

This lingual movement is important, for at the beginning of the stroke, the paracone of the upper molar extends into the V formed by the protoconid, metaconid, and hypoconid of the lower molar, to a position lingual to the junction of the second and third commissures, (see Figure 21A), so that without the lingual movement of the lower tooth, the cusps would not interdigitate, but would bite onto the commissures.

At this point, the hypoconid being lower than the protoconid, is not in contact with the upper teeth.

As the stroke continues, the lingual movement of the lower molar brings the junction of the second and third commissures to lie lingually to the tip of the paraconid, so that the paracone does not bite on to the third commissure~~s~~. This movement is shown in Figure 21A & B.

This lingual movement also serves to remove the food from between adjoining cusps of the upper teeth. If the movement were vertical, food would become jammed into the crevice between the paracone and metacone.

The ridges of the hypoconid and protoconid are curved slightly backwards from the tip. This curvature is the same as that followed by the mandible in its upward stroke. As the mandible moves upwards this curvature allows the commissures of the upper and lower teeth to keep in contact for the length of the stroke (see Figure 22). Without it the tall interlocking teeth would prevent the jaw from closing. Bohlin (1945) has shown that the teeth are curved so that maximum pressure is applied to the food as the jaws close.

The stroke continues until the hypoconid reaches the protoconal ridge, and the protoconid reaches the stop formed by the vestigal hypocone.

At the end of the stroke, the posterior face of the metaconid comes into contact with the anterior face of the protocone, thus preventing overclosing of the mouth. From this action the metaconid is worn away from the posterior side, and the protoconal ridge is worn away from the anterior side.

The fact that the protocones are progressively more anteriorly placed from M^1 to M^3 (see Pages 25 and 27) appears to be correlated with the fact that the metaconids are more anteriorly placed from M_1 to M_3 (see Page 29). Thus each protocone can bite against the corresponding metaconid.

Also, at the end of the stroke, the teeth in the opposite jaw come into contact. The hypoconid comes to lie just external to the protoconal ridge.

In this shearing action, the cingula on the buccal side of the lower molars, and on the lingual side of the upper molars, serve to protect the gum from the pulverised food. Also, the parastyle in each upper molar overlaps the tooth in front, and so prevents the food jamming between two teeth. Thus the protoconid bites into an enclosed V rather than into a gap between two teeth. Similarly, in the lower molar the paraconid extends forward to overlap the hypoconulid of the next most anterior tooth, so again there are no gaps between the teeth.

2) <u>The Lateral Grinding Movement</u> See Figure 17 (2 & 3).

The mandible, from the position at the end of stroke 1, moves laterally, so that the molars describe a greater arc than the antemolars in order to compensate for the convergence of the toothrows (see Page 37).

In Rhinolophus there is more room for lateral movement of the mandible between the upper canines. Correlated with this, the talonid basins and the protoconal ridges are wider in Rhinolophus than in H. beatus. Also the toothrows in Rhinolophus are less convergent, and it appears that in the lateral movement in this species all of the teeth transcribe the same arc (Mills 1961).

In H. beatus, stroke 2 causes the hypoconid to move across the protoconal ledge. At the same time, the protocone traverses the talonid basin moving from the posterior face of the metaconid to a position anterior to the hypoconid. This movement causes the wear facets shown in Figure 18B. With advancing age, a deep groove is worn in commissure 3 just ~~posterior~~ anterior to the tip of the hypoconid by the action of the protocone.

This stroke brings the teeth of the opposite side, as well as on the chewing side, into operation, (balanced occlusion). The action on the opposite jaw is the reverse to that on the chewing side. The tip of the hypoconid which was just lingual to the protoconal ledge before the stroke, moves across the ledge to cause wear on the protocone just posterior to the protocone tip, and on the lower tooth the protocone moves across commissure 3 of the talonid and into the talonid basin.

Thus, the protocone plays an important part in the lateral chewing stroke; its action can be likened to a pestle and mortar action as it traverses the talonid basin, becoming more like a millstone action as the protocone and the talonid become worn flat. It bites in turn against the metaconid and the hypoconid ridge.

The Effect of Age on the Chewing Action

In very young specimens, the height of the protocone tip prevents much lateral movement, but the tip soon wears down. As the bat ages, the cusps become blunted so that the vertical stroke becomes less efficient. As this happens, the lateral grinding movement in the chewing stroke become more important, (increased lateral chewing being a compensating factor). In very old bats, the cusps are worn flat, and the grinding movement becomes the only method of chewing.

The tropical bat Rhinolophus rouxi, according to Knud Anderson (1918), lives for 5 to 6 years. In the sixth year the teeth are worn to the gums. The British greater horse-shoe bat is known to live up to 10 years (Hoopers 1960, personal communication). The teeth of the older horse-shoe bats have not been examined, but the wear on the teeth may be a factor for limiting life span, as is believed to be the case in shrews.* It is possible that the British bat has double the life span of the tropical bat because it hibernates for half of the year.

Wear on the teeth is such that the action of interdigitating cusps is retained as long as possible. The lack of a hypocone allows the protoconid to be the tallest cusp on the lower molar, and to remain relatively unworn.

The metaconid is worn only from the posterior face, and the entoconid shows little wear until the lateral movement is such that it contacts the protocone. In the upper jaw, the region of the buccal styles remains unworn until an advanced age, due to the lateral movements being restricted by the canines. (At one stage, the styles are by far the highest cusps on the upper molars). Not until the lateral movement is excessive do the styles come into contact with the lower teeth.

It is interesting to note that in H. beatus those cusps believed to be homologous with the primitive single cusp of the reptilian tooth, viz: the paracone in the upper tooth and the protoconid in the lower tooth have little wear. Their main function is, as in reptiles, to pierce and hold the food, whilst those cusps that are thought to have evolved with the development of

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* Patterson, personal communication.

chewing in mammals, the talonid cusps and the protocone, have the most severe wear in the chewing action.

3) The Recovery Stroke

At the end of stroke 2, the mandible swings in a smooth arc downwards and across to come into the position shown in Figure 14 at x. From here another cycle begins.

The bat changes from chewing on the right to chewing on the left, or *vice versa*, by reversing the movement of the mandible at any stage during the chewing cycle.

CHAPTER IV

THE DEVELOPMENT OF THE CHEEK TEETH OF HIPPOSIDEROS BEATUS

In the earliest embryo, (Mn-length 0.58 cm), all the tooth germs are established. Of the first and second molars the cuspal pattern is fairly distinct, and calcification is in progress. In the case of the third molars, M_3 is an early cap stage, and M^3 is as yet merely a proliferation of the dental lamina.

In the most advanced embryo (Mn-length 0.97 cm) the molars are in a stage just prior to eruption. The crowns of all the molars are fully formed and calcified, and root formation is in progress.

Hence the material affords a study of the complete cuspal development of the third molars, and of the latter stages of development of the first and second molars.

A brief account of the histological development is given in Appendix A. The following points are of interest:

1) an enamel knot is present in M_3 and M^3 stage 1. In M^3 stage I, it appears to lie in a depression in the crown surface (see Figure 23) but later comes to lie on the summit of a cusp.
2) the stellate reticulum remains active and non-vascularised until calcification is fairly extensive over the crown surface.

In the following account the terms anterior, posterior, etc., will refer to the teeth as they will be in their final position and are irrespective of the varying positions of the teeth during development.

Ontogeny of the Upper Molars

Crown pattern of M^3

Stage 1 (Mn-length 0.58 cm)

The dental lamina has by stage 1 grown into the jaw tissue from the oral epithelium, the extremity has proliferated and become invaginated to form the enamel organ. The latter is lying closely adposed to the primordium of the dental papilla. Figure 24 shows the continuation of the lamina with the oral mucosa.

The crown appears as an elliptical cap of low relief. There is a central depression bounded by lingual and buccal grooves and into which extends the enamel knot. The lingual ridge is the highest point on the crown. The posterior surface is twisted so that it faces directly buccally. At this early stage no demarcation of the crown into cuspal areas can be seen, although a comparison with later stages suggests that most of the surface will give rise to the paracone.

Stage 2 and 3 (Mn-length 0.59 and 0.63 cms respectively) show a transition from bud to cap stage taking place. The crown surface is expanding rapidly, and at the same time the lingual ridge appears to be enlarging at the expense of the central depression.

The anterior region is growing in width more rapidly than the posterior region, so that the crown is becoming triangular in outline. By stage 3 the central depression has greatly diminished, and the lingual ridge has come to occupy the central region of the crown. The enamel knot now lies on the highest point of the lingual ridge, but also extends buccally into the remains of the depression.

In stage 3a(Mn-length 0.65 cm) the crown is still expanding rapidly, growing in height, width and length. However, the growth in width is most marked in the anterior region and growth in length in the posterior region. These are the regions in which the parastyle, protocone and metacone will develop.

Cusps other than the paracone appear to grow from the marginal regions of the crown. The crown is now triangular in outline. There is a central elevated region, the primordium of the paracone.

An area immediately buccal to the future tip of the paracone is forming a valley, causing the apex of the paracone to stand out from the rest of the crown. This valley continues to deepen to form the depression between the parastyle and mesostyle.

Stage 4 (Mn-length 0.66 cm)

The wax model of stage 4 shows the crown to have attained approximately half its final size, see Figure 25.

The primordia of the metacone and protocone have developed, and the parastyle and mesostyle regions are just discernable. In other words the cuspal pattern of the tooth is mapped out. However, the cusps (except for the paracone) are in low relief. The valley between the parastyle and mesostyle regions is deepening so that the summit of the paracone is now distinct. The latter has risen above the rest of the crown and dentinogenesis has commenced on its highest point.

The crown of M^3 stage 4 is markedly triangular in outline. The anterior part of the tooth is more sharply differentiated than the posterior region. At the extreme anterior region a cingulum is differentiating from the rest of the crown. The tooth germ so far has shown marked anterior to posterior and also buccal to lingual, growth gradients.

Stage 5 (Mn-length 0.68 cm) shows a continued expansion of the crown in all directions, but again most growth is taking place in the protoconal, parastylar and metaconal regions. The crown has grown considerably in height. The calcification on the paracone summit is spreading downwards. Its advance is most marked along the elevated ridges of the crown i.e. the paraconal ridge and the ridges extending to the parastyle and mesostyle regions.

Wax Models of stages 6 and 6a (Mn-length 0.69 and 0.69s cm) show that growth is taking place mainly in height. Ridges and cusps are becoming "sharper" and now stand out in high relief from the valleys.

Calcification has continued to spread from the summit of the paracone.

Stage 8 (Mn-length 0.75 cm) shows a further increase in height of the cuspal areas. Calcification has extended to and enveloped the parastylar region, and is rapidly approaching the metaconal region. At the same time a secondary calcification centre on the metacone is spreading to envelope the posterior buccal region of the crown. Also in stage 8, calcification has just commenced on the protocone.

By stage 9 (Mn-length 0.73 cm) the protoconal calcification becomes continuous with that of the metacone and of the paracone.

Calcification of an area prevents further growth, therefore, once calcification 'bridges' the distance between two cusps, these cusps are fixed in relation to each other. Thus by stage 8 the parastyle is fixed in relation to the paracone, and by stage 9 the mesostyle-metacone region and also the protocone is fixed in relation to the paracone. However, growth can and does continue in the uncalcified regions, causing the valleys to deepen.

The last regions to calcify and therefore to stop growth are:

1) the valley between the protocone and paracone and;

2) the antero-lingual margin of the tooth.

By stage 13 the whole of the crown has calcified and therefore attained its final form. Uneven depositions of enamel could modify the shape of the cusps, as in man, but as far as can be ascertained from the sections, and from a comparison with erupted teeth, the enamel does not appear to alter substantially the shape of the dentinal crown.

Figure 25A is designed to show growth in width of regions of the crown relative to the paracone. The models of M^3 are arranged so that the paraconal summits lie along a scale representing the

Mn-length of each stage. Lines drawn to connect homologous parts on each model diverge from stage 1 to stage 13 and so demonstrate the growth in width of the tooth. The most rapid growth (greatest divergence of the lines) occurs between stages 3 to 6a when the cells have differentiated and before calcification restricts growth. Thus after histological differentiation the rate of growth varies inversely with the degree of calcification. The figure shows that the buccal region of the tooth-germ develops and calcifies before the lingual region, and that growth in width, in the region buccal to the paracone summit, is very slow after stage 6, but continues steadily in the lingual region.

The line connecting the Protocones remains almost parallel with that connecting the Paracones, showing that the protocone, once established and calcified, remains at a more or less constant distance from the paracone (Gaunt 1955 has shown the same thing to be true of the cusps of mouse molars).

Figure 25B is constructed in a similar way to Figure 25A, but to show growth in <u>length</u> of M^3. Again the greater divergence of the lines between stages 3 and 6a demonstrates the rapid expansion of the tooth germ in the early stages.

After stage 6a the lines are almost parallel because the ventral aspect of the crown has calcified and growth is taking place in height rather than length.

Figure 26 demonstrates growth relative to the paracone by superimposition of successive stages of M^3. Commissures 1 and 2 (or primordia of these commissures) are drawn in.

Here it will be noticed, commissures 1 and 2 tend to become parallel with each other as growth continues. See Figure 27. At an early stage angle P is obtuse and commissures 1 and 2 diverge markedly, but in a later stage angle P becomes acute, shown as angle P^1 in Figure 27. But calcification has already commenced at P, whilst angle P was large. After calcification, no change in shape can occure therefore the tip of the paracone must remain as an obtuse angle. As calcification continues to spread along A and B from the paracone tip, A and B are growing more parallel to each other, so that although angle P at the tip of the paracone remains blunt, A & B calcify so that angle P^1 becomes more and more acute.

The Ontogeny of M^1 and M^2

The cusps of M^1 and M^2 develop in a similar way to those of M^3, i.e. as primordial humps from which a summit becomes elevated. Table II gives a summary of the cuspal development of M^1 and M^2 compared with M^3.

The triangular M^2 stage 1 shows a remarkable resemblance to M^3 stage 5; see Figure 28.

The tooth germs shown in Figure 28 are approximately the same size, the same shape, and in both only one centre of calcification is active, viz; that of the paracone. Therefore, one can assume that they are of the same developmental age.

However, closer examination reveals that the posterior region of M^2, even at this early stage, is relatively larger than the posterior region of M^3 and also the protocone is more posteriorly placed in M^2 than in M^3.

As development proceeds the differences between M^2 and M^3 increase. It is soon obvious that the posterior region of M^2 is growing at a faster rate than the anterior region, and by stage 6a, the tooth germ has lost its triangular form and the metaconal region has become as large as the paraconal region.

Thus in the embryos studied no stage of M^2 resembles exactly a stage in the development of M^3.

In M^2, as in M^3, the order of calcification of the cusps is the same, viz; paracone, metacone, protocone; but in M^2 there is a longer time interval between the first appearance of calcification on the metacone, and the first appearance on the protocone. In M^3 the protocone calcifies almost immediately after the metacone. (Table II shows the metacone and protocone of M^2 to calcify by stages 2 and 4 respectively and the metacone and protocone of M^3 to calcify by stage 8).

By stage 5 (Mn-length 0.68 cm) M^2 is in a developmental stage comparable with M^1 in stage 1 (Mn-length 0.58 cm). See Figure 29.

The tooth germs are approximately the same size, and in both calcification is active on the paracone, metacone and protocone. All the cusps are discernable and the crowns are essentially shallow miniatures of the completed forms. Each is approximately half the final size.

But M^1 stage 1 differs from its counterpart M^2 stage 5 in the relative position of the protocone. The latter is more anteriorly placed in M^2. There are also small differences in the angles between the commissures, and differences in the relative lengths of the commissures.

Again as development proceeds, the small differences between the two teeth become more apparent, so that in the embryos studied no stage of M^1 resembles exactly a stage in the development of M^2. Except for these small differences the general pattern of development in M^1, at least in the later stages, is the same as that in M^2.

There are indications that the early stages are also similar, for M^1 stage 1 shows the anterior part of the tooth to be larger and more advanced than the posterior region, and also shows the buccal cusps to be more advanced than the lingual cusps. Thus it would seem that M^1, as well as M^2 and M^3, show anterior to posterior, and buccal to lingual gradients, in crown development.

The varying extent of calcification on the main cusps of M^1 stage 1 (see Figure 37) suggests that the order of calcification is the same as in M^2 viz; paracone, metacone and protocone.

Notes on the Ontogeny of the Upper Molars

1) The molars develop in sequence from M^1 to M^3.
2) M^3, M^2 and probably M^1 develop as shallow triangular plates.
3) Within each tooth germ there is a marked anterior to posterior gradient of growth, and also a marked buccal to lingual gradient.
4) No stage of development in any upper molar resembles exactly a stage of development in any other molar.

5) Investigations suggest that the order of appearance and the order of calcification of the cusps is the same in all three molars, being paracone, metacone, protocone.
6) Separate calcification centres for the stylar cusps are not apparent in any of the stages. This does not preclude their existence, as such centres may appear shortly before calcification reaches and overrides them from neighbouring centres. They may be present in stages of Mn-lengths between 0.58 and 0.59 cm, or 0.66 and 0.68 cm, or 0.75 and 0.90 cm. Their presence could not be affirmed from a study of the dentine in the stylar regions.
7) In each tooth, calcification begins on the highest points and works downwards. The valleys and margins of the crown calcify last.

Ontogeny of the Lower Molars

Crown pattern of M_3

Stage 1 (Mn-length 0.58 cm)

In stage 1 the tooth germ of M_3 is in an early bell stage, being more advanced in development than the corresponding third molar of the upper jaw.

The dental lamina has lost its connection with the oral mucosa but the remnants of its attachment are still present. M_3 is positioned far back in the jaw occuring beneath the ascending ramus at a point where the jaw is not covered with oral mucosa. But the sections show that the dental lamina has grown inwards from the oral mucosa from a point just above the hypoconid of M_2.

In stage 1 the trigonid, or rather the protoconid of the trigonid, is precociously developed. It is shaped like a triangular prism. The remnants of the enamel knot are present on its summit. Three ridges extend downwards from its tip, anteriorly, buccally and postero-lingually. Calcification has not yet commenced on the protoconid, yet its summit is sharp and angular.

The metaconid at this stage is hard to distinguish from the base of the protoconid, but its future position is indicated by a small bulge at the base of the lingual ridge.

Of the paraconid which develops at the base of the anterior ridge, there is no sign.

In the basal part of the tooth the epithelium is growing rapidly downwards on the buccal and lingual sides to enclose the dental papilla, but is growing more slowly on the anterior and posterior sides. On the posterior side of the protoconid, the epithelium has ceased to grow downwards and instead has grown outwards to form a small nodule, which will give rise to the talonid. See Figures 30 and 31.

By stage 2 (Mn-length 0.59 cm) the tooth germ has grown in width and height and dentine deposition has commenced on the tip of the protoconid.

On the lingual side of the trigonid, a depression is forming. This will become the valley between the metaconid and paraconid. The talonid primordium has grown and is now distinct from the trigonid. However, the internal enamel epithelium has not yet grown over the posterior side of the talonid.

Stage 3 (Mn-length 0.63 cm) shows an advance in cuspal differentiation of both the trigonid and talonid. The trigonid basin is deepening. The internal enamel epithelium is growing downwards on the lingual side of the trigonid. At the base of the lingual and anterior ridges it is bulging outwards to form the primordia of the metaconid and paraconid respectively, the metaconid being the more advanced. On the lingual side of the talonid primordium at a point just below its top a bud is proliferating. Comparison with later stages shows that this bud will become the entoconid. The primordial nodule, from which it has arisen, will become the hypoconid. On the posterior side of the hypoconid, the dental papilla is still exposed.

In Figure 32, a section through the tooth germ shows the entoconid budding off from the hypoconid.

Thus by stage 3 the protoconid is well established and the primordia of 4 other cusps are discernable.

Stage 3a (Mn-length 0.65 cm) shows the entoconid and hypoconid to be separated by a valley.

By stage 4 (Mn-length 0.66 cm) the tooth germ has attained approximately half its final size. Calcification is spreading downwards from the summit of the protoconid. Its encroachment is uneven, being most rapid along the dorsal and lingual sides. Just before the calcification from the protoconid reaches the metaconid, a secondary centre is established on the latter.

The talonid region in stage 4 is growing rapidly. The papilla is no longer exposed on its posterior side. The valley between the hypoconid and entoconid has deepened.

The basal region of the trigonid is also growing rapidly, causing the protoconid to become considerably elevated relative to the talonid.

The paraconid is at this stage a small nodule on the anterior ridge of the protoconid. M_3 stage 4 is illustrated in Figure 30.

In stage 5 (Mn-length 0.68 cm) calcification is continuous between the protoconid and metaconid, and dentinogenesis has commenced on the tip of the paraconid and later on the hypoconid.

Stage 6 (Mn-length 0.69 cm) shows dentinogenesis to have commenced on the entoconid.

Between stages 5 and 6a calcification has bridged the area between the paraconid and protoconid. Also the hypoconulid has made its appearance as a small elevation on the rim of the talonid basin. It appears to have arisen as a bud from the base of the hypoconid, and its development as a cusp is shortly followed by its calcification.

By stage 6a (Mn-length 0.69 cm) all 6 cusps are linked by calcified bridges. Growth continues in the uncalcified areas viz; the talonid basin, and at the margins of the tooth.

Between stages 7 and 12 (Mn-length 0.71 to 0.90 cm) growth in width is particularly noticable in the waist region between the talonid and trigonid. The last regions to stop growth are the talonid basin and the extreme posterior margin of the tooth.

By stage 13 (Mn-length 0.97 cm) the crown surface is completely covered with dentine and enamel.

Table III demonstrates the relationship between the appearance of a cusp, the beginning of dentinogenesis, and the bridging of calcification between one cusp and another.

As was done for M^3, diagrams have been drawn to demonstrate regional growth of the crown (see Figure 31).

The models are arranged along a scale according to their Mn-length.

The divergent lines show that the most rapid growth is between stages 4 and 6a after cellular differentiation and whilst most of the tooth is uncalcified.

The divergent lines show that some cusps once established do not remain at a constant distance from each other, particularly the hypoconid and protoconid (see discussion page 102). Direct measurements on the models verified this to be so. Figure 31B shows growth in depth of the crown and demonstrates that growth in the paraconid region, causes the anterior part of the crown to bulge forwards so that the crown appears to tilt backwards (see later Chapter V).

Ontogeny of M_1 and M_2

In the finished dentition the first and second lower molars are more similar to M_3 than the first and second upper molars are to M^3.

The present investigation shows that the developments of the lower molars are more alike than are the developments of the upper molars.

Table III gives a summary of the cuspal development of M_1 and M_2 compared with M_3.

In all three molars the anterior part of the tooth develops first.

The protoconid is the primary cusp and develops well in advance of the rest of the tooth.

The order of appearance of the cusps judged by size in M_1 and M_2 (where earlier stages were not available), appears to be the same in all three molars viz: protoconid, metaconid, paraconid, hypoconid, entoconid and lastly the hypoconulid. Similarly the order of calcification of the cusps is the same. In each instance, the last regions to calcify are:

1) the waist region between the trigonid and talonid
2) the margins of the tooth and
3) the posterior border.

The dental papilla in the posterior regions of M_1 and M_2 remains exposed, as in M_3 until a late stage of development. This phenomenon has been shown to occur also in the human lower molar (Turner Ph.D. Thesis 1962).

Figure 33 shows comparative stages of M_2 and M_3 superimposed, and Figure 34 shows comparative stages of M_1, M_2 and M_3.

The differences in the tooth germs in Figure 33 are as follows:

1) The talonid is larger relative to the trigonid in M_2 than in M_3. This was established by superimposing squared paper over both occlusal and side view scale diagrams of the teeth, and counting the squares covering sections of the teeth. Also the talonid cusps of M_2 are taller and more sharply defined than in M_3.
2) When viewed from directly above the protoconid summit, the tooth germs differ in the positioning of the talonid, see (a) below.

Figure 34 shows corresponding stages in the development of M_1, M_2 and M_3, Figure 34d shows these stages superimposed. Again differences are apparent as follows:

a) The talonid relative to the trigonid is positioned progressively more buccally from M_1 to M_3, so that angle T becomes progressively smaller.

b) Also the lingual length of the trigonid becomes progressively smaller from M_1 to M_3. Therefore the metaconid is further forward relative to the paraconid from M_1 to M_3.

These differences between the developing tooth germs, quoted above, all occur in the completed molars, see page 29.

Notes on the ontogeny of the lower molars

1) The molars develop in sequence from M_1 to M_3.
2) The developing crown of M_3, in the bell stage, has a higher relief than the crown of M^3 in a similar stage.
3) The protoconid cusp is pointed and ridges from its tip are sharply demarcated before calcification commences.
4) Within each tooth germ there is an anterior to posterior, and a buccal to lingual, gradient of growth.
5) In the embryos investigated no stage of development in any lower molar resembles exactly a stage of development in any other molar.

6) Investigations suggest that the order of calcification of the cusps is the same in all 3 molars viz; protoconid, metaconid, paraconid, hypoconid, entoconid, hypoconulid.

7) Calcification begins on the highest points of the crown and works downwards. Thus cusps and ridges become calcified first.

8) In each molar the posterior border is the last region to calcify.

A Comparison between the Ontogeny of Upper and Lower Molars with Special Reference to the Development of Occlusal Relations

In the following account it is proposed to consider how the development of the upper tooth row is related to that of the lower tooth row, and to establish whether or not the cuspal patterns of the upper molars grow in step with the cuspal patterns of the lower molars.

As in the last section, no account will be made of the movements of the teeth during ontogeny, for this will be dealt with in Chapter V. Instead it will be supposed that the upper and lower teeth develop in two straight lines one above the other. In Chapter III it has been shown that occlusal relations in the erupted dentition can be divided into:-

1) those concerned with the vertical shearing stroke (buccal phase)
2) those concerned with the lateral chewing stroke (lingual phase)

Figure 16 shows the erupted teeth in a) centric and b) buccal occlusal positions.

Figure 35 shows, diagramatically, in side view, how the cusps of upper and lower teeth interdigitate.

The teeth of upper and lower jaws interlock so that each tooth bites against two teeth in the opposing jaw. The lower teeth are placed slightly anterior to the upper teeth, so that for example

M_2 bites against M^2 and M^1. When the development of upper and lower toothrows are considered separately, it is found that in both, development proceeds from the anterior to the posterior, e.g. M^1 develops in advance of M^2, which in turn develops in advance of M^3. When the development of the cheek teeth series is considered as a whole, a correlation in timing of development is observed. Those teeth that will later occlude, develop in a strict order, starting from the anterior region. Each lower molar develops in advance of the corresponding upper molar, and is always in a stage of development midway between the two upper molars against which it will eventually occlude.

This is shown in Figure 36 for the tooth germs in stage 1, but the same phenomenon is true for all stages investigated. See also Figure 37.

This correlation in the order of development is apparent not only for the tooth germs themselves, but also for the principal cusps that will later occlude.

If the buccal cusps are numbered according to the stage of development reached, it is found that the numbering alternates between upper and lower tooth rows. This is shown in Figure 36. For example the protoconid of M_3 is in a stage of development midway between the metacone of M^2 and the paracone of M^3.

This sequence of development is apparent in all stages investigated.

Figure 37 demonstrates the order of calcification of the cusps. Due to the buccal to lingual growth gradients in both jaws, the buccal cusps i.e. those concerned with the vertical shearing movement, are more advanced in development than the lingual cusps i.e. those concerned with the lateral chewing stroke. It can be seen that when the buccal cusps only are considered, the sequence of calcification alternates between occluding cusps in upper and lower jaws.

Similarly if the metaconids and protocones only are considered and numbered according to developmental age, the numbering will again alternate between upper and lower tooth rows.

Development of Occlusal Relations concerned in the Vertical Shearing Stroke

In the previous section it has been stressed that certain differences in the cuspal patterns of the molars are apparent from an early stage of development. And above, it has been shown that buccal cusps that will later occlude develop in sequence i.e. grow in step with each other along an anterior to posterior gradient. It is now proposed to show that development is such that at any stage, should growth cease, and the teeth erupt in position, they would fit together to form a functional chewing mechanism.

In doing this, a difficulty arises due to the fact that each lower tooth bites between two upper teeth, therefore, for example, one cannot compare the growth of M_2 with M^2 but must compare it with M^2 and M^1.

Therefore it is proposed to consider each region of the tooth separately and to compare the growth of occluding parts with the growth of the counterparts in the opposite jaw.

The Occlusal Relations of the paracone of M^3

The paracone bites between the protoconid and hypoconid of M_3.

The angle at the top of the paracone (angle P Figure 27) is wide in the early stages and becomes more acute as development proceeds.

However angle T see Figure 34C into which it bites is also wider in the early stages than in the later stages. These angles develop so that the paracone will fit into angle T at all stages. This is demonstrated in Figure 38 (prepared from wax model reconstruction).

The tip of the paracone calcifies early so that further growth ceases. The angle into which it bites does not become calcified until much later. Thus the summit stops growth before the region with which it occludes.

However, when the total growth of the occluding parts of the paracone are compared with the total growth of the corresponding parts in the lower molar, it is found that there is a strict correlation.

In the "V" of the paracone, calcification starts in the angle and proceeds towards the extremities, whereas in the "V" of the lower molar into which the paracone bites, calcification begins on the extremities i.e. on the tips of protoconid and hypoconid and proceeds towards the angle of the "V." The growth is such, that the total growth of the paracone "V" keeps pace with the total growth of the protoconid to hypoconid "V." See Figure 38.

Thus the surfaces of the paracone grow in step with those surfaces on the lower molar against which they occlude. These occluding surfaces were measured on the wax model reconstructions, and the results are shown graphically in Figure 39. The small diagram in Figure 39 gives details of the measurements taken, similar explanatory diagrams are shown in later graphs.

The Occlusal relations of the protoconid M_3

These are more difficult to investigate during development, because the protoconid bites into the embrasure between M^2 and M^3. Complicated movements of the tooth germs, described in Chapter V, prevent a significant measurement of the embrasure during development. However, the growth of the occluding surfaces of the protoconid can be compared with their counterparts in the upper tooth row. It has been shown above that the posterior face of the protoconid grows in step with the anterior face of the paracone of M^3. It is now proposed to show that the anterior face grows in step with the posterior face of the metacone of M^2, with which it will occlude.

The summits of the protoconid and metacone calcify early, the latter preceding the former, but the occluding surfaces both have regions that continue to grow until a late stage.

If the occluding length of commissure 1 of M_3 is compared with the occluding length of commissure 4 of M^2 their growth is found to be correlated. This is shown graphically in Figure 40.

The occlusal relations of the hypoconid of M_3

The anterior face of the hypoconid of M_3 bites against the posterior face of the paracone of M^3, and it has been shown above that these regions grow in step with each other (Figure 39). The posterior face bites against the anterior face of the reduced metacone. In the finished dentition the posterior face of the hypoconid is slightly curved so that the hypoconulid bites beyond the tip of the metacone of M^3, showing that M_3 is less reduced than M^3. It has been shown above that during development also, M_3 is less 'reduced' i.e. more like M_1 and M_2 than M^3 is to M^1 or M^2.

The result of plotting the growth of commissure 3 M^3 against that of commissure 4 M_3 is shown in Figure 41. It will be observed that the graph curves steeply upwards. This is due to the hypoconulid region being included in the measurement of commissure 4. When the hypoconulid is not included in the measurement i.e. when only occluding surfaces are considered, the graph in Figure 42 is obtained; this shows the growth to be correlated.

This correlation in growth that occurs between occluding buccal cusps in the third molars, can also be observed in the other molars. e.g.: in the occlusal relations of M^2.

The Occlusal Relations of the Metacone of M^2

The metacone bites into the embrasure between M_2 and M_3 and the latter cannot be measured significantly. However, it has been shown above that the posterior face of the metacone grows in step with the anterior face of the protoconid of M_3 (Figure 40). Below it is shown that the anterior face of the metacone grows in step with the posterior face of the hypoconid of M_2 (Figure 43).

The occlusal relations of the hypoconid of M_2

The hypoconid of M_2 bites between the paracone and metacone of M^2 see Figure 43. The paracone (M^2), hypoconid (M_2) and metacone (M^2) calcify in sequence, calcification occuring first on their summits and working along the adjacent commissures. The tip of the hypoconid calcifies before the mesostyle against which it will eventually occlude, in the same way the summits of the paracone, and metacone calcify before the regions with which they will occlude. However when the width of the hypoconid area, (B) in Figure 43, is compared with the width between the paracone and metacone of M^2 (A) in Figure 43, it is found that these two areas grow in step with each other, so that at all times, the hypoconid of M_2 is able to fit between the paracone and metacone of M^2. In other words the growth of lengths (A) and (B) in Figure 43 is correlated.

The buccal shearing action mainly concerns the cutting edges. As in a pair of scissors, the depth of the blades is relatively unimportant. Mills (1961) points out that the edges of the teeth are like guillotines, and slope downwards from the cuspal summits. Thus, when the teeth are in the buccal phase, the occluding surfaces are such that the deepest parts in the upper teeth are adjacent to the lowest parts in the lower teeth, and _vice versa_. Therefore, in the vertical plane, occluding surfaces do not grow at the same rate.

Occlusal Relations in the Lateral Chewing Stroke

In the lateral chewing stroke, the protocone traverses the talonid basin, from the posterior face of the metaconid, to the third commissure between the metaconid and hypoconid. As this happens, the hypoconid traverses the protoconal ledge.

It will be remembered that the protocone is increasingly more anteriorly placed from M^1 to M^3, and correlated with this, the metaconids are more anteriorly placed from M_1 to M_3. In the last section, it has been shown that these differences are present from an early stage of development. Therefore, if the widths of the protoconal ridges and the talonid basins develop at the same rate, these cusps would always be in their correct positions relative to each other. However, this does not seem to occur.

From Figure 37, it appears that the protocone is slightly retarded in development. In all three molars the protocone develops and calcifies later than the metaconid that bites in front of it, but does not calcify before the entoconid that bites behind it. From Figure 38 it appears that the protoconal ridge does not grow in width quite so fast as the talonid basin. However, the difference is not great enough to prevent models of the upper and lower teeth fitting together at all stages. At all times the protocone still bites against the posterior face of the metaconid.

Growth in width of the protoconal ridge continues later than the growth in width of the talonid basin so that, in the completed tooth, the widths of these regions are almost equal.

Figure 37 shows that the development of the hypoconulid is retarded in M_1 and M_2.

At the beginning of the lateral chewing stroke it lies adjacent to the tip of the metacone, therefore a certain amount of retardation can be expected. For, just as angle T (Figure 34) becomes calcified much later than angle P (Figure 27), it follows that the hypoconulid would calcify much later than the tip of the metacone. This allows for the growth of commissure 4.

Conclusion on crown development

The cuspal patterns of occluding molars develop in step with each other. At all stages wax models of the crown patterns of upper and lower teeth will fit if put together. This suggests that a single growth factor governs the development of upper and lower teeth.

CHAPTER V

MOVEMENT OF THE TEETH DURING ONTOGENY

In the insectivorous bats where the teeth have high interlocking cusps, it is essential for their functioning that the teeth erupt in their correct positions.

Figure 44 and 45 illustrate the maxillary and mandibular toothrows in various stages during their development, and Figure 16 shows them in their erupted condition.

It can be seen from Figures 44 and 45 that the initial positions of the tooth germs are dissimilar to their final positions, and that the teeth move relative to each other during their development.

The study of movement in embryonic growth is complicated since all the tissues are differentiating and growing at different rates.

In the embryonic head no tissue can be taken as stationary, and it is necessary to define a reference point to which the movements of the teeth can be related.

In the present study, different reference points are used at different times, and for different purposes, as this proves more convenient than relating all movement to an artificially imposed standard. The elongation of the snout in H. beatus prevents such a standard as the Frankfurt mandibular plane from being a satisfactory standard.

Movement can be rationalised into three planes, namely, horizontal (frontal plane), vertical (sagittal plane), and transverse. Alternatively, it can be analysed as translatory movement as opposed to tilting movement.

Factors effecting the movement of the tooth germs are:

A) <u>Intrinsic Growth of the Tooth Germs</u>

This causes both translation and tilting of the teeth as follows:

1) <u>Translation or Drift</u>

As the tooth germs grow they occupy more space and so pressures are set up in the surrounding tissues. The fibrous sheaths of the follicles prevent the teeth themselves from becoming distorted by these pressures, instead the follicles press against each other and are caused to spread in the direction of least resistance.

2) <u>Tilting</u>

Intrinsic growth may cause tilting of the crown relative to the surrounding tissues, e.g. the paracone of M_3 grows at a greater rate than the base of the posterior region, causing the anterior region to bulge, which in turn appears to causes the crown of the tooth to tilt backwards see page 60.

B) Growth of the Other Tissues in the Head

1) Growth of the non-dentary tissues may cause movement of the tooth germs indirectly by causing movement of the mandibular and maxillary bones that support them. The growth of the supporting bones directs the movements of the tooth germs by allowing space for them to spread out i.e. allowing drift or tranlatory movement. 2) Also, uneven deposition of bone immediately surrounding the tooth germs can cause them to tilt.

It is proposed to consider first the growth of the mandible and the effect that this has on the growth movement of the lower teeth, and then to discuss the growth of the maxilla and its effect on the maxillary teeth.

Growth of the Mandible and Movement of the Mandibular Molars

The mandible is formed as a membrane bone in association with Meckel's cartilage. In the earliest stage (Mn-length 0.58 cm), calcification is in progress along its entire length. However, Meckel's cartilage is still prominent (apparent in Figure 51).

The alveolar bone calcifies at the same time as the mandibular shaft. It is continuous with it and is similar in appearance. The mandibular shaft together with the alveoli form a gutter enclosing the tooth follicles. See Figure 9.

Once calcified, the mandible grows in height and width by apposition of bone, and in length by a subperiosteal growth centre on the mandibular condyle. However, until the symphysis between the shafts of right and left mandibles becomes closed, growth may also occur in the anterior region. But if so, this growth would be by apposition of bone, and would be small compared with the subperiosteal growth at the mandibular condyle.

Figure 46 shows the mandible in stages 1, 4 and 13 superimposed to show growth. As the increase in length takes place mostly in the condylar region, the anterior part of the shaft has been used as a reference point for superimposition. It is evident from this figure that the ascending process of the mandible keeps a constant proportional relation with the condyle throughout development. It therefore follows that much remodelling of this region must take place. The histological study of the sections shows a thick layer of large dense cells, osteoblasts and osteoclasts, to be present along the margins of the ascending process indicating that bone is resorbed from the anterior margin, and subsequently deposited along the posterior margin.

Movement of the Teeth in the Sagittal Plane

The alveolar bone around the periphery of the tooth follicles is thickest and most stable on the buccal and lingual sides. The bone is trabeculate and is deposited fairly rapidly. (During development a ledge of alveolar bone grows between the tooth follicles and the mandibular nerve, thus the latter comes to lie in a bony canal, the mandibular nerve canal.)

In the early stages the tooth germ follicles develop precociously so that the straight anterior part of the mandible is too short to support them linearly. In Figure 47 it is evident that the tooth row curves dorsally in the posterior region. Between stage 1 and 5 this dorsal curvature is increased. It appears that the growth of the mandible does not keep pace with the growth of the tooth follicles, and so the latter are pushed backwards and upwards into the only space that is made available to them i.e. towards the mandibular condyle.

After stage 5 the dorsal curvature of the toothrow flattens out. The mandibular nerve sinks downwards and the alveolar gutter with the enclosed teeth, follows.

Thus it appears that after stage 5 the growth of the toothrow slows down, whilst the mandible continues to grow, this causes the condyle to grow backwards away from M_3. It can be seen from Figure 47, that the relative distance between the condyle and M_3 increases in the later stages. M_3 is directly below the ascending process in stage 5, but is left in a possition anterior to it by stage 13. Figure 48, shows the length of the mandible plotted against the length of the toothrow. As would be expected there is a peak at stage 5.

It will be remembered from Chapter IV that the period of most rapid growth of the tooth germs is from shortly after histological differentiation of the cells to the onset of calcification of the crowns. For the third molars this is between stages 3 and 6a

(Mn-length 0.633 to 0.660 cm respectively). The first and second molars and the antemolars finish their period of most rapid growth before stage 6a for by this stage they are almost completely calcified see Figure 37. Thus it can be assumed that the peak at stage 5 in Figure 48, is due to the slowing down of growth of the toothgerms, due to calcification of the latter.

The bases of the teeth keep a constant relation with the mandibular nerve, therefore in the early stages the crowns of the posterior molars face anteriorly. As the nerve descends, the posterior region of each tooth moves more than the anterior region, so that the teeth come to face dorsally.

But the teeth are growing in height. Therefore in the posterior teeth, as the bases of the teeth are sinking, the crowns of the teeth are moving upwards. Thus the crowns of the teeth do not descend to the same extent as their bases, and in fact the crowns do not "descend" but always grow upwards relative to the base of the mandible.

Thus the flattening out of the toothrow causes a rotational movement of the teeth, whereby the crowns of M_2 and M_3 tilt backwards. This movement is helped by the fact that the protoconal region of the crown grows more than the posterior basal region, thus increasing the tilt of the tooth by intrinsic growth.

Hence the movement of the teeth in the sagittal plane can be said to be the resultant of three component forces, as follows:

1) A downward component force caused by the sinking of the toothrow as the mandibular condyle grows backwards.

2) A backward component force due to the increase in size of the tooth follicles, causing them to spread out backwards.

3) An upward component force due to the growth in height of the teeth.

The reorientations of the teeth in the sagittal plane between stages 1 and 13 are shown in Figure 49. Here stages 1,5, & 13 are superimposed, and arrows show the movement of the principal cusps relative to the mandibular symphysis.

Movement of the Teeth in the Horizontal Plane

Figure 50 illustrates horizontal movements of the teeth between stage 1 and 13 relative to the midline and the anterior end of the mandible.

The figure shows that the mandibular condyle grows laterally as it grows backwards. With this lateral growth there is some adjustment in the region of the symphysis, so that the original anterior part of the mandible rotates slightly. The rotation appears to be in a lingual direction. This is surprising since the tissues between right and left mandibles are increasing in size. However, it is less surprising when the shape of the finished jaw i.e. when it is elongated and narrow, is compared with the embryonic short snouted form.

In Figure 50 the arrows show the relative movements of the main cusps. It is evident that M_1 moves backwards and slightly laterally, whilst M_2 and M_3 move almost directly backwards i.e. their buccal cusps move buccally and their lingual cusps move lingually.

It will be noticed that there is a horizontal rotation of the teeth. The posterior half of each molar swings lingually. This is due to the re-orientation of the mandible and also to rotation of the tooth germs within their alveoli. The latter is caused by the intrinsic growth of the tooth germ and the directing influence of the enclosing tissues.

Movement of the Teeth in the Vertical Plane

It has already been stated that, as the teeth increase in height, the base of the toothrow keeps a constant relation with the mandibular nerve. However, when transverse sections are studied, it can be demonstrated that it is the lingual region that remains close to the nerve, whilst the buccal basal region grows upwards away from it, so that the base of the crown tilts markedly. The tilting appears to be directed by an uneven deposition of bone. When measured from the base of the mandible, the bone deposited beneath the lingual basal margin is found to be greater than that deposited beneath the buccal basal margin.

The tilting of the tooth base increases as development proceeds. For M_1, this is shown in Figure 51 a & 52b where the sections are transverse to the tooth rows. The same thing occurs for M_2 and M_3.

Plates a and b in Figures 51 & 52 pass through the talonid region of M_1 in stages 1 and 13 (Mn-length 0.58 and 0.97) cm.

Summary of movement of lower molars

1) Movement of the lower molars is due to an interrelation between the growth of the tooth germs and the growth of the mandible, the latter affording space for the former.
2) The growth in length of the toothrow is not proportional to that of the mandible.
3) An unfurling of the posterior dorsal curvature of the toothrow occurs whereby the crowns of the molars tilt backwards and at the same time their bases tilt buccally. The movement can be visualized as a process whereby the molars slide down an expanding inclined plane, the floor of which is tilted lingually in the posterior region and buccally in the anterior region. See Figure 62.

Growth of the Maxilla and Movement of the Maxillary Molars

The maxilla like the mandible forms as a membrane bone.

In the region of M^1 in stage 1, bone formation is fairly advanced, but the degree of calcification tapers off towards the posterior end, so that in the region of M^3 calcification has not yet commenced. The maxilla in this region consists of tracts of connective tissue.

The alveolar bone develops in a similar way to that in the lower jaw i.e. it is laid down around the periphery of each tooth follicle, particularly on the buccal and lingual sides so that the follicles become enclosed in a tooth row "gutter".

Just as the tooth follicles exhibit a marked gradient in their development, so does the alveolar bone that surrounds them. Thus throughout development it is more extensive in M^1 than in M^3. In stage 1 it has not yet developed around the third molar.

During development a ledge of bone arises above the follicles so that the maxillary nerve becomes enclosed in the maxillary nerve canal (Cf mandibular nerve canal).

From the wax model reconstruction of the tooth follicles and enclosing alveolar bone in stage 1, it can be seen that the alveolar bone encroaches between the tooth follicles, particularly on their lingual sides. This also happens in the lower jaw, but due to the difference in the shapes of upper and lower molars, it is less marked in the latter.

In stage 1 the tooth follicles are packed closely together, and in the region of M^2 and M^3 the tooth row curves markedly towards the lingual side. The crowns of the upper molars are tilted to face slightly posteriorly. This posterior tilt increases from M^1 to M^3.

When the tooth row is viewed from the side, a slight dorsal curvature in the posterior region and a marked dorsal curvature in the anterior region can be seen, see Figure 57 stage 1.

As growth in length of the maxilla probably occurs both at the anterior and at the posterior margins, it is proposed to use a point near the centre of the bone viz; the position of M^1 as a reference point, from which to measure developmental movements of the molars.

In Figures 53 and 54, a tracing of stage 1 is superimposed on to a tracing of stage 13, and arrows indicate the movements of the molars.

Figure 55 illustrates the molars in various stages during development, and indicates the position of the maxillary nerve. It is evident that the molars keep a constant relation to this nerve. The latter runs diagonally above the toothrow from the anterior buccal region of M^1 to the posterior lingual region of M^3 in all stages.

Movement of the teeth in the Horizontal Plane

In stage 1 the tooth germs are located along the buccal border of the maxilla, however, there is insufficient room for all of them, and it can be seen that the posterior teeth develop so that the toothrow curves lingually. Between stages 1 and 5 this lingual curvation increases. It would appear that this is due to the tooth germs growing faster than the supporting bone, and therefore the most posterior ones are "pushed" into the only space available to them, which is lingually.

Figure 45 shows that during development the upper toothrow keeps a constant relation with the buccal border of the maxilla.

After stage 5 the growth in length of the latter is greater than the sum of the growth in length of each maxillary tooth. Thus during development the toothrow is drawn towards the buccal border and the lingual curvature diminishes.

M^1, M^2 and M^3 move buccally and rotate buccally, and M^3 moves from a position lingual to M^2 to a position posterior to M^2.

The posterior margin of the upper tooth row keeps a constant relation to the zygomatic process of the maxilla. In stage 1 M^2 is the most posterior tooth, and is positioned diagonally across the anterior margin of this process. By stage 13, M^3 is in the position that M^2 occupied in stage 1.

Thus although the individual teeth do not grow at the same rate as the maxilla, the anterior to posterior length of the tooth row does. This is shown graphically in Figure 56.

How the unfurling of the tooth row comes about is open to speculation. In the following account it is proposed to describe observations which may throw light on this topic, and to offer a possible explanation:-

When the "unfurling" of the toothrow is examined more closely, it is found that much of the unfurling is due to <u>intrinsic growth</u> of the tooth germs.

When the toothrow in stage 1 is considered, it is found that the lingual border of the toothrow is only slightly curved, and that it is the buccal border which exhibits the marked curvature. This suggests that much of the curvation is due to the shape of the tooth germs.

The young tooth germs are wedge-shaped. The anterior and buccal regions develop first. These facts, together with the marked gradient in size of the follicles from M^1 to M^3, causes the excessive curvature. By stage 5, M^3 has also developed into a wedge-shaped form, and, as has been shown, the curvature of the tooth row in stage 5 is even more marked than in stage 1.

After the wedge-shaped stage is reached, the growth in the posterior regions of the crowns takes place, and this causes an apparent rotation of the tooth relative to the surrounding tissue.

When a line is drawn joining the paracone and metacone of M^2 in stage 1 and stage 13, it is found that the rotation of this line relative to the midline of the head is only 8½°. Whereas the apparent rotation of the tooth measured by the rotation of the buccal border is 29°. The discrepancy between the actual rotation and the apparent rotation is due to the growth of the metaconal region. In M^3 the posterior region does not increase in size to the same extent as the anterior region. The tooth remains wedge-shaped, and it will be noticed, the buccal border remains sloping in a lingual direction even in the erupted dentition.

But the intrinsic growth does not account for all the horizontal rotation during development. The intrinsic growth of M^3 does not account for the buccal and posterior movement of this tooth relative to M^2. However the <u>distal</u> <u>drift</u> of the teeth may play a part in this process.

Drift in the upper molars is not so easily explained as in the lower molars. For the former are the wrong shape to cause a direct anterior or posterior movement merely by enlarging and pressing against each other. Direct pressure along the anterior and posterior borders of the wedge-shaped tooth germs would cause an increase rather than a decrease in the curvature of the toothrow. Indeed this appears to happen in the very early stages before the alveolar bone has developed between M^2 and M^3.

However as development proceeds, the tooth germs are not in contact along their entire anterior and posterior surfaces. Re-entries of alveolar bone develop between their tapering lingual regions, so that the tooth germs are only in contact with each other towards their buccal parts.

It is conceivable that reciprocal pressure applied in these regions i.e. where the follicles are in contact may help in causing an anterior or posterior movement together with some unfurling of the tooth row. This may happen in the following way:-

> In Figure 55 growth of the buccal region of M^2 and M^1 would cause pressure at point X where they are in contact. This pressure acting against the metacone of M^1 would cause a tendancy for M^1 to rotate buccally.
>
> In the same way, with the development of M^3, see Figure 55, M^3 would press against the metacone of M^2 (at point Y) and cause a tendancy for M^2 to rotate buccally. But M^2 is also receiving pressure from M^1 at point X.

It is possible that the pressures would be such that with the increase in size of the teeth and the tendency for the metacones of M^1 and M^2 to move buccally, there would be a distal drift of the teeth accompanied by a buccal rotation, and therefore a straightening out of the anterior region of the molar toothrow.

However, this would not explain why the curvature in the region of M^3 is reduced, and why M^3, which lies lingual to M^2 in stage 1, should be posterior to M^1 by stage 13.

The movement of M^3 could be explained as follows:-

There is very little re-entry of bone between M^2 and M^3 until shortly before eruption, so that these teeth are in contact along their respective posterior and anterior sides, Y-Z in Figure 55. Reciprocal pressure can therefore occur along Y-Z. During development, the lingual region of M^2 grows backwards to develop a posterior heel. As the latter develops it is conceivable that pressure would be directed against M^3 at Z. At the same time M^3 is pressing against M^2 at Y and M^2 is pressing against M^1 at X. Also all the teeth are increasing in size and cannot move forwards because of the development of the anterior teeth.

Therefore with the increase in the posterior region of M^2, and with the backward pressure of the teeth, M^3 would be made to move backwards into the space made available for it by the growth backwards of the maxilla. This backward buccal movement would depend on there being a resistant lingual margin of alveolar bone to prevent a lingual movement of M^3.

Alternatively, the growth of the supporting bone, e.g. growth centres in the maxilla, may be the factor that causes the posterior drift of the teeth, and the buccal horizontal rotation.

Whichever factor initiates the movement, it is made possible by the maxilla growing in the posterior region, and so providing space for it to take place.

Movement of the Teeth in the Sagittal Plane

The posterior movements in the sagittal plane has been dealt with above.

From Figure 57, it is evident that the bases of the upper molars keep a constant relation with the maxillary nerve, therefore with growth, the crowns move downwards away from this nerve.

In the early stages the crowns are inclined slightly in a posterior direction, however during development this inclination is reduced.

Its reduction appears to be partly due to <u>intrinsic</u> <u>growth</u> as follows:- in the early stages, the paracone develops first, and so is higher than the metacone, and therefore the crown slopes posteriorly. But growth of the metacone soon exceeds the growth of the paracone, so that the former becomes as large, if not larger than, the latter. Therefore the posterior tilt of the crown is lost. In M^3 the metacone is never as large as the paracone, and it can be seen that the crown always tilts slightly backwards.

The anterior to posterior gradient in the development of the underlying bone accentuates the posterior tilt of the teeth in the early stages. In the later stages, the gradient is less marked, and so its effect on the tilting of the teeth is reduced.

Movement of the Teeth in the Vertical Plane

When transverse sections are studied it is found that in the early stages the bases of the tooth germs are approximately horizontal, but that during development they become tilted in a lingual direction. The base of the lingual region of each tooth germ keeps at a constant distance from the maxillary nerve, whereas the buccal region grows downwards away from it.

This process appears to be aided by an uneven deposition of bone around the basal region of the tooth germ.

When measured from the floor of the orbit, more bone is deposited along the buccal border of the maxilla, than along the lingual side, thus the buccal part of each tooth germ comes to lie on a ridge of bone, and so is lower than the lingual region. Figures 51 and 52 demonstrate the tilting of M^1 during development. Plates a and b pass through the protoconal region of M^1 in stages 1 and 13.

(Mn-length 0.58 and 0.97 cm). These sections are chosen because they are transverse to the toothrow, however the same occurs in M^2 and M^3.

Summary of Movement of upper molars

1) As in the lower jaw, the movements appear to be due to an interrelation between the growth of the tooth germ and the growth of the supporting bone, the latter affording space for the former.
2) Growth in length of the toothrow is proportional to that of the maxilla, this is because the lingual curvature in the posterior region of the upper toothrow is drawn laterally during development, and unfurls against the buccal border of the maxilla. The process is not complete by stage 13.
3) As the lingual curvature unfurls, the molars rotate buccally, and at the same time they tilt forwards, and their bases tilt lingually.

The process can be visualised as the tooth germs moving on the underside of a helical plane, the posterior region of which is twisted lingually yet faces in a buccal direction, and the anterior region of which is tilted in a lingual direction. See Figure 62.

A Comparison of the Developmental Movement of the Upper and Lower Toothrows with Special Reference to Their Occlusal Relations

Figures 57 and 58 show graphic reconstructions of upper and lower toothrows 'in situ' in the head in side-view and plan-view in various stages during development.

In Figure 59 a tracing of the side-view reconstruction of stage 1 (Mn-length 0.58 cm) is superimposed on to a side-view reconstruction of stage 13 (Mn-length 0.97 cm) to show movements of opposing occlusal points relative to the maxillary nerve and M^1. Points that will later occlude are joined by brown lines. Red arrows show movements of these points.

In Figure 57 hypothetical lines are drawn through opposing occlusal points.

In the previous section it has become clear that the growth movements are dependent upon the intrinsic growth of the teeth and on the growth of the supporting tissues, the latter affording space for the tooth germs.

The intrinsic growth of upper and lower teeth is co-ordinated (see Chapter IV), therefore, it would appear that any differences in their growth movements is due to a difference in the growth of their supporting tissues particularly the maxilla and mandible.

When the increase in length of the mandible is plotted against that of the maxilla, see Figure 60, it is found that their growth in length <u>is</u> co-ordinated, the bones grow at the same rate. However, the maxilla is always significantly shorter than the mandible, yet the sum of the lengths of all the maxillary teeth is not much shorter than that of all the mandibular teeth. From Figures 57 and 58 it is evident that the maxillary teeth are more crowded than the mandibular teeth. And it would appear that this overcrowding, together with the fact that the maxilla and mandible are different shapes, causes the differences in the growth movements of the follicles.

In the early stages, in both upper and lower jaws, the teeth grow faster than their supporting bones. In both cases the younger tooth germs are pushed into the only spaces made available to them (see appendix B). The lower teeth advance backwards and upwards towards the mandibular condyle, whereas the maxillary teeth (A) advance lingually around the posterior edge of the maxilla and (B) increase the upward curvature in the anterior region. Thus, the curvatures that ensue are in different directions in the two jaws. The increase in the convergence of the hypothetical lines between stages 1 and 5 in Figure 57, shows that compression of the teeth is greater in the upper jaw than in the lower jaw.

After stage 5, the teeth spread out, but to attain their correct occlusal places, the upper teeth must spread out at a greater rate than the lowers. The fact that they do this is evident from Figure 57, for the lines joining opposing occlusal positions gradually become parallel. The graphs in Figures 48, 56 and 60, can be compared directly with each other in Figure 61. A fourth graph representing Mn-length plotted against age is also given. In this figure, graphs A and B converge slightly up to stage 5, showing the toothrow to grow slightly faster than the mandible: after stage 5 the graphs diverge showing that the growth of the toothrow slows down. Graphs B and D demonstrate that the maxillary toothrow is always shorter than the mandibular toothrow, but that the greatest difference in their lengths occurs at stage 5. Before this stage, the upper teeth are compressed more than the lower teeth (shown by divergence of the graphs). After this stage the upper teeth spread out at a faster rate than the lower teeth, (shown by the convergence of the two graphs) so that, by stage 14, the upper toothrow is almost as long as the lower toothrow.

The lines in Figure 57 show that the greatest compression in the upper tooth row occurs in (1) the posterior region and (2) the anterior region, denoted by lines AB, DE, respectively.

In the final dentition (stage 14), $\frac{AB}{A_1B_1} = 1$ and $\frac{CD}{C_1D_1} = 1$.

But in the early stages $\frac{AB}{A_1B_1}$ and $\frac{CD}{C_1D_1}$ both equal less than one.

The figure shows that the most marked contrast in regional lengths between upper and lower toothrows occurs in the posterior region i.e. $A A_1$ to $B B_1$. This is due to the marked lingual curvature in the M^2 M^3 region.

The occlusal lines in Figure 57 illustrate another phenomenon viz: the teeth that will later occlude tend to face each other at all stages, in the saggital, the transverse and the horizontal planes.

Movement of the Molar Teeth

In the Sagittal Plane

The lower molars are tilted forward so that they face the upper molars and the latter are directed backwards.

With growth, the crowns of the lower molars tilt backwards and the crowns of the upper molars tilt forwards, at the same time the lower molars move forwards relative to the uppers. In other words, during development the upper molars no longer face backwards but rotate so that they face ventrally, and the lower molars no longer face forwards but rotate so that they face dorsally, as this happens the lower molars move forwards underneath the uppers so that at all times upper and lower teeth that will later occlude, face each other.

In the Transverse Plane

It will be remembered that the bases of the upper molars tilt lingually, whereas the bases of the lowers tilt buccally. The tilting is such that the bases of occluding upper and lower teeth remain parallel throughout development. The titlting is equal, but opposite, in both upper and lower teeth, and is such that, as the teeth grow towards each other and overlap, the buccal sides of the lower teeth come to be adjacent to the lingual sides of the upper teeth. This equal but opposite rotation is demonstrated in Figures 51 and 52.

In the Horizontal Plane

The posterior upper molars rotate buccally, whilst the lower molars rotate slightly lingually. However the rotation is such that the molars, that will later occlude, tend to face each other.

These rotational movements are difficult to demonstrate from plan- and side-view reconstructions, therefore a diagramatic representation of the movement is given in Figure 62. The figure was drawn from a three-dimensional model, made of strips of paper, twisted to simulate the shape of the toothrows. The developmental movements of the molars can be visualised as a process whereby the lower molars slide down the lower helical plane in Figure 62 and the upper molars move on the underside of the upper helical plane.

Movement of the Antemolars

Of the antemolars, it can be seen from Figure 57 that the upper teeth in the early stages are splayed in such a way as to face their occlusal opponents in the lower jaw. In the later stages the upper teeth become less crowded, and less splayed, and move downwards to take their positions between the lowers.

It will be noted that in the early stages there is plenty of room for the lower teeth in the region $C_1 D_1$ and that as the teeth grow they just fill up the space available, and consequently there is little expansion of this region, and little pressure exerted on the posterior teeth.

Therefore the difference in the proportion $\frac{CD}{C_1D_1}$ during development is mainly due to the spreading of the upper teeth.

From stage 5 onwards the upper antemolars spread backwards relative to the lower antemolars. Space is allowed for this by the backward movement of M^1 relative to M_1.

General

In the molar region, AB becomes equal to A_1 B_1; again by spreading out of the upper teeth relative to the lowers, but here, there are no spaces between the lower teeth in the early stages, and so A_1 B_1 grows considerably during development due to intrinsic growth of the lower molars. However, the increase is not so great as that of A B, for the latter grows not only by intrinsic growth, but also by the movement of M^3 from a position lingual to M^2 to a position posterior to M^2. Thus A B is increased by the length of one tooth. But even so the unfurling of the toothrows is not sufficient to account for all the backward movement of the upper molars relative to the lowers.

It has already been stated that M^1 moves backwards relative to M_1. This causes a subsequent movement of M^2 and M^3. This is sufficient to account for the backward change in position of M^3 relative to M_3.

This process is more easily explained if one accepts that the whole maxilla translates backwards relative to the mandible, rather than that M^1 moves backwards along the aveolar gutter. In the former case the spreading out of the upper antemolars could only be explained by growth at the anterior end of the maxilla, allowing them space to move forwards, thus leaving the posterior upper teeth close to the jaw joint, whilst the lower teeth are pushed forwards away from the jaw joint.

Eruption

By stage 13 the teeth are not quite in their final positions. The upper anterior teeth have come to lie directly dorsal to their occluding opponents in the lower jaw, and already overlap to a considerable degree in the sagittal and transverse planes. But the degree of overlap and finalisation of positioning is progressively less as one proceeds backwards along the toothrow. The posterior upper molars still exhibit a lingual curvature, so that the embrasure between M^2 and M^3 is too narrow for the protoconid of M^3 to fit into. Also the occluding lingual and buccal surfaces of the upper and lower molars respectively are not quite vertical. No stages showing erupting teeth were available. But, for the teeth to attain their final positions from those that they occupy in stage 13, it is necessary for:

1) M^3 to rotate buccally from M^2,
2) for the occluding sides of upper and lower teeth to become vertical and
3) for the teeth to grow towards each other and increase their overlap.

It will be noticed that these movements are a continuation of the developmental movements. Therefore it would appear that eruption is but the terminal phase in the process whereby the teeth attain their final occluding positions.

By stage 13 (Mn-length 0.97 cm) the growth of the crown has ceased, however intrinsic growth can still play a part in causing developmental movements. The work of Sicher (1942) and Orban (1928) show that root formation is an important factor in eruption. In H. beatus root formation could account for most of the movement that takes place between the latest embryonic stage studied and the final stage.

In M^3 the roots develop at an angle, they grow forwards and lingually away from the tooth. This would help M^3 to rotate backwards and buccally, and so open the gap between M^3 and M^2.

Sicher (1942) has shown the presence of a hammock ligament at the base of single-rooted teeth, and suggests that this acts as a resistant layer, so that growth of the root pulp causes an upward movement of the tooth. No hammock ligament could be discerned at the bases of the single-rooted teeth in the bat. However, the formation of trabeculate bone between the roots of the multi-rooted teeth (also described by Sicher), and around the tapering roots of the single-rooted teeth, could well be a factor in lifting them bodily through the tissues in the process of eruption.

Rink (1929) has shown that in the rabbit, the eruption of incisors takes place when the animal is at rest, and the incisors are out of occlusion i.e. when there is no pressure on the crowns. Therefore eruption appears to be a continuation of the process whereby the teeth move in the direction of least resistance.

Conclusions on tooth movement

1) Due to the maxilla being shorter than, and a different shape from, the mandible, the growth movements of upper and lower toothrows differ from each other.
2) There is always more space available in the lower, than in the upper jaw, so that the upper teeth are more compressed during development. Compression is greater in the posterior region.
3) However there is a marked tendency for occluding teeth to face each other throughout development.
4) The teeth do not attain their final positions by the time the crowns are fully calcified, and it is probable that eruption is merely a continuation of the developmental movements of the teeth.

CHAPTER VI

DISCUSSION

In Chapter IV the order of calcification of the main cusps in the upper molar has been shown to be paracone, metacone, protocone. Kraus (1960) has shown the order in the human upper molar to be paracone, protocone, metacone. As the dentitions of both man and bats are presumed to have evolved from the same primitive insectivorous form, ontogeny in this case does not recapitulate phylogeny. Instead the factors controlling the order of development appear to be:

1) the height of the cusps in the finished dentition, and

2) the growth gradients in the tooth germ.

The tallest cusps tend to differentiate and calcify first, followed by the next tallest etc. Thus, the protoconid is the highest cusp in the lower molar and develops first. However, this order is interrupted by the growth gradients in the tooth germs. Thus in the upper molar, the metacone develops later than the paracone, irrespective of the fact that the metacone in M^1 and M^2 becomes the tallest and largest cusp.

Whether growth gradients throw light on the homologies of regions of the crown, is a debatable point. In man (Korenhof 1959 and Turner 1960) and in H. beatus (present investigation) the growth gradients are anterior to posterior and buccal to lingual in both upper and lower teeth, therefore suggesting that the anterior parts of upper and lower teeth are homologous, and also that the buccal parts of oposing teeth are homologous. However in the mouse (Gaunt 1955, 1956) the gradients are reversed in the upper teeth, suggesting that in these animals the anterior part of an upper tooth is homologous with the posterior part of a lower tooth.

However, it is difficult to find homologies of the cusps of the mouse with those of other mammals.

As the more complex patterns of upper and lower teeth have evolved together (Butler 1941), homologies between the cusps of upper and lower teeth do not necessarily arise; except perhaps for the primary cusps, which are believed to be homologous with the single cusp of the canine, evolving via the reptiles, from a placoid scale.

In the present study the cusps develop as small nodules or elevations. These are at first rounded but soon a small area becomes elevated to form the summit of the cusp. The shape of the summit is determined before the onset of calcification. Whether the elevation is due to cessation of mitosis in the cuspal region, so that the surrounding region grows downwards away from it (Butler 1956), or, whether the cuspal region is elevated by an increase in mitosis at the summit, is at present being investigated by Anga Ramadan, at the Royal Holloway College.

Except for the primary cusp, the cusps bud off from the margins of the crown, for example, the metaconid develops from the trigonid margin, and the protocone from the lingual margin of the paracone. Gaunt's figures (1955 p. 263) suggest that the cusps arise in this manner in the mouse.

In the lower tooth, the paraconid, metaconid and hypoconid, bud off from the base of the protoconid, however the hypoconid itself gives rise to cusps, i.e. the entoconid and hypoconulid. Therefore, the hypoconid can be regarded as the "primary" cusp of the talonid. In a similar way, the protocone, parastyle and metacone appear to bud off from the margins of the paracone, but the metacone also gives rise to cusps i.e. the metastyle and vestigial hypocone, therefore the metacone can be regarded as the "primary" cusp of the posterior region of the upper tooth.

The statement that "once established, the distances between the major cusps remain the same throughout" (Gaunt 1955 p. 258), does not apply to <u>H. beatus</u> unless modified to "Cusps once established and <u>calcified</u> remain at a constant distance from each other". Once the summits of the cusps are calcified, growth of the tissue between them is mostly in depth i.e. causing a deepening of a valley, but the distance between the summits cannot be truly fixed until calcification has completely bridged the gap between them.

In both upper and lower jaws the greatest difference in development between the anterior molars and the third molar, is in the posterior region. In the lower molar the difference is mainly in the size of the hypoconulid. The latter does not develop until a late stage, and its appearance is followed almost immediately by its calcification (see figure 37 stage 6a) thus allowing very little growing time. In M_1 and M_2 the hypoconulid develops relatively earlier, and more growth occurs both before calcification begins on its summit and before calcified bridges link it with its neighbouring cusps. Similarly, in M^3, the metaconal region develops relatively late, and its calcification occurs soon after its development, so that further growth is prevented.

Within the same jaw therefore, the differences in shape between the molars appears to be due to differences in the timing of appearance of the cusps, and the onset of their calcification. However, it could also be due to a difference in the amount of original material available in either the enamel organ, or the pulp tissue. Grüneberg (1961) has shown that if there is insufficient material in the jaw tissue, a tooth germ will not develop. This same principle may apply to the cusps. The marked anterior to posterior growth gradient, makes it possible that insufficient material would prevent the posterior region from developing.

The important conclusion from this section of the investigation is that M_3 and M^3 are "reduced" from an early stage, i.e. at no time do the third molars resemble any other molars.

The present study has shown that the growth of upper and lower teeth is correlated. Occluding cusps develop in step with each other, and when differences occur between adjacent upper teeth, corresponding differences can be found in the opposing lower teeth. These differences are present throughout development. Thus unerupted, even uncalcified teeth will fit if put together.

This correlation is the more remarkable in that the tooth germs of the two jaws are far removed from each other in the head, and must undergo complex movements in order to attain their functional positions. This suggests that there is a common factor, possibly one gene, governing the growth of both upper and lower teeth.

Work by Hörstadius and Sellman (1946), and Sellman (1946), on urodele embryos shows that tooth germs are partly derived from neural crest material that streams downwards from the dorsal part of the head at an early stage of development. Therefore it is possible that physiological gradients in the neural crest material, common to upper and lower jaws, could account for both the growth gradients that are found in the dentition and for the apparent metamerism that is exhibited.

The single growth factor theory first postulated by Butler 1941 i.e. that upper and lower teeth are expressions of the same gene is supported by other evidence.

It is known that homologous cusps in a variety of mammals can be identified by their occlusal relations (Butler 1952). In other words, occlusal relations appear to remain constant during evolution.

From the present study of *H. beatus* it is evident that although reduction occurs in the third molars, it is such that the same occlusal relations are present as in the second molars.

In the Microcheiroptera, a series can be found ranging from bats with third molars similar to the second molars, to those with the third molars very markedly reduced and even absent (Miller 1907).

Investigations by Butler (unpublished) and separately by the writer, on the collection of Microcheiroptera in the British Museum have shown that there is a high degree of correlation between the reduction in the upper and lower third molars, and always the cusps have the same occlusal relations as homologous cusps in the second molars.

It has also been pointed out by Butler (1962) that molar teeth show a high degree of individual variation, even in species with closely interlocking cusps. The latter is borne out in the present study, for example the paraconid varies in M_1 in different individuals. These small deviations could result in serious malocclusion and yet malocclusion does not appear to occur. This is because either 1) a compl~~i~~ementary variation is found in the opposing tooth or 2) the variation occurs on a part of the tooth that does not occlude or 3) the variation is so small that it is obliterated by wear as soon as the teeth become functional.

The fact that a significant variation on an occluding surface is always accompanied by a complimentary variation on the opposing tooth and the fact that growth of upper and lower teeth is correlated throughout development, gives strong evidence that the growth of opposing teeth is controlled by the same genetic factor.

Dickson 1959 clearly supports the theory that a single gene is responsible for tooth development; page 34, he states "Apart from (such) pathological accidents it would appear that a single genetic factor governs tooth size as, despite gross variations in size and shape of upper and lower jaws, the upper and lower teeth regarded as <u>sets</u> always match. No one for instance is found with a set of large upper teeth and small lowers". Later page 69, he says it is occasionally possible for the teeth and jaws to differ in size, and still more rarely for the jaws to differ in size relative to each other.

The present investigation therefore gives strong support to the theory already expressed by others that an indivisible factor controls the growth and evolution of the whole dentition. This is in opposition to the classical theory that suggests natural selection acts independently upon variations of individual teeth, so that, only those animals whose upper and lower teeth happen to fit are able to survive.

Although the shapes of the teeth of <u>H. beatus</u> throughout development allow them to fit if placed together, the investigation has shown that the shapes of the tooth rows do not.

Thus, although the teeth tend to face each other at all times, models of upper and lower toothrows, even in a stage just prior to eruption, will not fit if placed together. This is due to the growth curvatures in the toothrows. The dorsal curvature in the lower toothrow and the lingual curvature in the upper, do not allow sufficient space between the teeth for the opposing teeth to interdigitate between them. The curvatures appear to be caused by the lack of space in the supporting bones, see Appendix B.

The dorsal curvature in the posterior region of both upper and lower toothrows can be compared with the curve of Spee in the human dentition. It appears to be a general feature of mammalian dentitions, and is particularly marked in the elephant. (An exception however is found in the rodents where the molars develop in a straight line on a ridge of bone that juts lingually from the mandible).

In H. beatus the molar toothrows appear to develop as helicoids. The helicoids unfurl as development proceeds, and at the same time the crowns of upper and lower teeth grow towards each other and overlap. Eruption appears to be the terminal phase in this process of unfurling.

In many mammals e.g. Hyrax, Rhynchocyon and Seniculus and to a certain extent in H. beatus the helical formation of the tooth rows is apparent in the erupted dentition. Thus it appears that eruption has occurred before the process of unfurling is complete. The helical formation of the occluding surfaces is most apparent in animals with a large number of molarised teeth each with cusps of relatively the same size.

From the present study, a picture emerges of a highly complex system of growth involving both intrinsic growth of the tooth germs and of the surrounding tissues. The relative positions of the tooth germs when they first appear and the order in time of their appearance must be controlled, so that as the teeth erupt they are both the right shape and in the right positions to function. Disturbances of this system are responsible for malocclusion.

Studies of tooth germs <u>in vitro</u> and <u>in vivo</u> suggest that the potentialities of each tooth germ are determined at an early stage, for transplanted teeth (Glasstone 1938, Gerstner and Butcher 1957, 1958, Flemming 1955) show powers of organised development.

This suggests that teeth, once established, are not so markedly affected in their development by physiological or mechanical disturbances in their surroundings, as for example is bone. Mellanby 1960, has shown that diet can affect bone formation, as can stresses set up in the surrounding area by external factors (Stallard 1925) or by tension at the muscle attachments (Moore 1960 unpublished). These facts together with the results shown by the present investigation namely, that growth of upper and lower teeth is more intimately correlated than is growth of upper and lower jaws, makes it not surprising that malocclusion in man is more often due to malformation of bone, than to malformation of the tooth crowns.

Many reasons have been put forward why man and domestic and captive animals should suffer more than others from malocclusion.

One of the main causes in man seems to be the timing of eruption of decidous and permanent teeth, the position of the first permanent molar being an important factor (Graber 1954, Hellman 1942, Cohen, Oliver and Berwick 1942 and others). It is known that much malocclusion in children, rights itself by the time the teeth have all erupted (Hellman 1942), but that disturbances in the order of eruption or premature removal of deciduous teeth can cause permanent disturbances in the dentition.

Pressure exerted by the descent of the tongue in embryonic and young stages has been put forward as a factor necessary for normal occlusion, in that it causes the dental arches to increase, therefore allowing space for the teeth (Baker 1944, Dickson 1959).

Wallace (1904) points out that the syndrome of Cretinism includes the growth of a large tongue and also of large dental arches. He also points out that these 2 factors, a large tongue and large dental arches are found in Eskimos and suggests that it is the large tongue which causes the growth of the large dental arches.

Bad facial habits in children involving lips, tongue or finger sucking have all been put forward as factors causing malocclusion.

Stallard (1925) has an interesting theory that "pillowing" i.e. the position of the head during sleep has a great effect on the development of the jaws. The swaddling of babies, e.g. amongst Ancient Greeks, Red Indians, and Laplanders, taught them to lie straight. In these tribes the face develops evenly (although the occiput often becomes flat or asymmetrical), whereas modern

American children are often "face pillowers" and malocclusion is prevalent, (whilst the crania are symmetrical and well-formed).

Malocclusion can also be due to genetic factors. For example, it is known that the size of upper and lower dentitions are always proportional (see page 106), but if a large upper jaw is inherited from one parent and a small lower jaw from the other, or if large teeth are inherited from one parent and small jaws from the other, then badly fitting teeth could result.

However the prevalence of malocclusion in man may be due to quite another factor. Mills (1955) and Butler have pointed out that in primates other than man, and indeed in mammals generally, the cusps slide between grooves in the opposing teeth and so are guided during functional occlusion; also the high canines (particularly in bats see pages 34 and 35) act as guides for attaining correct occlusion. But in man the canines are small and blunt, and the cusps of the molars are obtuse and do not have marked grooves, therefore the teeth are not kept in their correct positions by the action of chewing. Therefore gaps that arise by the loss of deciduous teeth are not kept open by chewing acting upon the adjacent teeth, thus the gaps tend to close, and so leave insufficient room for the permanent teeth, and this results in malocclusion.

Another factor is that the cusps of the deciduous teeth in man, do not interdigitate as they erupt. In <u>H. beatus</u> (where malocclusion does not arise) the stage just prior to eruption, shows that the teeth, although not yet through the oral mucosa, overlap and interdigitate, so that during eruption the movement of upper teeth against the lowers would tend to re-adjust any small discrepancies in spacing of the teeth. This does not happen in man.

Work done by Hellman, however, on the height of the cusps in human molars, has shown that malocclusion is most prevalent in man, in subjects with high-cusped dentitions and least prevalent in short-cusped dentitions, but this does not detract from what has been said above, because even in relatively tall-cusped dentitions the grooves are less distinct, and the canines are less suitable as "guides", than, for example in the dentition of apes.

Conclusion

The work has shown that the attainment of normal occlusion has a basis in ontogeny. The dentition develops as part of a highly complex growth system incorporating both development of the teeth and of the supporting tissues.

The most significant result of the investigation has been to show that the growth of opposing teeth is correlated throughout development. At all stages, wax models of the crowns of teeth that will later occlude, will fit if put together, this supports the theory that a single growth factor is responsible for the growth of both upper and lower teeth.

Whereas opposing teeth have complimentary growth patterns, the opposing jaws do not, so that the tooth germs must undergo complicated movements during ontogeny in order to attain their correct occlusal positions.

In showing that the growth of upper and lower teeth is more intimately correlated than the growth of upper and lower jaws, the investigation suggests that malocclusion in man would be due more often to anomalies in the growth of the jaws than in the growth of the teeth, which is what in fact occurs.

SUMMARY OF THESIS

1. The purpose of the work is to elucidate the growth processes involved in ensuring a correct mutual positioning of upper and lower teeth.
2. Previous work on ontogeny of tooth germs and on occlusal relations of the teeth is reviewed.
3. The material studied consisted of sectioned preparations of a series of 14 embryos of Hipposideros beatus, dried skull specimens and preserved specimens of H. beatus and related species, and live specimens of Rhinolophus ferum equinum insulans.
4. Modifications of the classical methods of graphic and wax model reconstruction are given. These modifications include a method for determining reference points in material that is cut and mounted, and a method of reconstructing material that is cut obliquely.
5. First the dentition of an adult bat is investigated.
6. The morphology of the teeth in the adult H. beatus is described.
7. The occlusal relations in the adult dentition of H. beatus and R. ferum equinum insulans are determined. This is done by
   - i. A study of the wear facets of the teeth.
   - ii. A slow motion cinematograph study of the chewing action in live bats.
   - iii. Examination and dissection of freshly killed and preserved bats.

7. The occlusal relations in a single chewing stroke are found to be
    1) A vertical shearing stroke involving the buccal cusps.
    2) A lateral grinding stroke, in which the protocone grinds across the talonid basin.
    3) A recovery stroke in which the jaws open and swing back to begin a second stroke.
8. The ontogeny of the teeth, particularly where it involves occlusal relations is then investigated, using the series of sectioned embryos of *H. beatus*. The investigation is divided into two parts
    1) An account of the development of crown pattern.
    2) An account of the movements of upper and lower teeth relative to each other during development.
9. In both parts the development of the upper teeth is compared with that of the lower teeth.
10. The molar tooth germs are found to develop in a strict sequence as follows M_1 M^1 M_2 M^2 M_3 M^3. Thus, for example, M_2 develops after the tooth that will occlude in front of it, and before the tooth that will occlude behind it.
11. This sequence of development alternating between upper and lower toothrows is also found to be true of cusps that will later occlude, thus, for example, the protoconid of M_2 develops after the Metocone of M^1 and before the protocone of M^2.
12. Surfaces that will later occlude are found to develop in

step with each other.

13. The result of this, is that models of teeth that will later occlude fit together at all times during development. This is remarkable in that the toothgerms develop in positions f~~o~~ar apart from each other in the head.

14. The teeth are found to undergo complicated movements in order to attain their correct occlusal positions relative to each other.

15. These movements are described and are found to differ in upper and lower jaws.

16. The development of the mandible with its one main growth centre at the condyle, differs from that of the maxilla with its more diffuse marginal growth. Also the mandible is always larger than the maxilla and so affords more space for the developing toothgerms. These differences in the growth of upper and lower jaws appear responsible for the differences in the growth movements of upper and lower teeth.

17. Although the movements of the teeth in upper and lower jaws differ from each other, teeth that will later occlude tend to face each other throughout development.

18. The most significant result of the investigation has been to show that the crown patterns of opposing teeth grow in step with each other, this supports the theory that a single growth factor is responsible for the development of both upper and lower teeth.

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APPENDIX A

THE HISTOLOGICAL DEVELOPMENT OF THE MOLARS

In the series observed, the earliest stage of development is seen in M^3 and the description below applies mainly to this tooth germ. Except for details of contour and shape of the crown surface, the histological development of the other molars (in the stages available) is essentially similar.

Histological development of M^3

M^3 stage 1 (Mn-length 0.580) is in a very early cap stage of development.

The enamel organ is differentiated into:-

1) Internal enamel epithelium, this consists of tall columnar cells with large dense nuclei, the latter almost filling the interior of the cells. The epithelium appears to be more than one cell thick. The cells are densely packed but all orientated at right angles to the membrana praeformativa, many mitotic figures are present and nuclei occur at all levels. However, in the region of the enamel knot, many of the nuclei have migrated towards the enamel pulp.
2) External enamel epithelium, this consists of columnar cells with large nuclei very similar to those of the internal enamel epithelium, but less tall. Mitotic figures are present.

3) Stratum Intermedium which lies adjacent to the internal enamel epithelium and consists of a layer 3 to 4 cells thick of ovoid cells with large nuclei and little cyloplasm. Dividing cell walls cannot be distinguished even under oil immersion.

4) Enamel knot - This structure first described by Ahrens, consists of a dense concentric aggregation of cuboidal cells lying against the internal enamel epithelium and extending into the enamel pulp, however it also extends in the opposite direction causing the internal enamel epithelium to bulge towards the papilla, thus causing a concave area on the otherwise convex crown surface. See Figure 23.

5) Enamel Cord - Cells towards the apex of the enamel knot are strung out to form what is known as the enamel cord.

Stellate reticulum The remainder of the epithelial cells within the enamel organ appear as star-shaped typical embryonic cells resembling mesenchymal connective tissue. They are separated from each other, except for cytoplasmic bridges, by a colourless fluid. The stellate reticulum contains no vascular elements. That part of the stellate reticulum adjacent to the external enamel epithelium resembles the stratum intermedium; its cells being closely packed together.

The Dental Papilla

This consists of an aggregation of cuboidal mesenchymal cells with large nuclei tightly packed against the membrana praeformativa. Interspersed between these cells are numerous small blood vessels.

The Dental Sac

Continuous with the dental papilla and surrounding it and the enamel organ, mesenchymal cells are in the process of orientating themselves to form a protective connective tissue sac or follicle.

These cells are elongated, and orientated along the circumference of the tooth germ. Their nuclei are long and spindle shaped.

The dental sac is heavily vascularised.

Thus in stage 1 (Mn-length 0.58 cm) the tooth germ of M^3 is in an early embryonic state of rapid proliferation, and mitotic divisions can be seen in most of the tissues. The nuclei are all large and active, and the cells are in the process of differentiating into their respective roles.

The internal and external enamel epithelia differ little from each other, each consisting of columnar cells, each having a dense cell layer immediately adjacent to them, and in each, numerous mitotic divisions can be seen.

At this early stage no demarcation of the crown cuspal areas can be made. Figure 23 shows a transverse section of the tooth germ and demonstrates the position of the enamel knot lying above the central depression. It also shows the lingual and buccal grooves (see page 47). The figure compares almost exactly with those shown by Ahrens (1913) Hoffman (1925) Santoné (1935) and Gaunt (1955) of other mammals including Guinea pig, cat, calf, mouse and rat. However, Lefkowitz (1953) in the case of the rat believed the enamel knot and cord to be an artifact due to oblique sectioning.

By stage 2 (Mn-length 0.59 cm) the cells are more definable as their respective tissues. The dental lamina has lost its connection with the oral mucosa, and is about to lose its connection with the dental lamina of M^2. The cells of the lamina have become small and rounded.

Internal enamel epithelium

The cells have become taller, but are still rapidly dividing. Many mitotic figures are present. Nuclei are seen at all levels in the cells.

External enamel epithelium

The cells are becoming less tall, and so are more easily distinguishable from internal epithelial cells, however they can still be regarded as a columnar epithelium.

Stratum Intermedium

The cells have become more flattened and distinct from the stellate reticulum, but otherwise show little change from stage 1.

Enamel knot

This structure is very prominent, more so than in stage 1, due to the difference between it and the surrounding stellate reticulum. However, whereas in stage 1 the enamel knot was lying in a central depression on the crown, by stage 2, it has come to lie partly on the elevated lingual groove.

Enamel Cord

This is also prominent.

Stellate reticulum

The stellate reticulum is less dense than in stage 1, the cells themselves having large ovoid nuclei with chromatin material and a nucleolus clearly visible in otherwise almost transparent nucleoplasm.

The colourless fluid between the cells has increased in volume and the cytoplasmic bridges afford the cells a stellate appearance. Cell walls are difficult to demonstrate. The layer of cells adjacent to the external enamel epithelium are now less distinguishable from the other areas in the stellate reticulum.

The Dental papilla, and the dental sac have grown in volume but otherwise show little difference from stage 1.

By stage 4, (Mn-length 0.66 cm) the enamel knot and enamel cord have disappeared, and the remaining components of the enamel organ are very distinct from each other. The tooth germ is no longer connected to the dental lamina. The latter has been constricted off and reduced.

The internal enamel epithelium is one cell thick, and consists of tall regular columnar cells. Those in the region where calcification is in progress and those where calcification is about to begin, were very tall (length = approx 5x width). The nuclei are packed at the distal ends of the cells (towards the enamel pulp) and fill approximately 1/3 of the length of the cell. Towards the future dentino-enamel junction, the ameloblasts are drawn out into trabecular processes.

The calcification in stage 4 consists of dentine deposition only, the ameloblasts having not yet deposited enamel.

The external enamel epithelium is reduced to cuboidal cells, tending to become squamous at the apex of the enamel organ.

Stratum intermedium is present against the ameloblast cells only, the cells formerly lining the external enamel epithelium having differentiated into stellate reticulum cells.

The stellate reticulum has increased in volume, however the developing crown has grown into it, so that relative to the rest of the tooth germ, it appears to be reduced. The stellate reticulum has become less dense due to an increase of fluid between the cells, but the nuclei are still large and active, and a few cell divisions can be seen. At this stage, when calcification has commenced on the paracone, the stellate reticulum is still devoid of vascular elements.

The dental pulp has become differentiated into odontoblast cells occurring adjacent to the membrana praeformativa, opposite to the ameloblast cells and enamel pulp cells.

The odontoblast cells are arranged more or less as an epithelium. Under the organisation of the ameloblast cells (Glasstone 1936) they are giving rise to, or about to give rise to, dentine. In the less advanced regions of the crown the odontoblast cells are not regularly arranged and differ little from undifferentiated dental papilla cells.

The remainder of the dental papilla consists of fibrous connective tissue. It is highly vascularised.

The dental follicular sac has formed external to the tooth germ. It consists of fibrous elements and blood capillaries are prominent. External to the sac, condensations leading to alveolar bone formation is occurring.

By stage 5 (Mn-length 0.68 cm) amelogenesis has commenced on the highest part of the crown (paracone), and the area of fully differentiated ameloblasts has increased, as has also the area of differentiated odontoblasts. No cell divisions can be seen in these cells; however mitotic figures are still present in the less developed regions of the crown i.e. in the regions of low relief.

The external enamel epithelium of stage 5 has become syncytial and squamous, being 2 to 3 cells thick, but is still complete, and has no infoldings. However, it is itself invaded by blood vessels; large vessels full of erythrocytes can be seen within its syncytial layers, but none has penetrated through into the stellate reticulum.

The stellate reticulum is no longer keeping pace with the growth of the crown, and so is becoming reduced, but the cells still have large active nuclei.

The dental lamina has become invaded by blood vessels and its cells have become rounded off as epithelial rests.

Stage 6 (Mn-length 0.69 cm) shows an increasing number of internal enamel epithelium cells taking on an ameloblast form, and similarly the number of odontoblast cells is increasing. In stage 6, the stellate reticulum has become invaded by blood capillaries. The external enamel epithelium is more or less complete, and the stellate reticulum cells retain their characteristic appearance.

Stage 7 (Mn-length 0.71 cm) shows an advance in dentino - and amelogenesis. Amelogenesis follows the advancing front of dentinogenesis.

Stages 8, 9, 12 and 13 (Mn-lengths 0.75 to 0.97 cm) show increasing disruption of the external enamel epithelium and invasion of the stellate reticulum by blood vessels.

By stage 13 (Mn-length 0.97 cm) calcification has extended over all of the crown surface. The last regions to become calcified and therefore to be differentiated into ameloblasts and odontoblasts are the valley between the paracone & protocone, and the margins of the tooth.

Always the differentiation of ameloblasts preceeds the differentiation of odontoblasts. Both of these differentiate into their respective types well before the onset of calcification.

Histologically the development of M_3 from the bell stage onwards is similar to that of M^3. In stage 1 an enamel knot and enamel cord are present on the apex of the protoconid. Also in stage 1, an enamel niche can be seen, but no corresponding structure was found in M^3.

In M_3 and in all of the molar tooth germs studied, the stellate reticulum remains active and unvascularised until a late stage i.e. until calcification is advanced on the crown. Similarly all the toothgerms show the external enamel epithelium to become syncytial and to contain many blood vessels prior to the vascularisation of the enamel pulp.

APPENDIX B

A POSSIBLE EXPLANATION OF THE TOOTHROW CURVATURES

There is some evidence that the youngest tooth germs are 'forced' to develop out of line with the rest of the toothrow due to the precocious development of the anterior molars and lack of space in the supporting bones.

In stage 1 in the lower jaw, the origin of M_3 from the oral mucosa occurs in a position far anterior to where M_3 is developing. No earlier stages were available, but stage 1 suggests that M_3 is unable to develop directly below its origin, because M_2 occupies this position. The presence of alveolar bone in the toothrow gutter prevents it from growing lingually or buccally and therefore it is left with no alternative but to grow backwards. As a consequence of this M_3, in the early stages, faces directly anteriorly i.e. towards its origin.

Between stages 1 and 5 the toothrow continues to grow at a greater rate than the mandible, and so M_3 is displaced further backwards and upwards towards the condyle. It appears that between these stages the process causing the curvature is still in operation.

Similarly in the upper toothrow, the origin of M^3 is not directly beneath the developing tooth germ, but in this case is in a buccal position. It would appear that the precocious development of M^1 and M^2 cause these teeth to move backwards and occupy all the space available along the buccal border of the maxilla. Due to their wedge shapes and the lack of room on the maxilla the growth of these tooth germs would tend to cause a lingual curvature in the posterior region, and 'force' the young tooth germ of M^3 to develop in a position lingual to M^2. The origin of M^3 from the oral mucosa is very close to that of M^2 and as the dental lamina between these two teeth is continuous, this suggests that the dental lamina does not show the same marked curvature as the toothrow. Figure 24 shows the early development of M^3, and it can be seen that the dental lamina has grown inwards from the oral epithelium at a point buccal to where M^3 is developing.

APPENDIX C

RESULTS OF DETERMINING THE OBLIQUITY OF CUT IN THE SECTIONED EMBRYOS OF HIPPOSIDEROS BEATUS

Obliquity of cut is resolved along three co-ordinates. Each embryonic head is said to 'roll' in the transverse plane, 'pitch' in the sagittal plane and 'yaw' in the frontal plane (see Figure 2).

The angle of 'roll' is not recorded because it is easily determined on each section, and is automatically corrected in plan and side-view reconstruction. The angles of 'pitch' and of 'yaw' are given below.

Stage number & Mn-length	Angle of pitch	Angle of yaw
1 (0.580 cm)	5.0°	1.00° Left of midline
2 (0.590 cm)	0°	0°
3 (0.633 cm)	8.0°	0.75° Left" "
3a (0.650 cm)	0°	0°
4 (0.660 cm)	3.5°	2.00° Right "
5 (0.680 cm)	3.5°	5.50° Right "
6 (0.690 cm)	0°	3.50° Right "
6a (0.693 cm)	7.0°	0°
7 (0.710 cm)	4.5°	5.50° Left "
8 (0.753 cm)	-1.0°	3.00° Left "
8a (0.750 cm)	0°	2.00° Left "
9 (0.727 cm)	4.0°	1.00° Left "
12 (0.903 cm)	0°	3.50° Right "
13 (0.973 cm)	4.0°	5.00° Left "

A negative angle of pitch means the head was tilted backwards, e.g. Stage 8. In all others the head was tilted forwards.

TABLE A

Stage (Gaunt's figures)	HEAD LENGTH	MANDIBULAR LENGTH
1	1.09 cm	0.580 cm
2	1.10 cm	0.590 cm
3	1.20 cm	0.633 cm
3a	1.20 cm	0.650 cm
4	1.28 cm	0.660 cm
5	1.30 cm	0.680 cm
6	1.32 cm	0.690 cm
6a	1.32 cm	0.693 cm
7	1.37 cm	0.710 cm
8	1.40 cm	0.753 cm
8a	1.40 cm	0.750 cm
9	1.45 cm	0.727 cm
12	1.63 cm	0.903 cm
13	1.68 cm	0.973 cm

TABLE I

Active Occlusion During the Vertical Stroke

	Lower Jaw		Upper Jaw	
M_1	Ant. surface of Prd. M_1	against	Post. flange of PM^2	
	Post. " " Prd. M_1	"	Ant. surface of Pa M^1	M^1
	Ant. " " Hyd. M_1	"	Post. " " Pa M^1	
	Post. " " Hyd. M_1	"	Ant. " " Me M^1	
M_2	Ant. " " Prd. M_2	"	Post. " " Me M^1	
	Post. " " Prd. M_2	"	Ant. " " Pa M^2	M^2
	Ant. " " Hyd. M_2	"	Post. " " Pa M^2	
	Post. " " Hyd. M_2	"	Ant. " " Me M^2	
M_3	Ant. " " Prd. M_3	"	Post. " " Me M^2	
	Post. " " Prd. M_3	"	Ant. " " Pa M^3	M^3
	Ant. " " Hyd. M_3	"	Post. " " Pa M^3	
	Post. " " Hyd. M_3	"	Ant. " " reduced MeM^3	

Abbreviations :

Ant. = Anterior
Post.= Posterior
Prd. = Protoconid
Hyd. = Hypoconid
Pa = Paracone
Me = Metacone

KEY to Tables II and III

The word 'bridged' signifies that calcification between the named cusps is continuous e.g. Prd-Med bridged, means that the Protoconid and metaconid are joined by a calcified 'bridge' and so are fixed in relation to each other.

Coloured lines join corresponding stages in cusp development in the three molars.

In these tables it is the lines that cross others (shown in red) and lines that converge or diverge from the third molar to the first molar that are of interest, for these show that the time between the appearance of a cusp or region and its calcification, differs in the three molars e.g. the hypoconulid is calcified immediately after its appearance in M_3 (Table III) but several stages afterwards in M_2 and M_1.

Abbreviations of cusp names are as follows:

Pa = Paracone
Me = Metacone
Pro = Protocone
Past = Parastyle
Mes = Mesostyle
Met = Metastyle

Prd = Protoconid
Med = Metaconid
Pad = Paraconid
Hyd = Hypoconid
End = Entoconid
Hyld = Hypoconulid

TABLE II

Crown Development in the Upper Molars

Table II

Stage No. & Mn-length	M^3	M^2	M^1
Stage 1 0.580 cm	Early cap stage of development. Buccal and lingual grooves present.	Late bell stage of development. Pa summit calcified. All cusps present.	All cusps present. Pa, Me and Pro and calcified. Pa calcification has reached the Past
Stage 2 0.590 cm	Early cap stage of development. Crown becoming triangular.	Me summit calcified.	Past-Pa-Mes-Me-Met bridged.
Stage 3 0.633 cm	Pa primordium present.		
Stage 3a 0.650 cm	Pa distinct. Crown is distinctly triangular in outline.		Pa-Pro bridged.
Stage 4 0.660 cm	Pa summit calcified. Me and Pro primordia present. Past and Mes Met primordia present.	Pro summit calcified. Pa calcification has reached the Past.	
Stage 5 0.680 cm	All cusps present.		
Stage 6 0.690 cm		Past-Pa-Mes-Me-Met bridged.	
Stage 6a 0.693 cm			
Stage 7 0.710 cm		Pa-Pro bridged.	
Stage 8 0.753 cm	Me summit calcified. Pro summit calcified Pa calcification has reached the Past.		
Stage 9 0.727 cm	Past-Pa-Mes-Me-Met bridged. Pa-Pro bridged.		Crown is completely calcified.
Stage 12 0.903 cm	Crown is completely calcified.	Crown is completely calcified.	

TABLE III

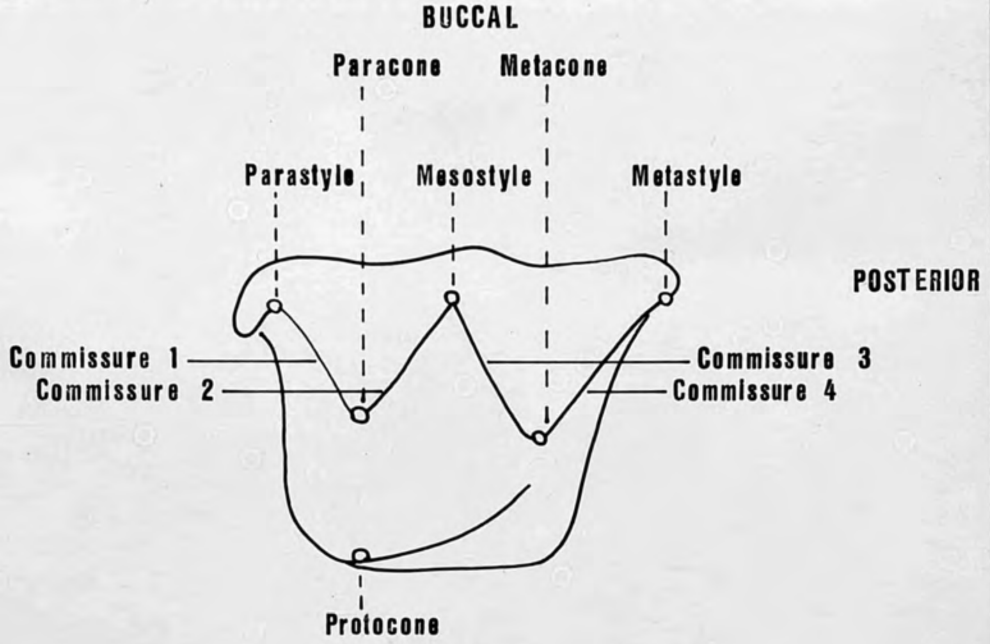
Crown Development in the Lower Molars

Table III

Stage No. & Mn-length	M_3	M_2	M_1
Stage 1 0.580 cm	Early bell stage of development. Prd present. Talonid primordium present.	Prd Med Pad Hyd and End present. Prd and Med summits calcified.	All cusps present. Prd, Med, Pad, Hyd and End summits calcified. Prd-Med and Prd-Pad bridged.
Stage 2 0.590 cm	Prd summit calcified. Hyd primordium present. Med primordium present.	Hyd summit calcified. Prd-Med bridged. Hyld primordium present.	Med-End bridged. Hyld primordium present.
Stage 3 0.633 cm	Med & Hyd present. Pad primordium present. End budding off from Hyd.	Pad summit calcified.	Prd-Hyd bridged.
Stage 3a 0.650 cm	End and Hyd separated by a valley. Pad distinct.	End summit calcified. Prd-Pad bridged.	Hyld summit calcified. Hyd-Hyld-End bridged.
Stage 4 0.660 cm	Med summit calcified. Epithelium now grown over posterior side of Hyd.	Hyld summit calcified. Hyd-Hyld-End bridged. Med-End bridged.	Growth continues in uncalcified regions i.e. in the valleys and at the margins of the crown.
Stage 5 0.680 cm	Hyd summit calcified. Prd-Med bridged. Pad summit calcified.	Prd-Hyd bridged.	
Stage 6 0.690 cm	End summit calcified Prd-Pad bridged. Hyld present and calcified.	Growth continues in uncalcified regions i.e. in the valleys and at the margins of the crown.	
Stage 6a 0.693 cm	Hyd-Hyld-End bridged. Med-End bridged. Prd-Hyd bridged.		
Stage 7 0.710 cm	Growth continues in uncalcified regions in the valleys and at the margins of the crown.		Crown is completely calcified.
Stage 8 0.753 cm			
Stage 9 0.727 cm		Crown is completely calcified.	
Stage 12 0.903 cm	Crown is completely calcified.		

FIGURE A

UPPER MOLAR - OCCLUSAL VIEW



LOWER MOLAR - OCCLUSAL VIEW

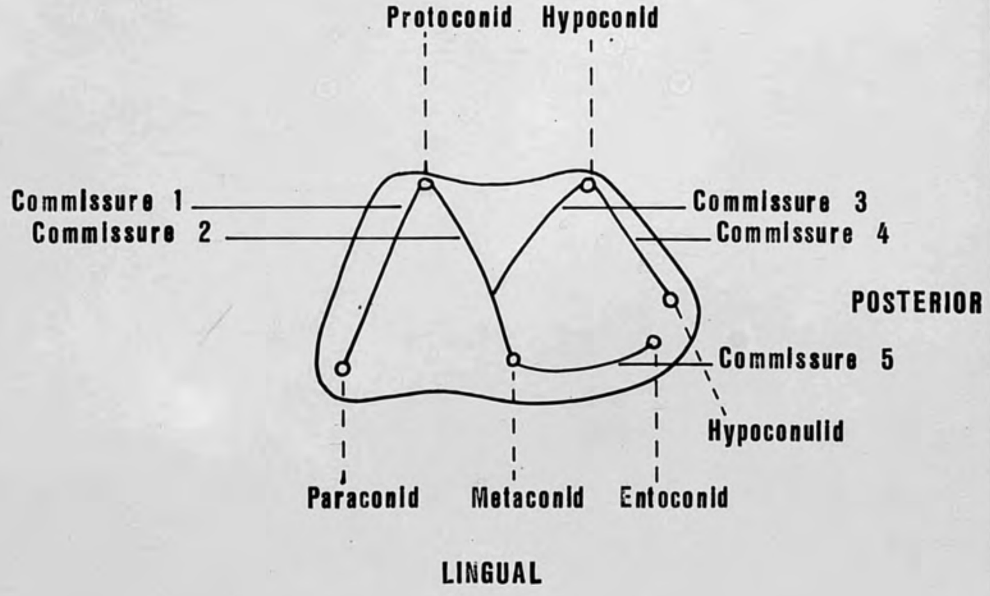
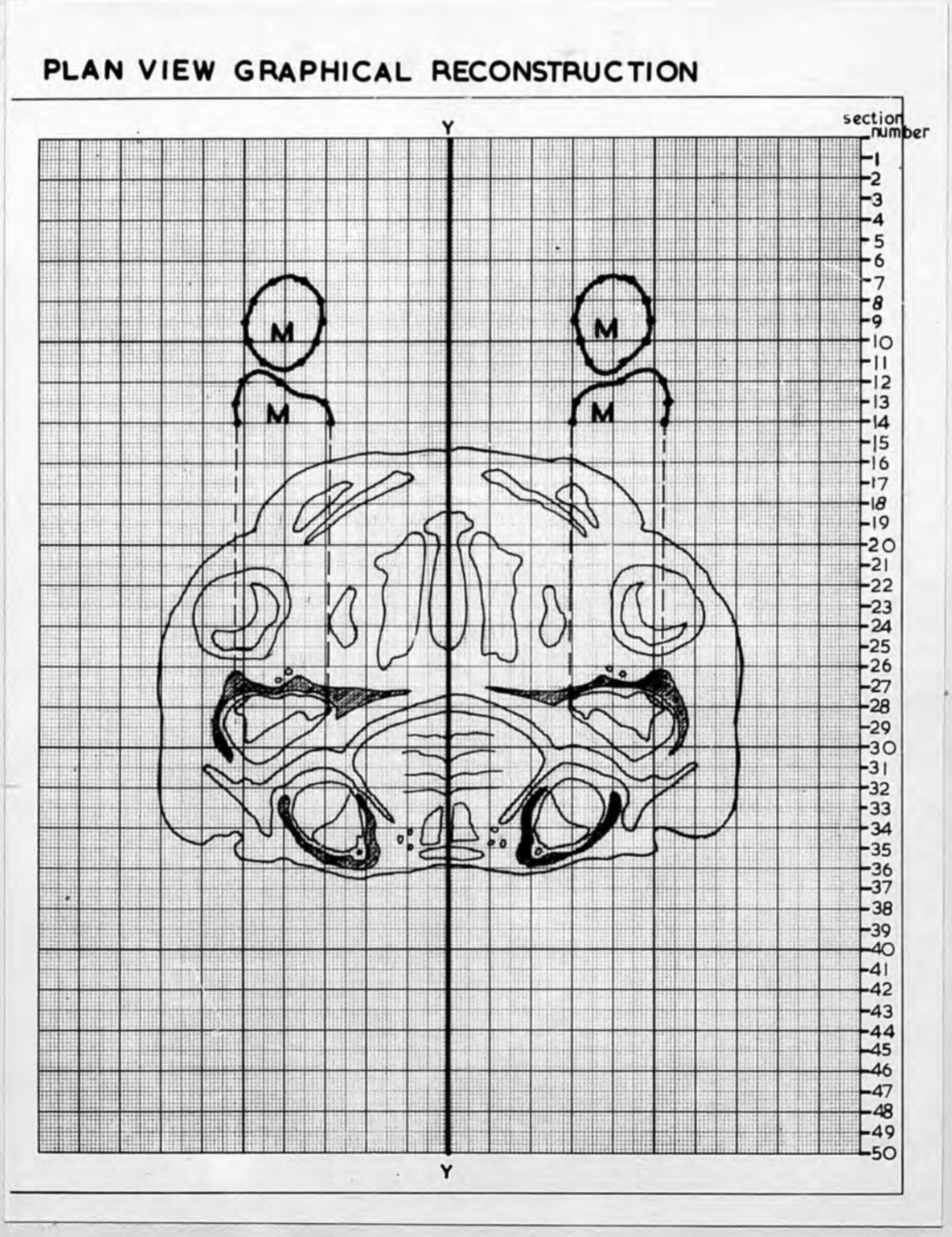


FIGURE 1. Diagram to show method of graphical reconstruction of the upper teeth in plan-view. Section 14 is projected onto the graph paper.



<u>**FIGURE 2**</u> Diagrams demonstrating the head cut obliguely in three planes.

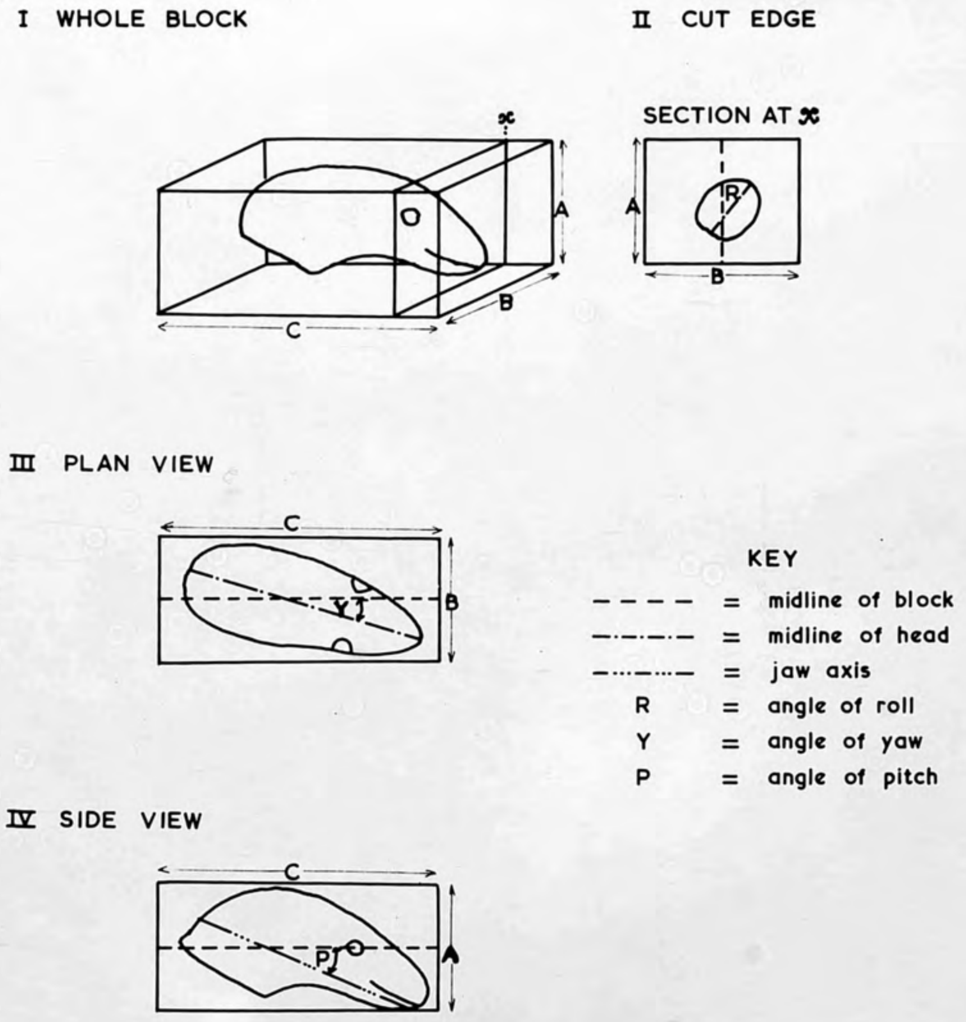


FIGURE 3 To show the method used for determining the angle of yaw.

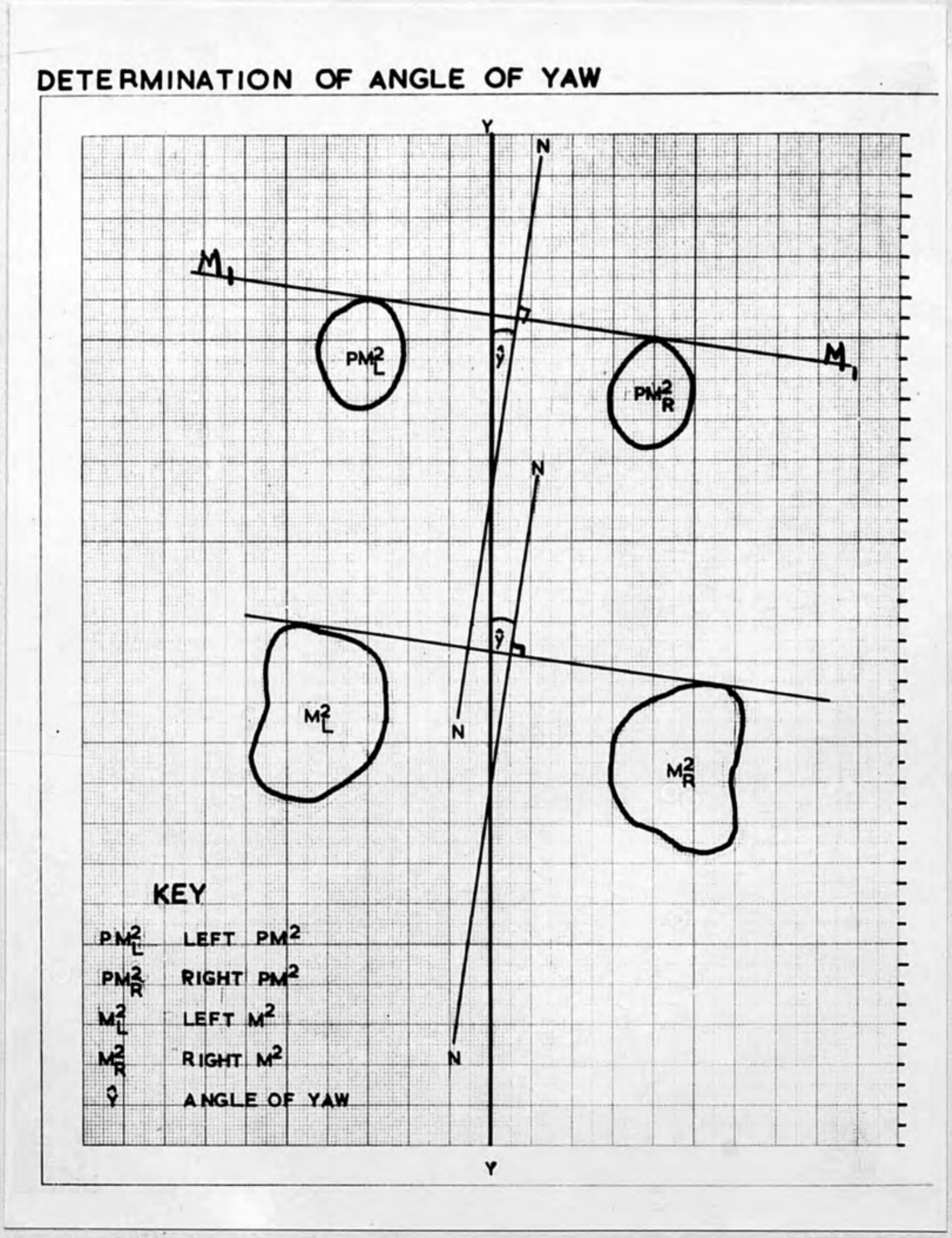
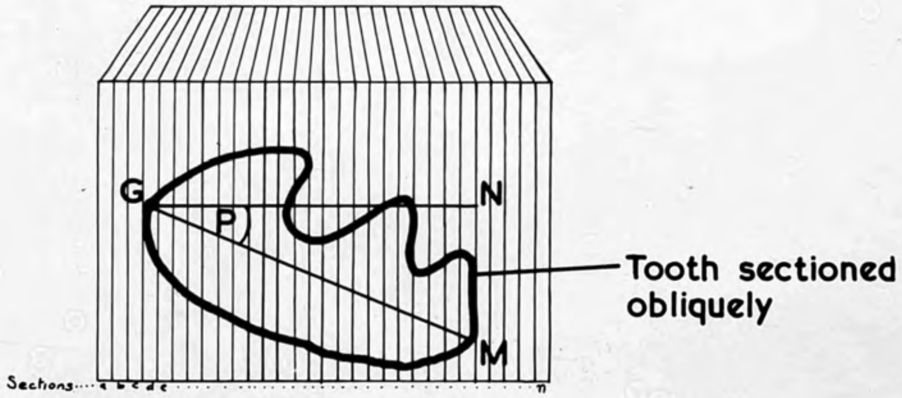


FIGURE 4 To show method of determining the true length of an object cut obliquely.

TOOTH SECTIONED OBLIQUELY



GM = long axis of tooth
" = true length
GN = apparent length in plan view
P = angle of pitch

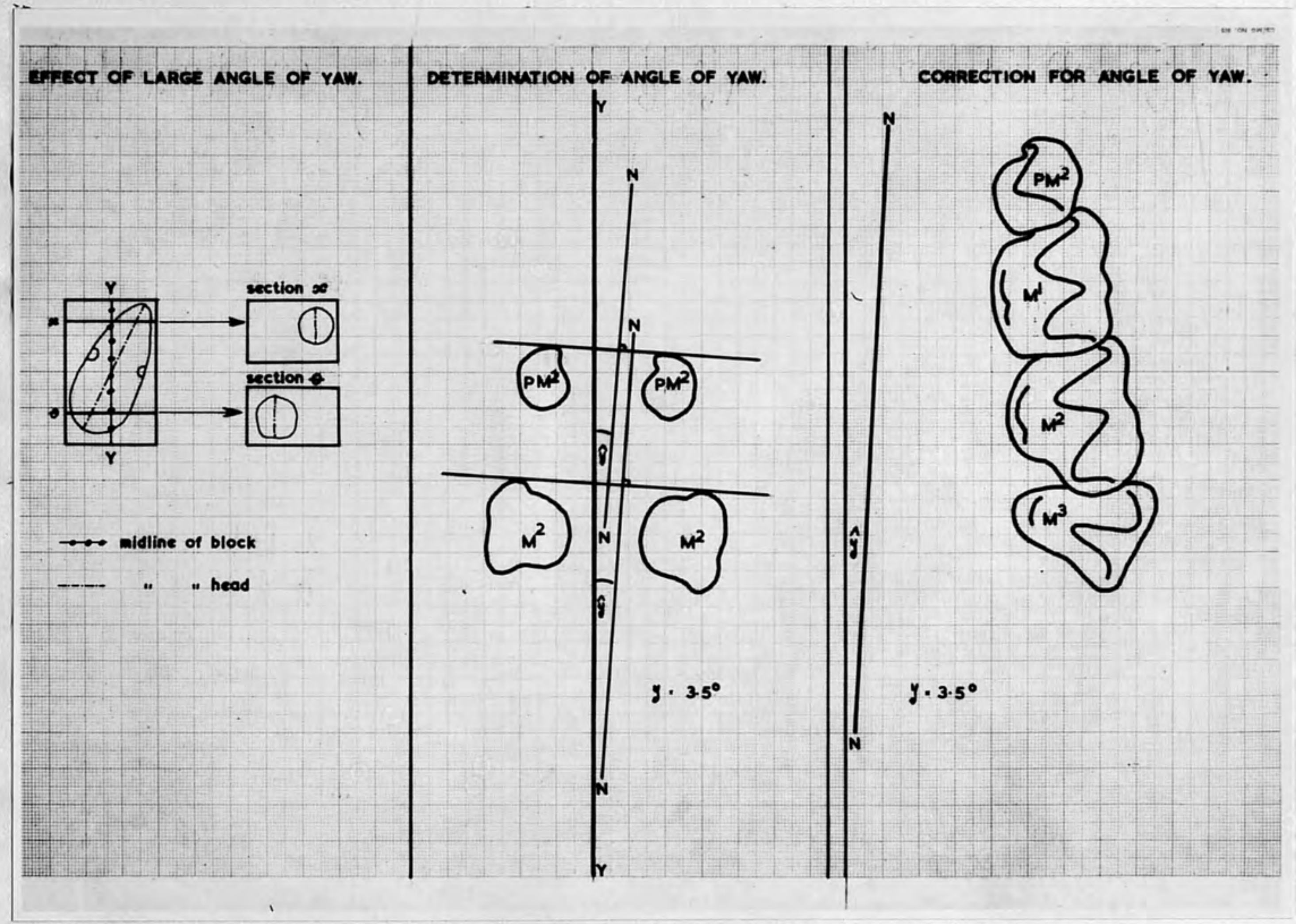


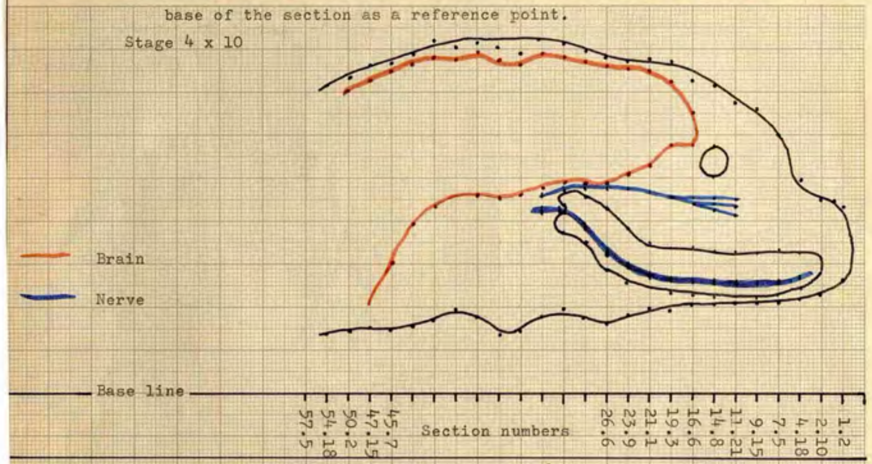
FIGURE 5 Diagram to show the effect, the method for determining, and the method of correcting the angle of yaw.

FIGURE 6

FIGURE 6 To show method of side-view reconstruction

1. Primary graphic reconstruction of gross structures in the head using the base of the section as a reference point.

Stage 4 x 10



2. Final graphic reconstruction of Stage 4 (unfinished) using mandibular nerve as base line. Section number 14.8 is projected onto the graph paper.

x 20

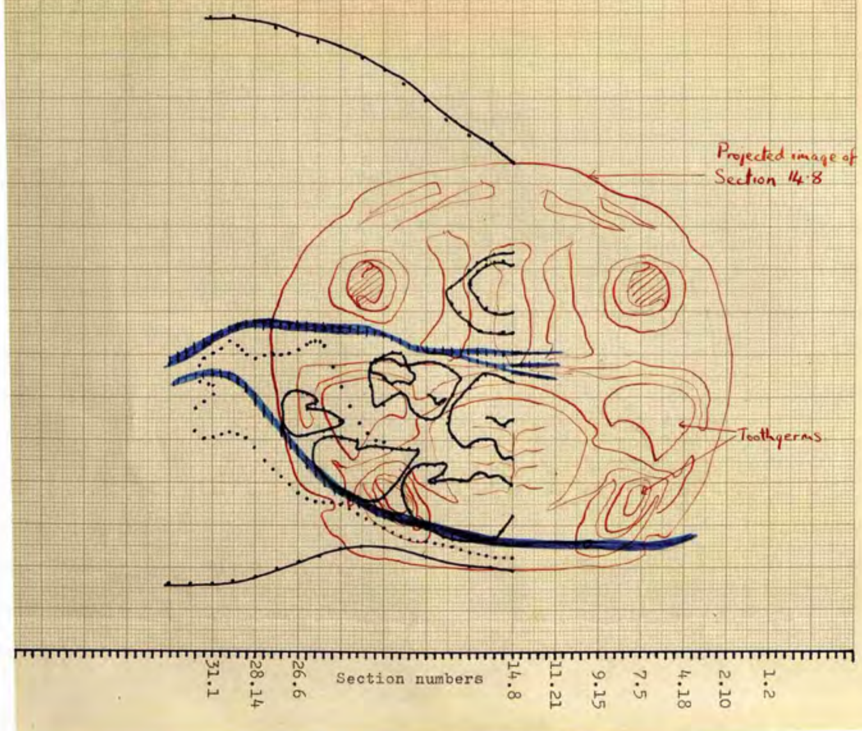


FIGURE 7 Diagram to demonstrate method of wax model reconstruction.

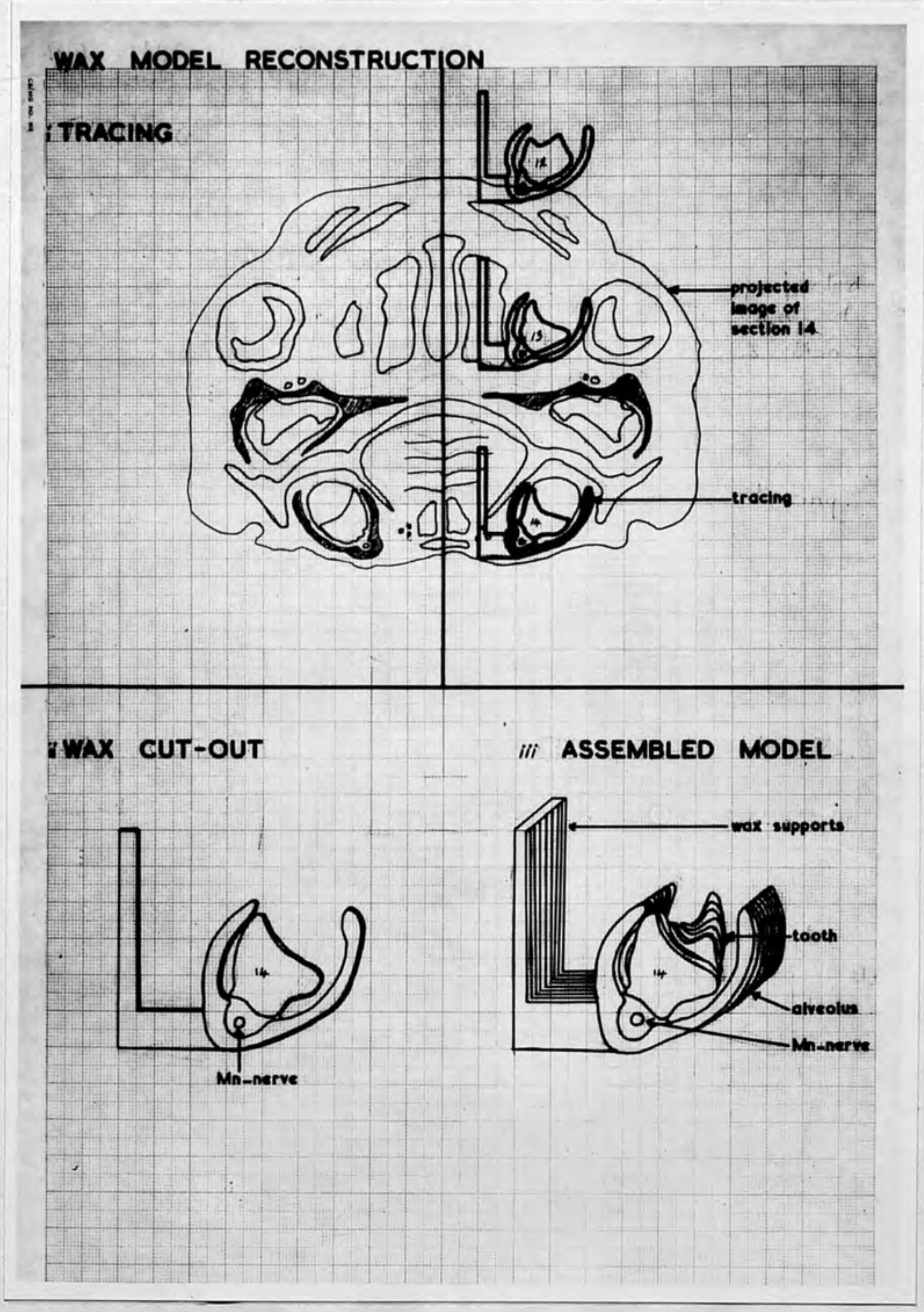
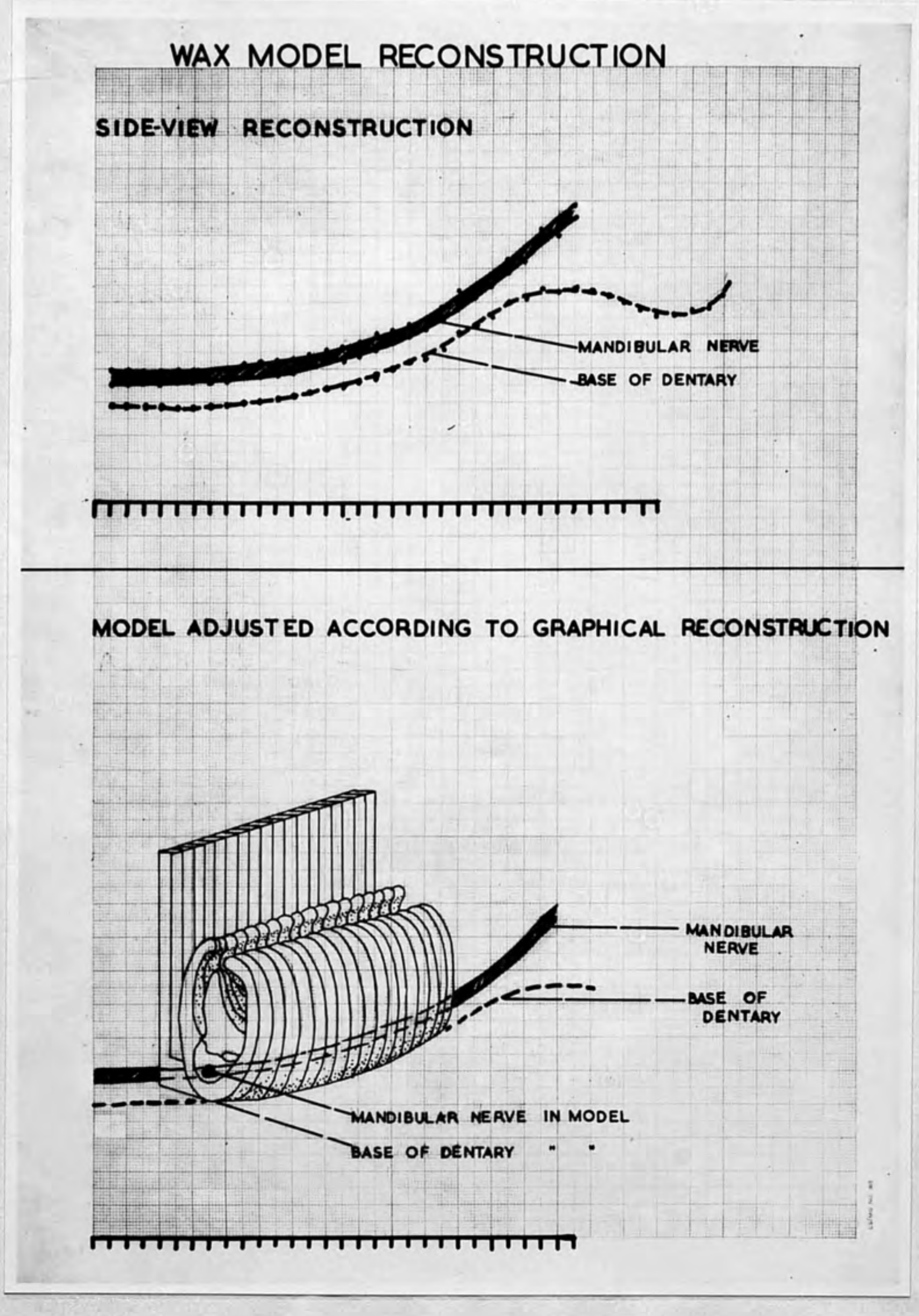


FIGURE 8 Method of wax model reconstruction continued.



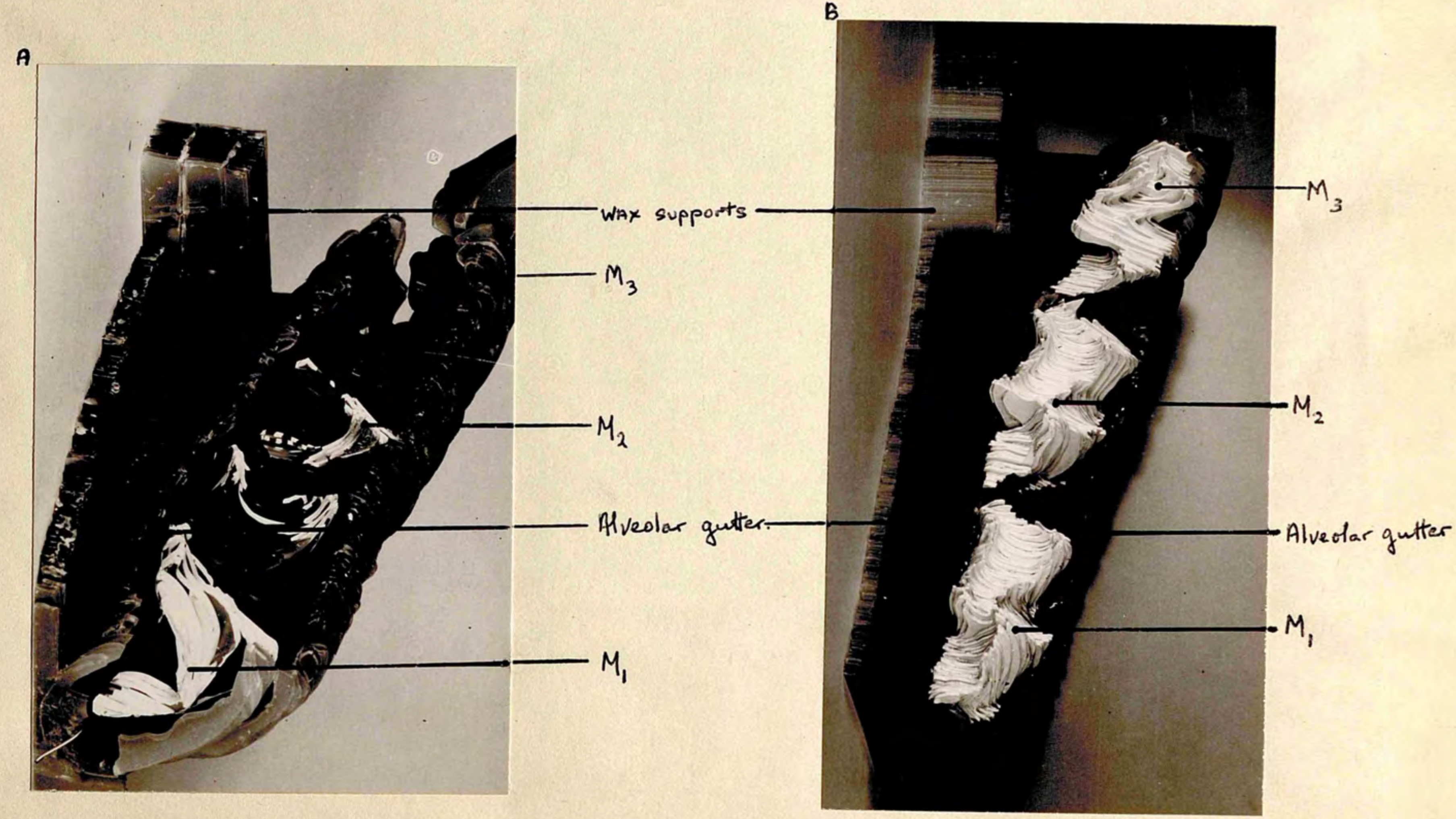
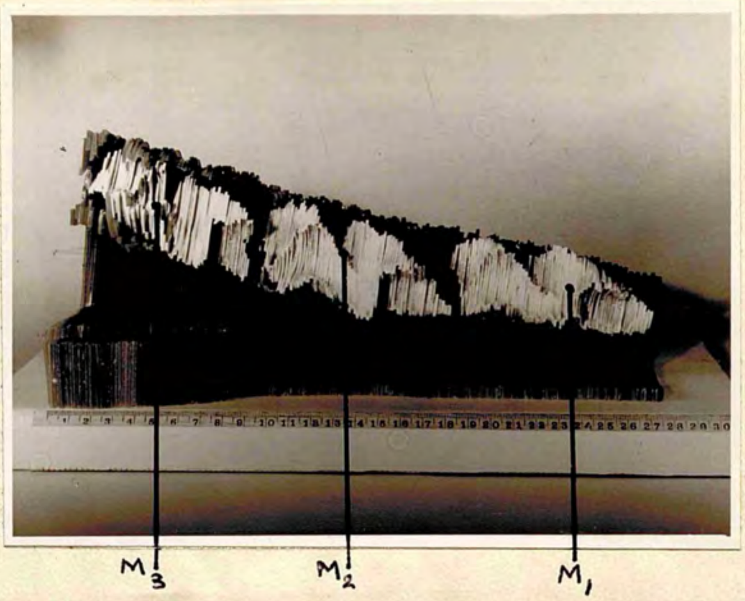


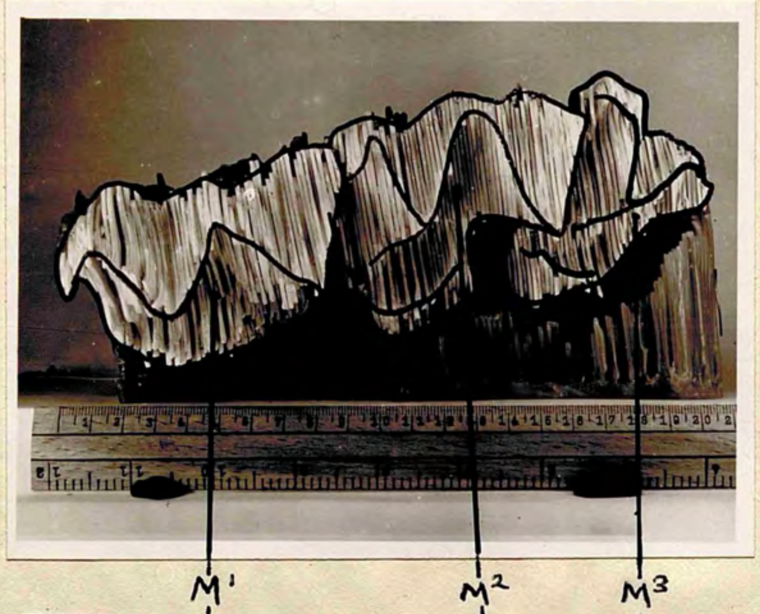
FIGURE 9 Wax models of M_1 M_2 M_3 lying in alveolar gutter

A Stage 1 Mn-length .58 cm. B Stage 13 Mn-length .97 cm.

FIGURE 9 Photographs of some of the wax models.



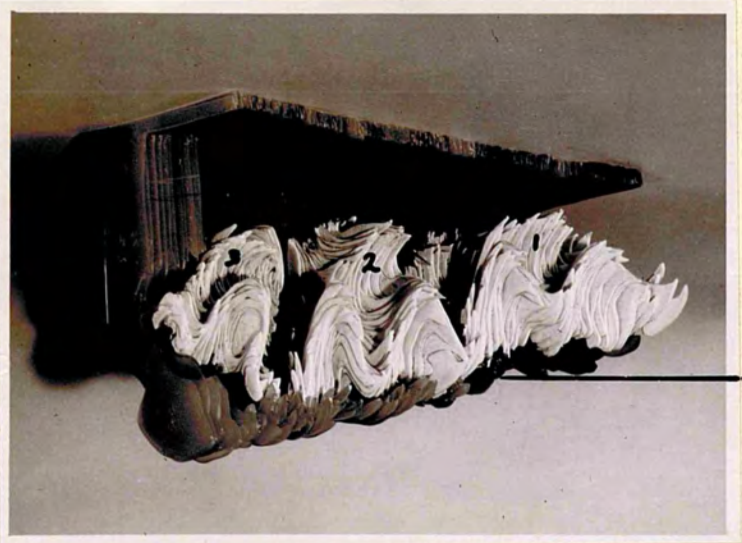
M_1 M_2 & M_3
Stage 13
lying in alveolar
gutter



M^1 M^2 & M^3 Stage 13

M^1 M^2 & M^3 Stage 1

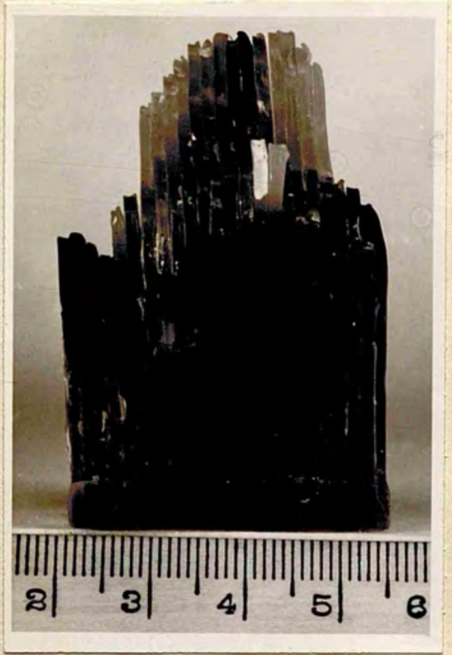
FIGURE 10 Photographs of some of the wax models.



M^1 M^2 & M^3 Stage 13

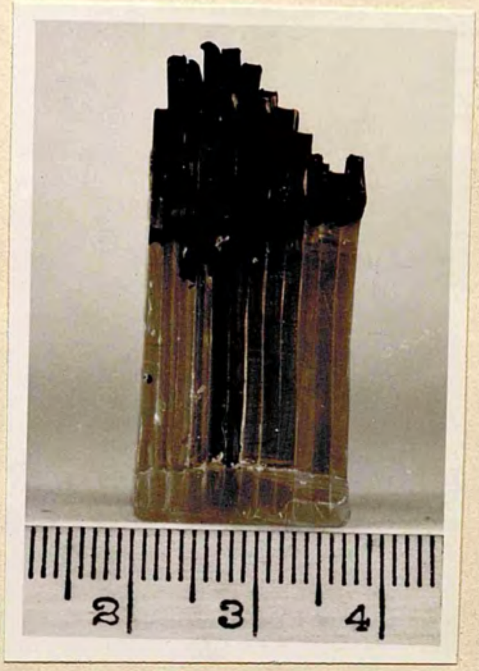
Occlusal-posterior view

showing alveolar bone



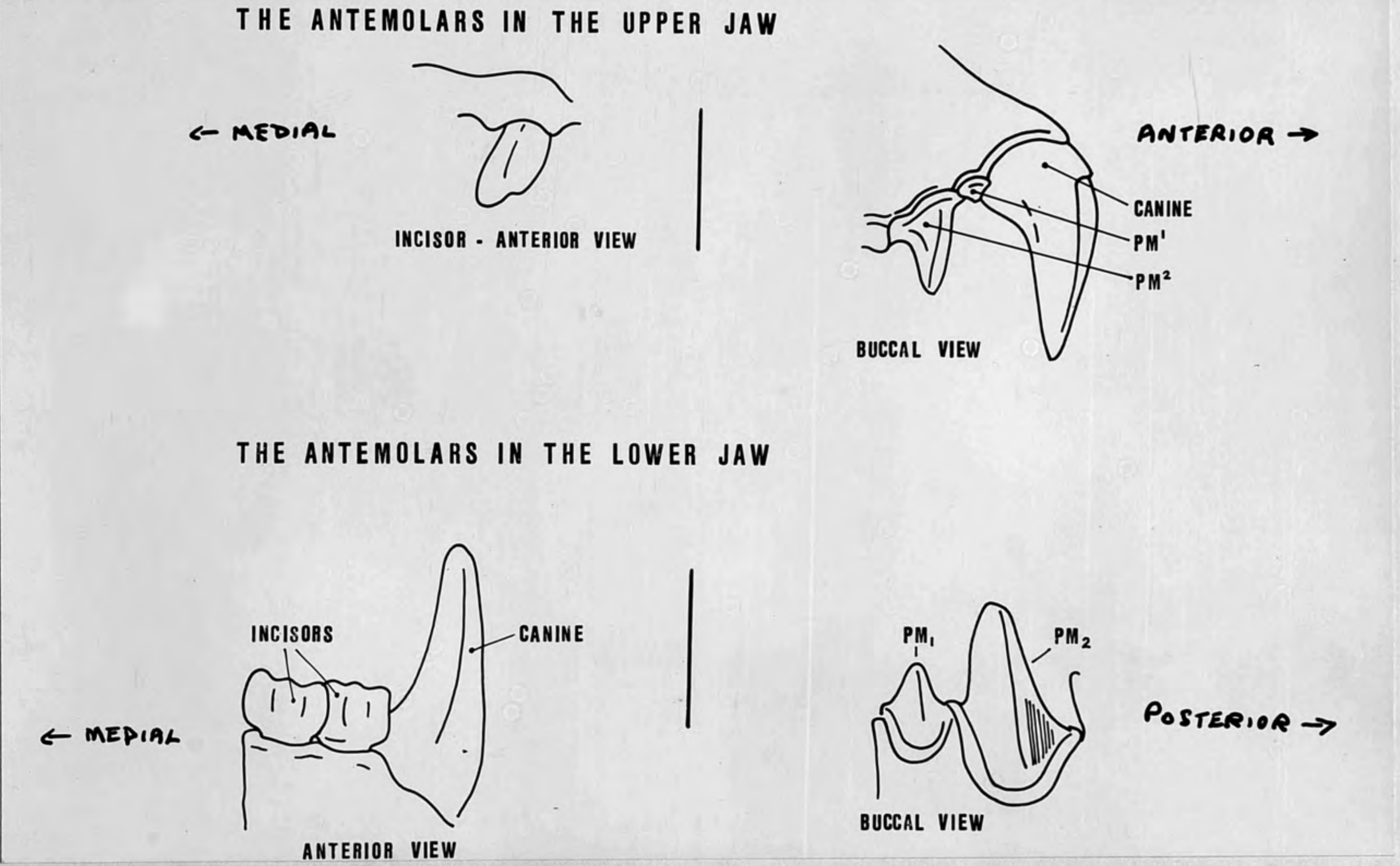
M^3 Stage 4

Occlusal view



M^3 Stage 1

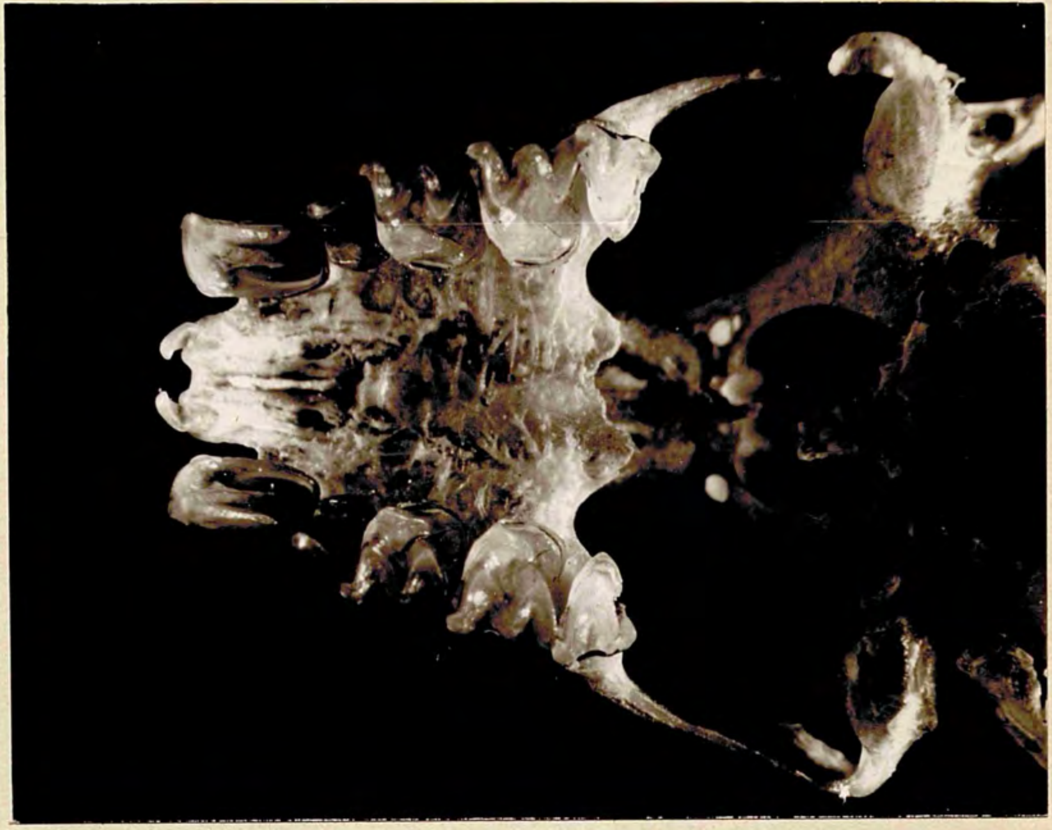
Occlusal view


THE ANTEMOLARS IN THE UPPER JAW

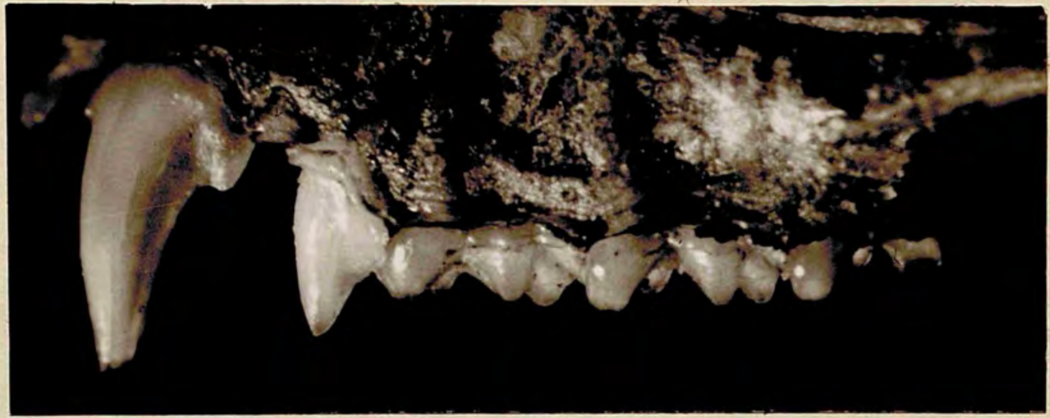
THE ANTEMOLARS IN THE LOWER JAW

FIGURE 11 The Antemolars of H. beatus.

FIGURE 12 Upper molars. Occlusal view.

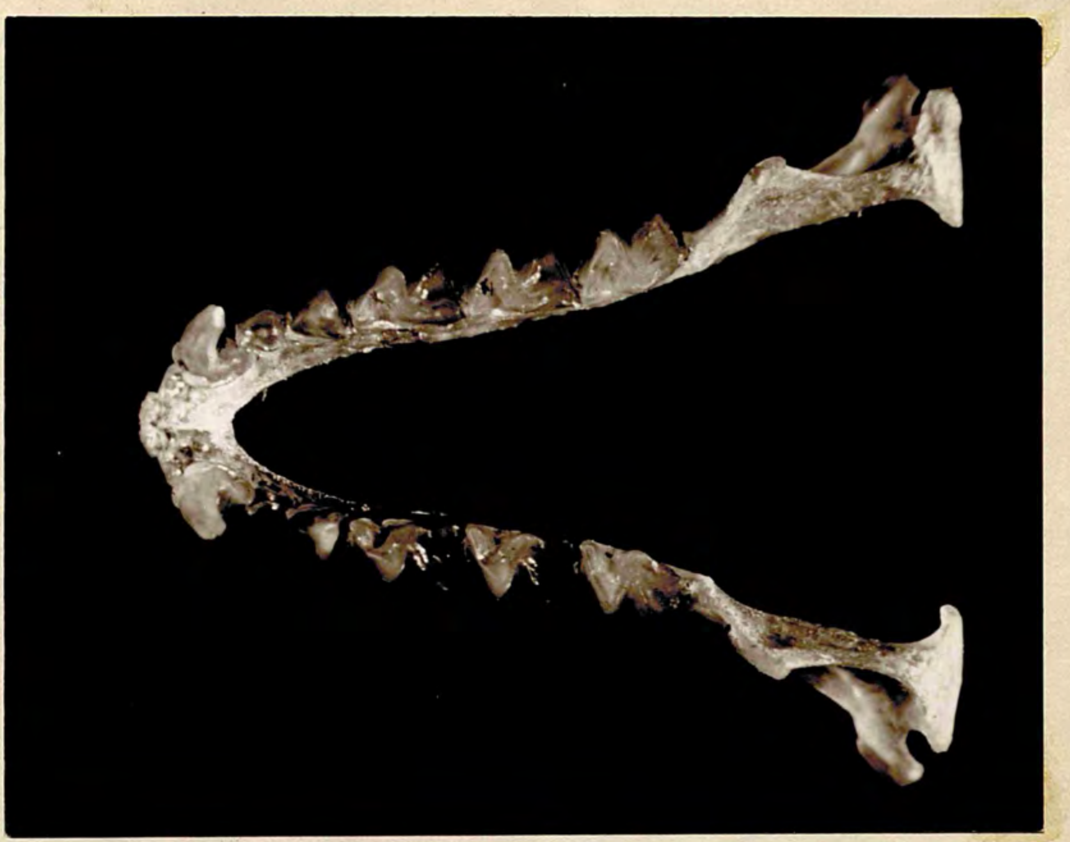


Buccal view. Left teeth.



Lingual view. Right teeth.

FIGURE 13 Lower molars. Occlusal view.



buccal view left teeth lingual view right teeth.

FIGURE 14 An anterior view of the path followed by the mandibular symphysis in two separate chewing cycles: a right-hand chewing cycle (black line) and a left-hand chewing cycle (dotted line). This diagram was made by tracing the mandibular symphysis in successive frames of the film, throughout 2 complete chewing cycles.

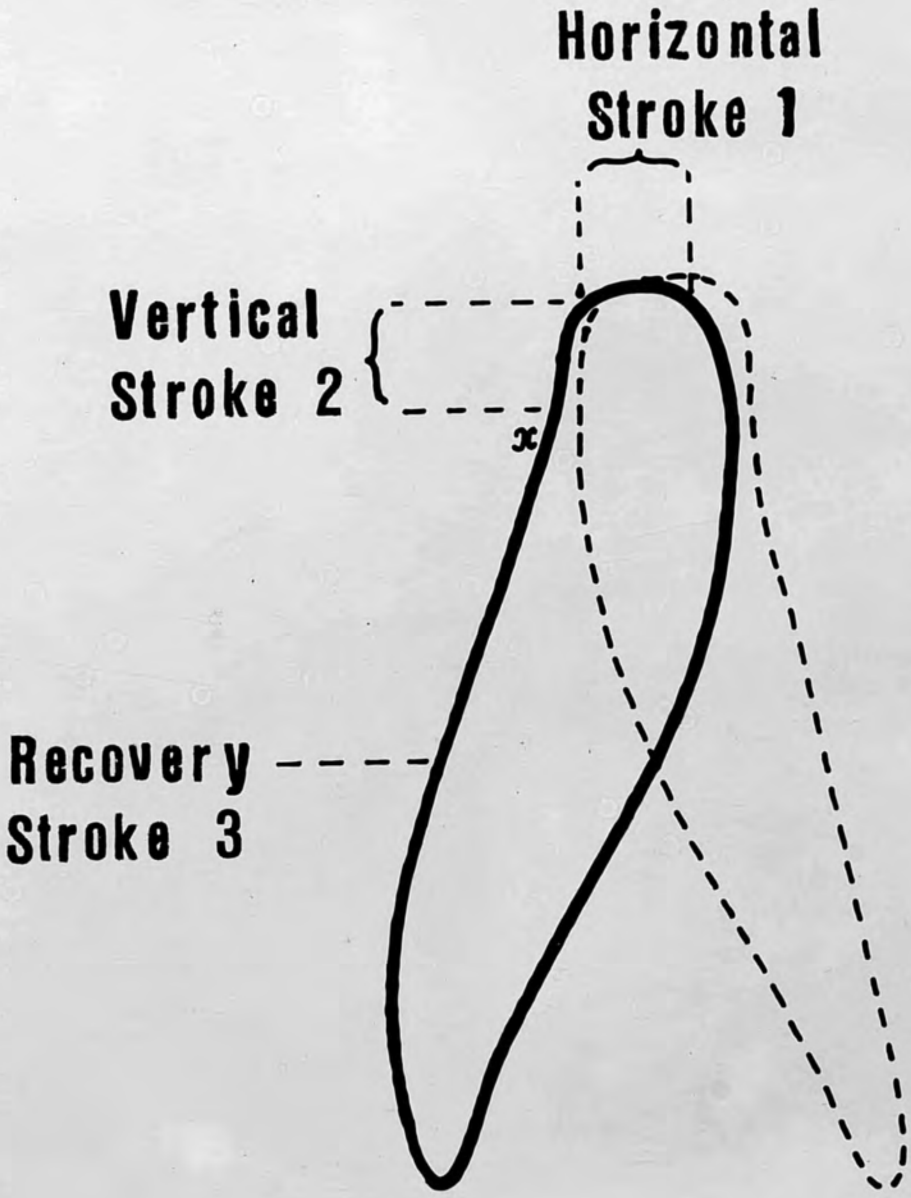
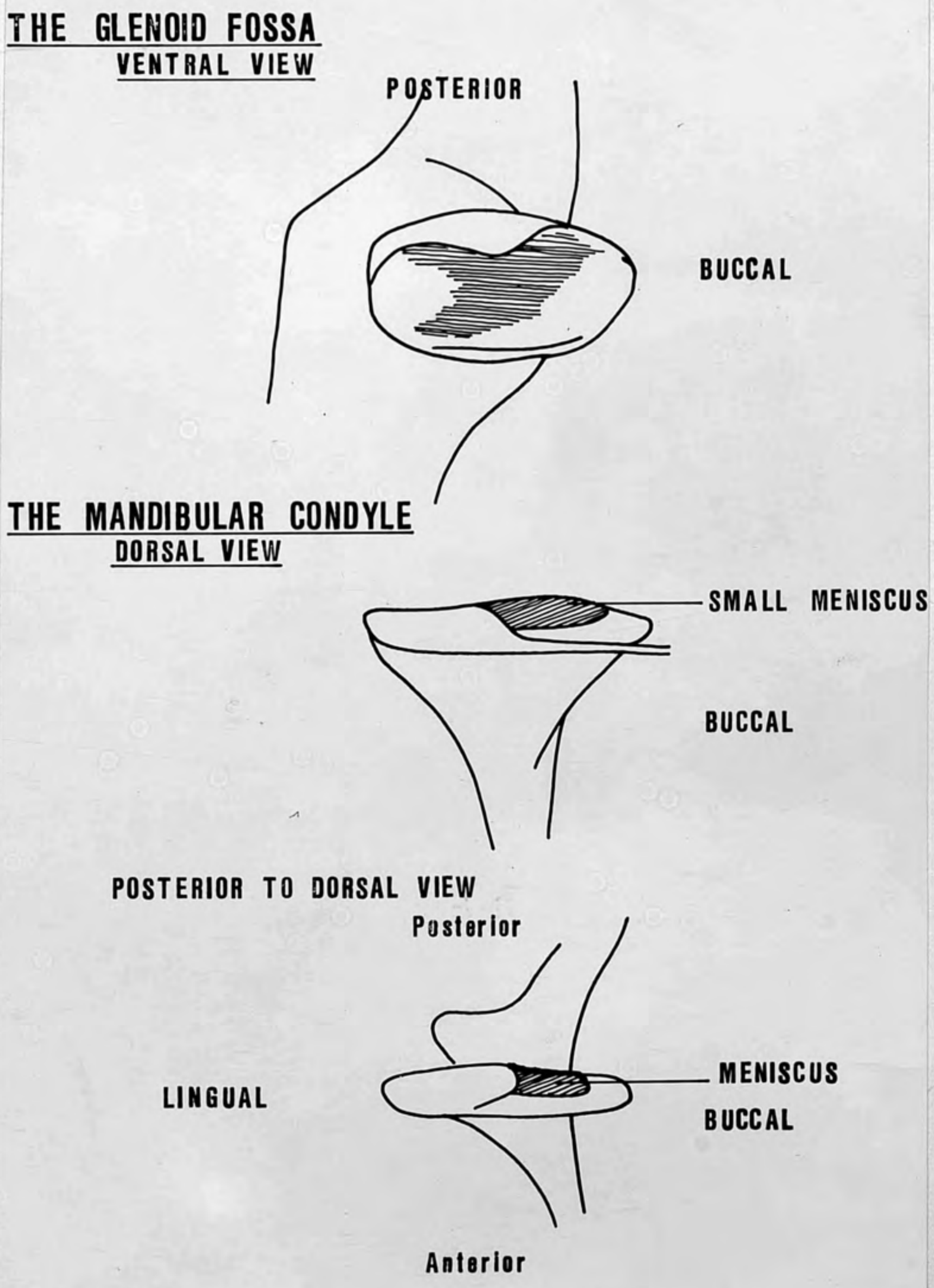


FIGURE 15 The jaw-joint of *H. beatus*



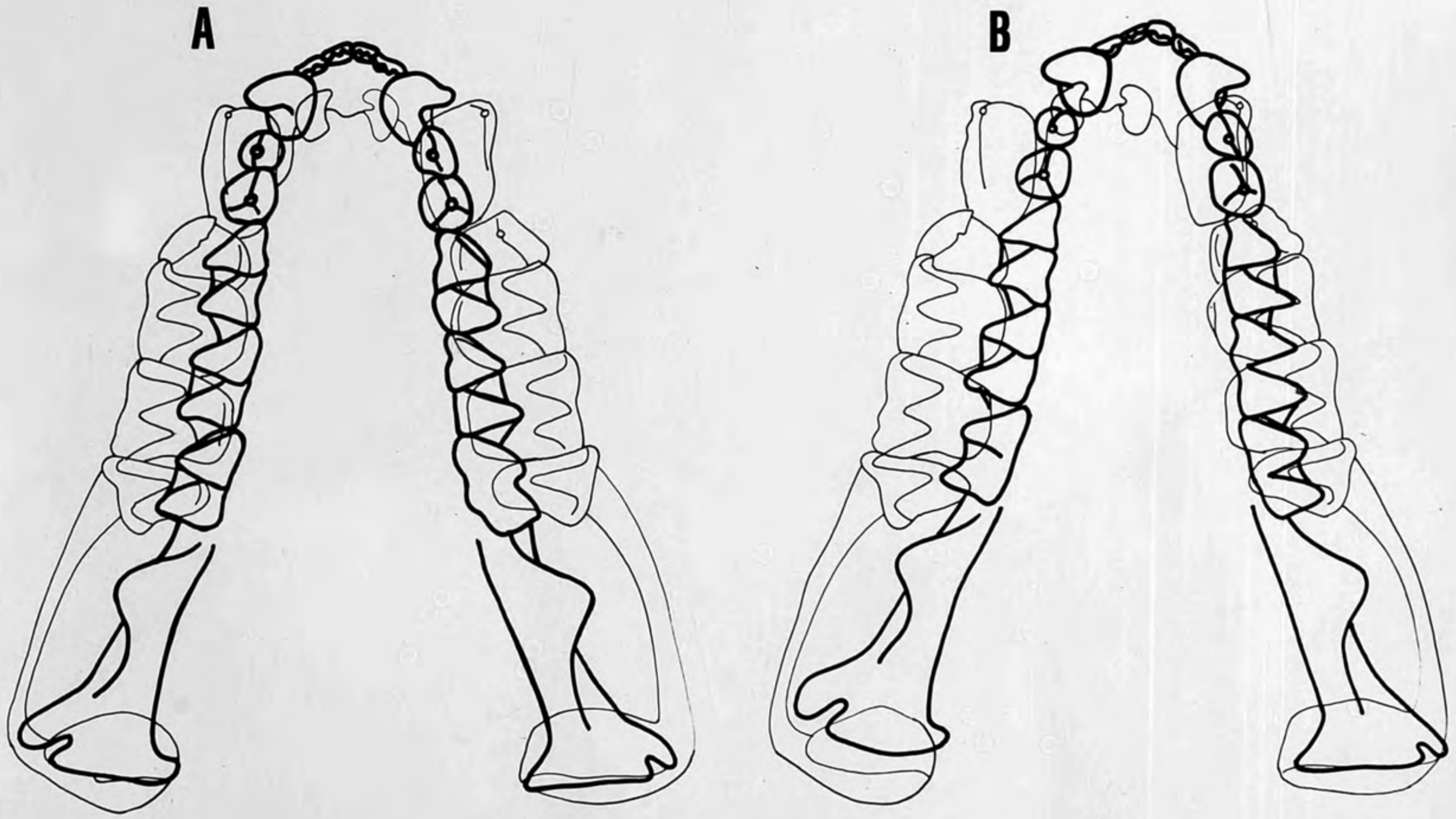


FIGURE 16 Occlusal position of the teeth in:

A centric occlusion B buccal occlusion

FIGURE 17 Three photographs of the teeth during a left-hand chewing stroke.

Figure 17 To show chewing action. Buccal to Ventral view of Left teeth. of *H. beatus*.

1. Teeth in position just prior to vertical stroke.

2. Vertical stroke, buccal occlusion.

3. Lateral stroke centric occlusion.

FIGURE 18 Occlusal view of teeth showing wear facets.

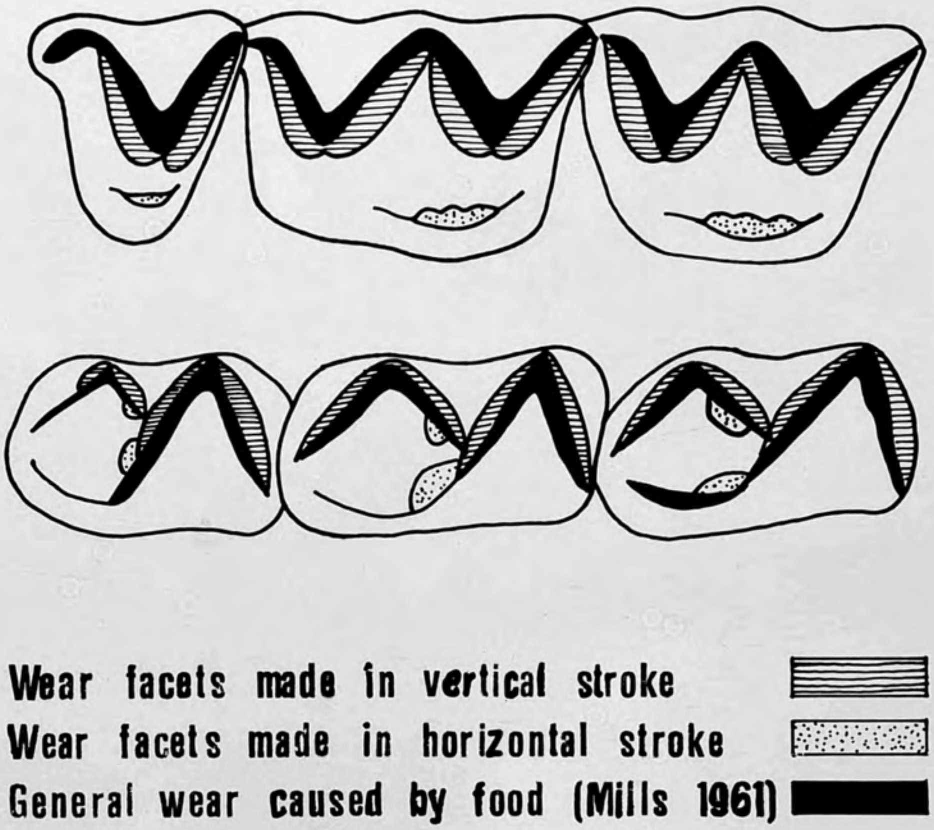
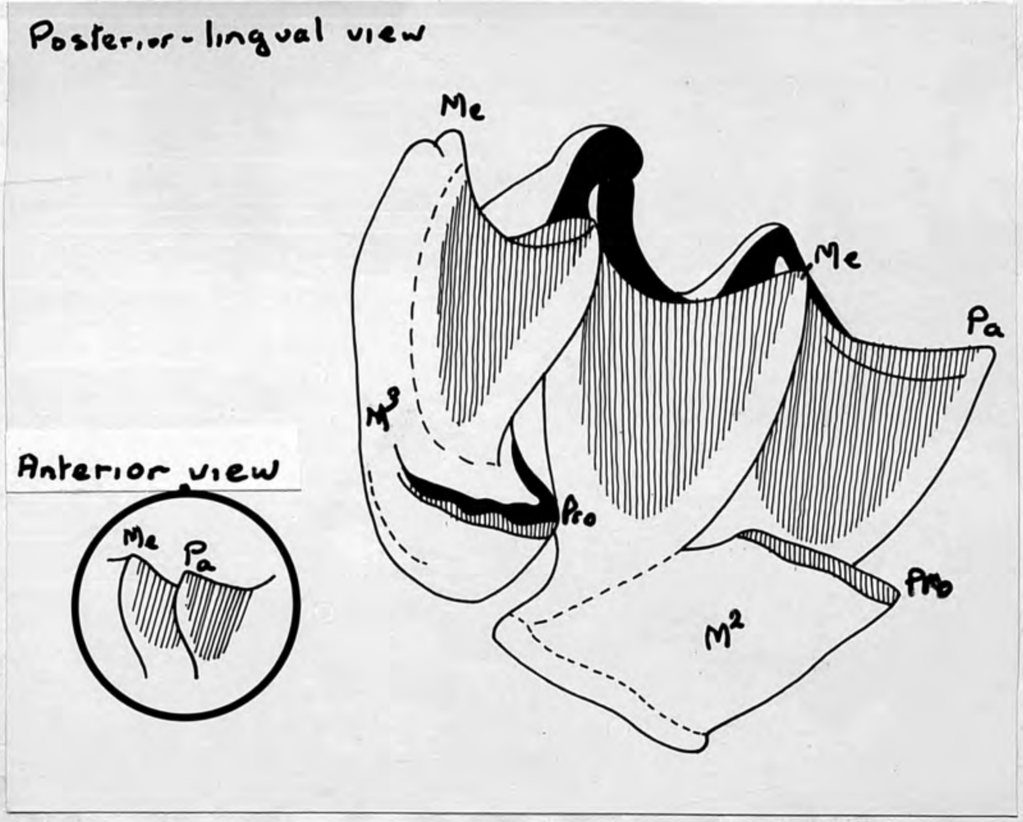


FIGURE 19 Wear facets and scratch marks made in vertical stroke.

a) Upper molars right M^2 and M^2 Posterior to lingual view.



b) Lower molars left M_2 and M_3 Anterior-buccal view.

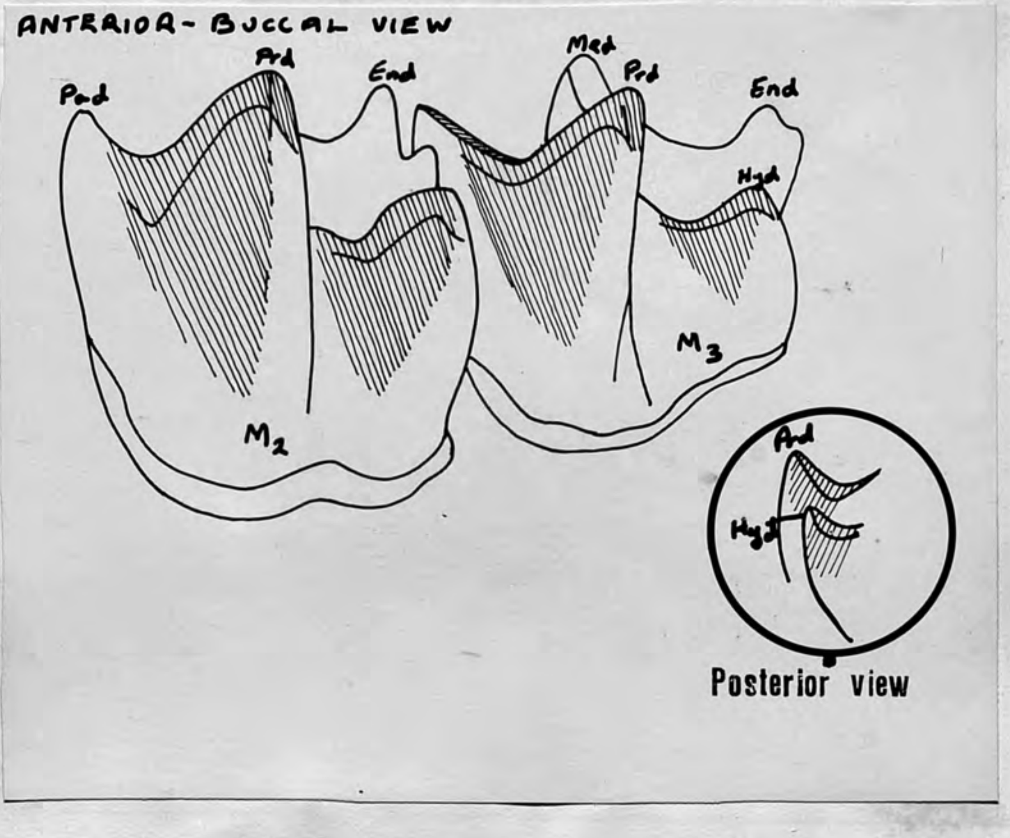


FIGURE 20 Posterior view of hypoconid and protoconid cusps, showing that the outer ridges curve outwards from the tip of the cusp.

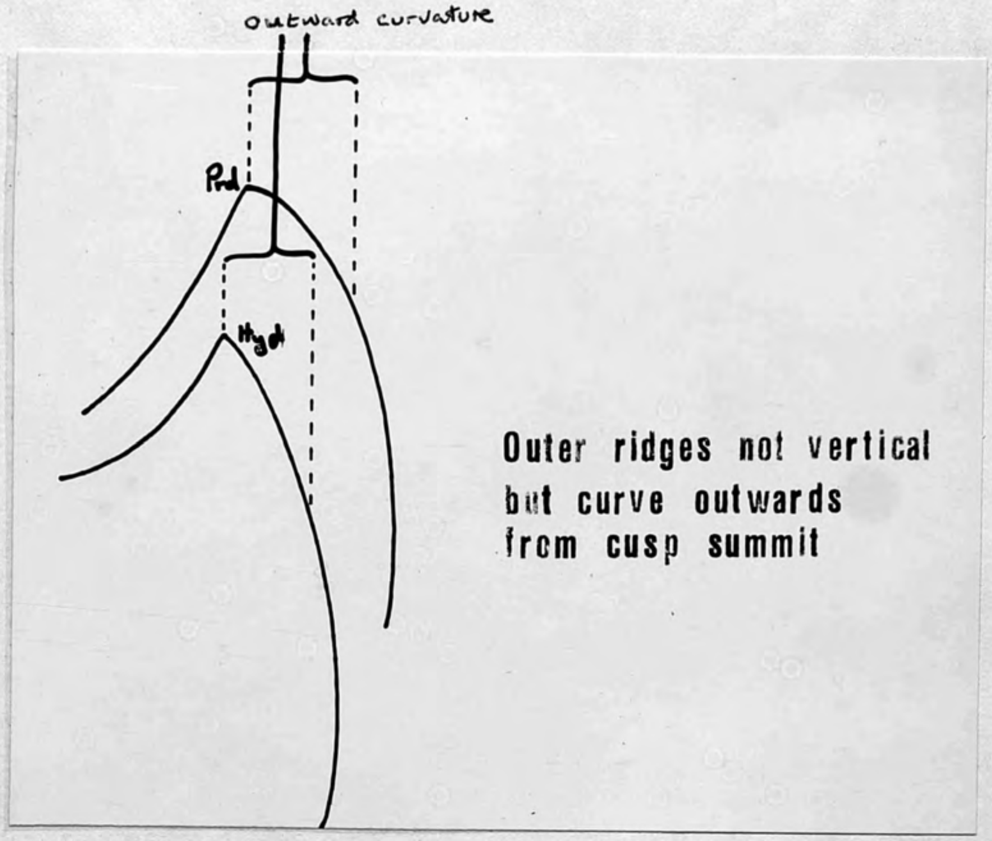
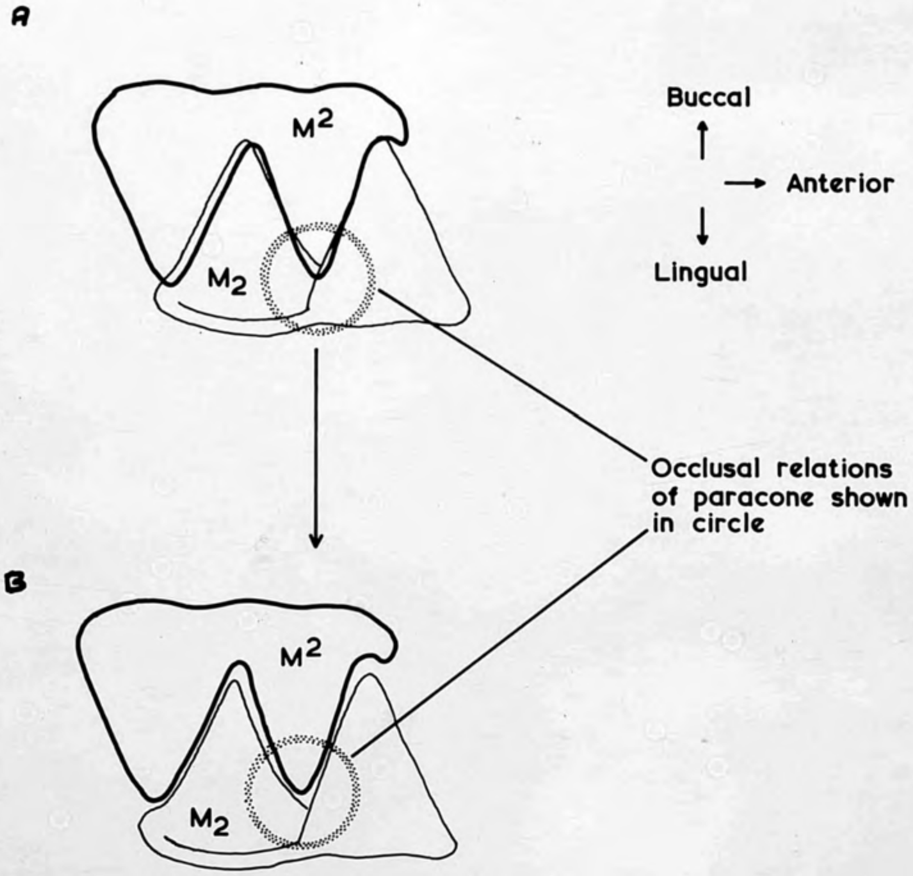


FIGURE 21

DIAGRAM TO ILLUSTRATE LINGUAL MOVEMENT OF LOWER MOLAR DURING 'VERTICAL' CHEWING STROKE.

Plan views of M^2 and M_2



DIAGRAMMATIC REPRESENTATION OF TOOTH CURVATURES

(to permit closing of mouth)

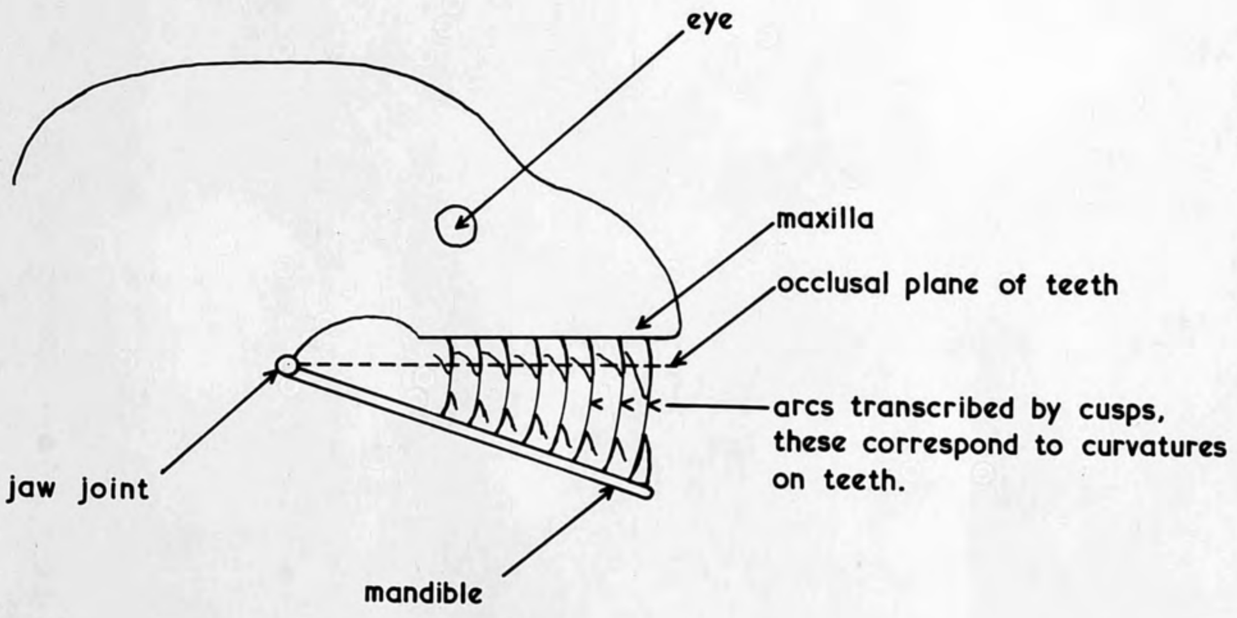


FIGURE 22

FIGURE 23 Transverse section through the tooth bud of M^3 to show the enamel knot lying in a central depression on the crown.

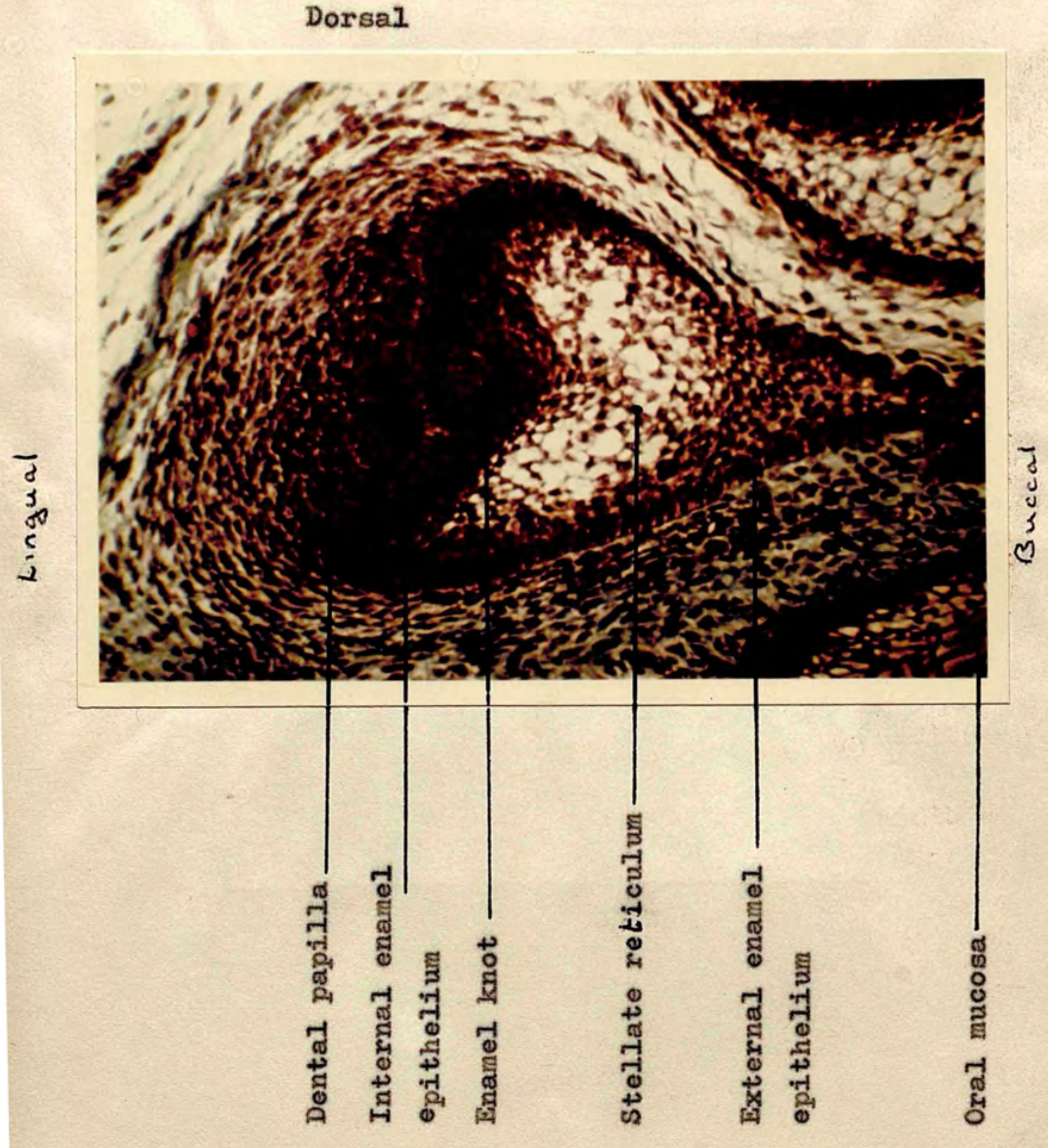


FIGURE 24 Another transverse section through the toothbud of M^3 Stage 1 to show the connection between the external enamel epithelium and the oral mucosa

A SCALED DIAGRAM TO SHOW GROWTH IN WIDTH OF M^3.

B SCALED DIAGRAM TO SHOW GROWTH IN LENGTH OF M^3.

KEY: Stages of M^3 are placed according to age along line AB. Lines joining homologous parts diverge to show growth.

All stages are shown from an occlusal viewpoint. ▨ = calcified areas. ------ = valley.

FIGURE 25

FIGURE 26 Outlines of successive stages of M^3 from an occlusal view-point superimposed to show growth. Stages 1, 3, 4, 6a, 8 and 13 are shown.

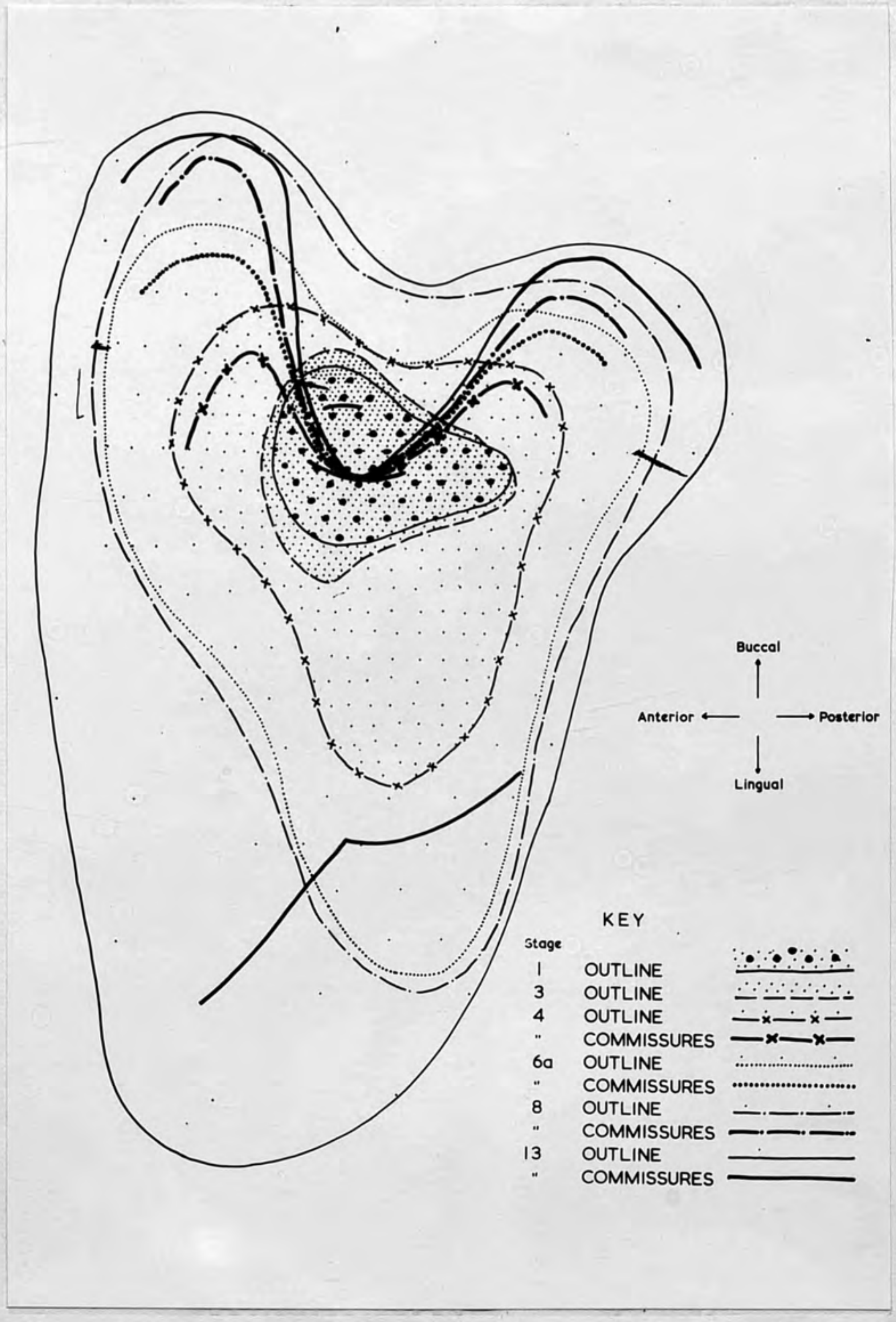


FIGURE 27 Occlusal view of M^3 to show the blunt tip of the paracone.

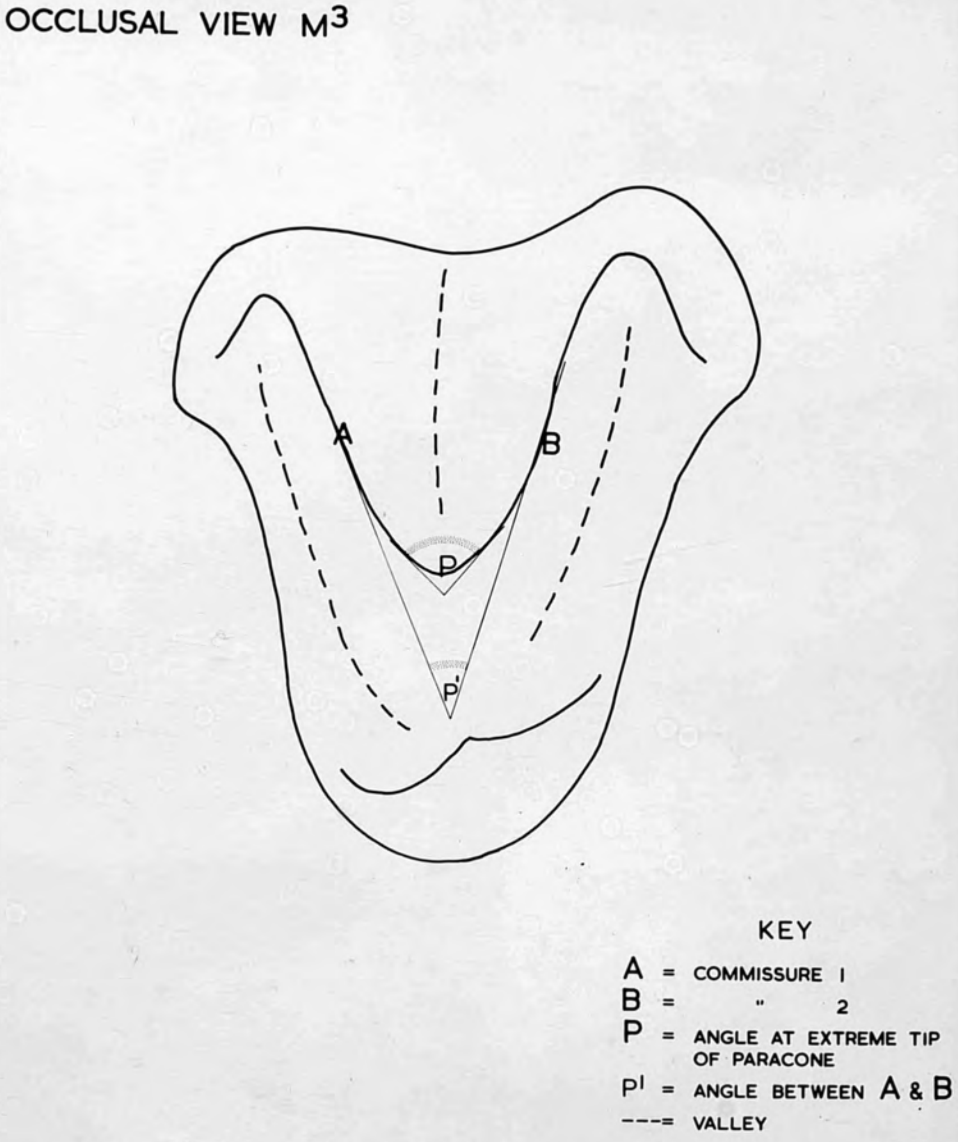
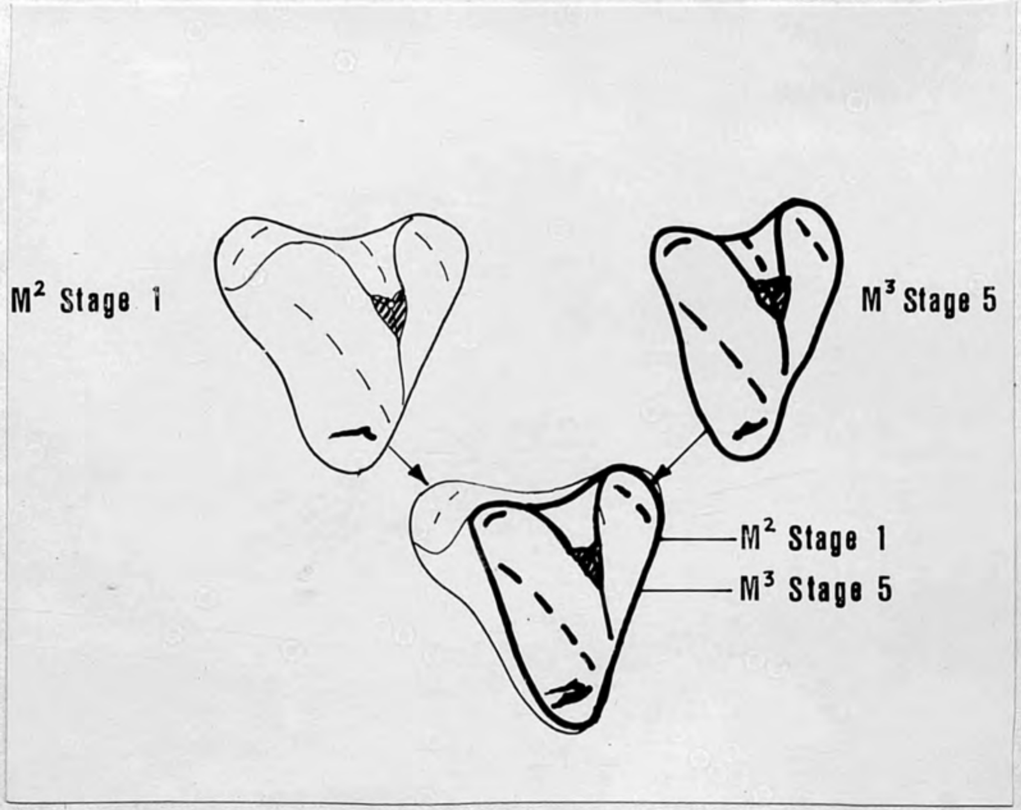


FIGURE 28 Corresponding stages of M^2 and M^3

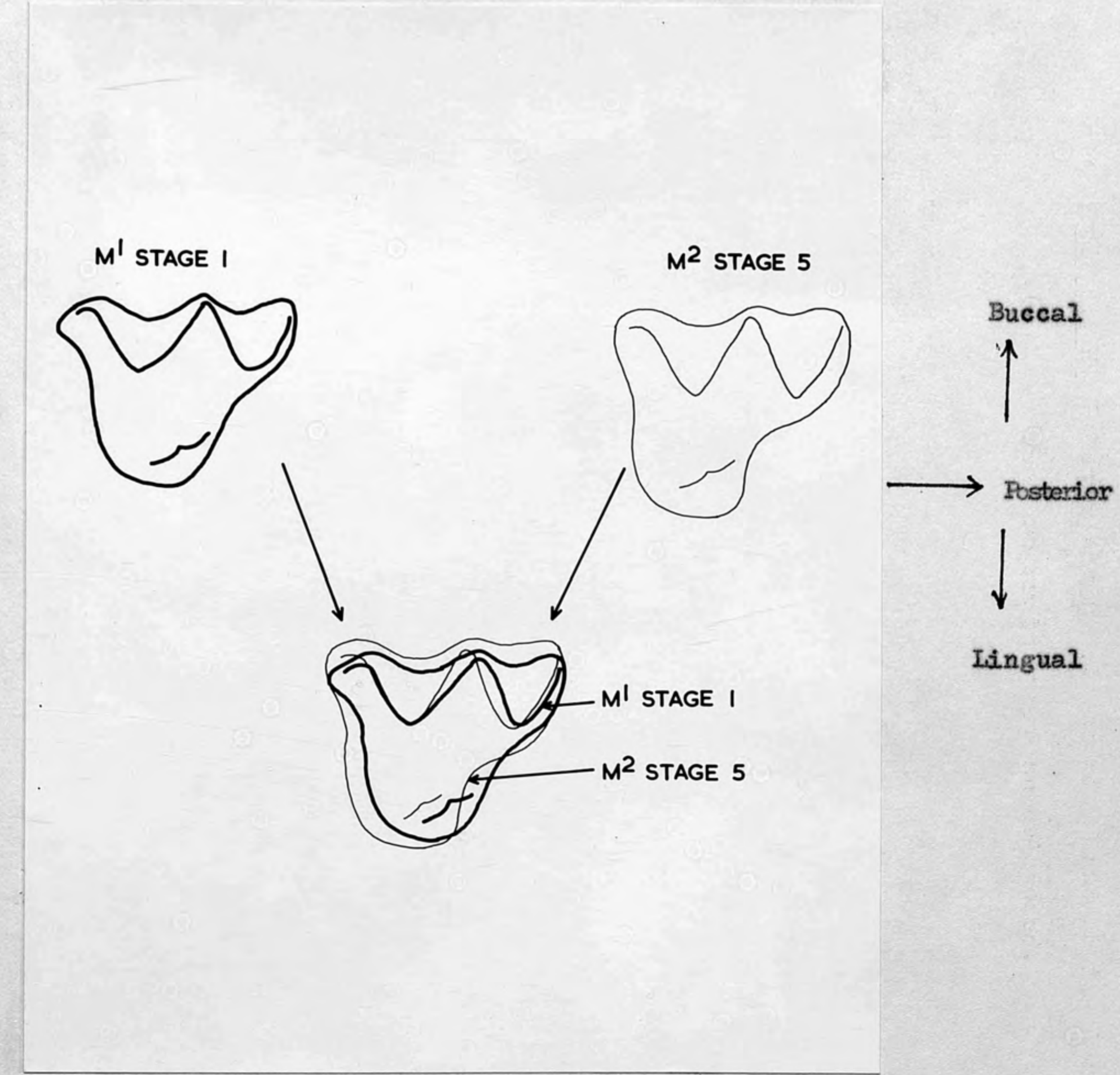
Occlusal view.



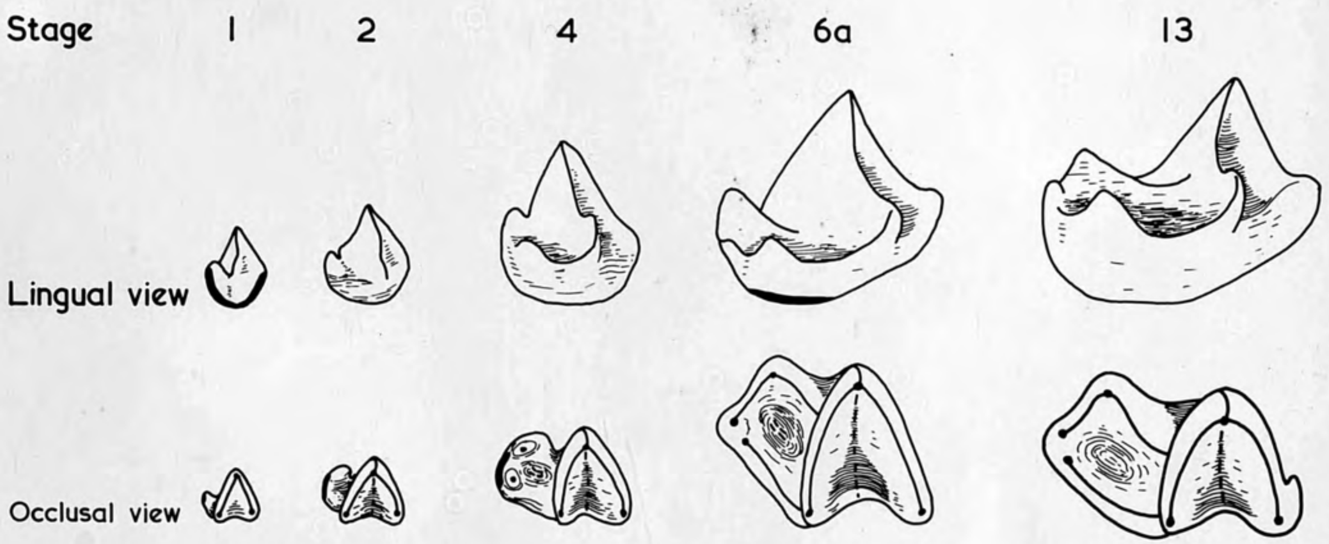
KEY ▨ = calcified area

Buccal
↑ ——→ Anterior
↓
Lingual

FIGURE 29 Corresponding stages of M^1 and M^2 in plan-view drawn separately and superimposed.



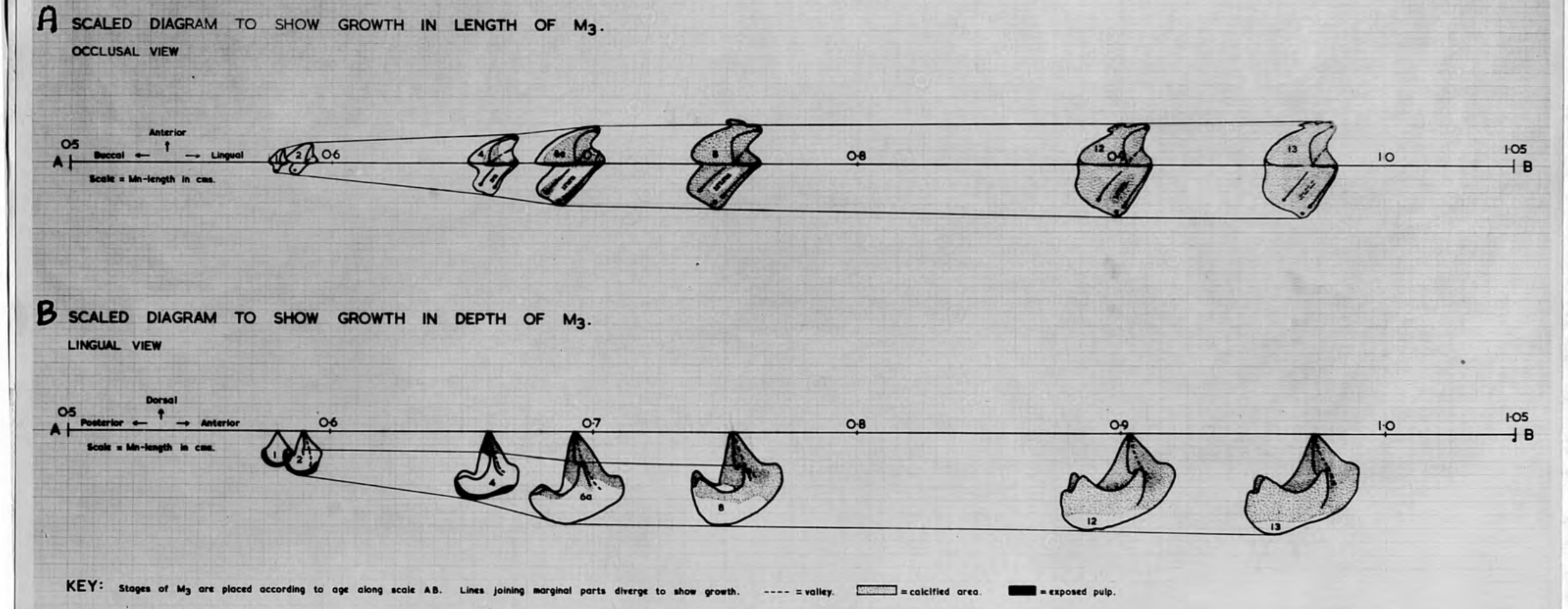
STAGES OF M_3 DRAWN FROM MODELS



KEY: Shaded to give 3 dimensional aspect. – – – = valley

■ : exposed dental papilla.

FIGURE 30



A SCALED DIAGRAM TO SHOW GROWTH IN LENGTH OF M_3.

OCCLUSAL VIEW

B SCALED DIAGRAM TO SHOW GROWTH IN DEPTH OF M_3.

LINGUAL VIEW

KEY: Stages of M_3 are placed according to age along scale AB. Lines joining marginal parts diverge to show growth. ---- = valley. ▨ = calcified area. ■ = exposed pulp.

FIGURE 31

FIGURE 32 Transverse section through the mandible in the region of the ascending ramus, showing M_3 cut horizontally. This section shows the entoconid budding off from the hypoconid, and the dental papilla still exposed on the posterior side of the hypoconid.

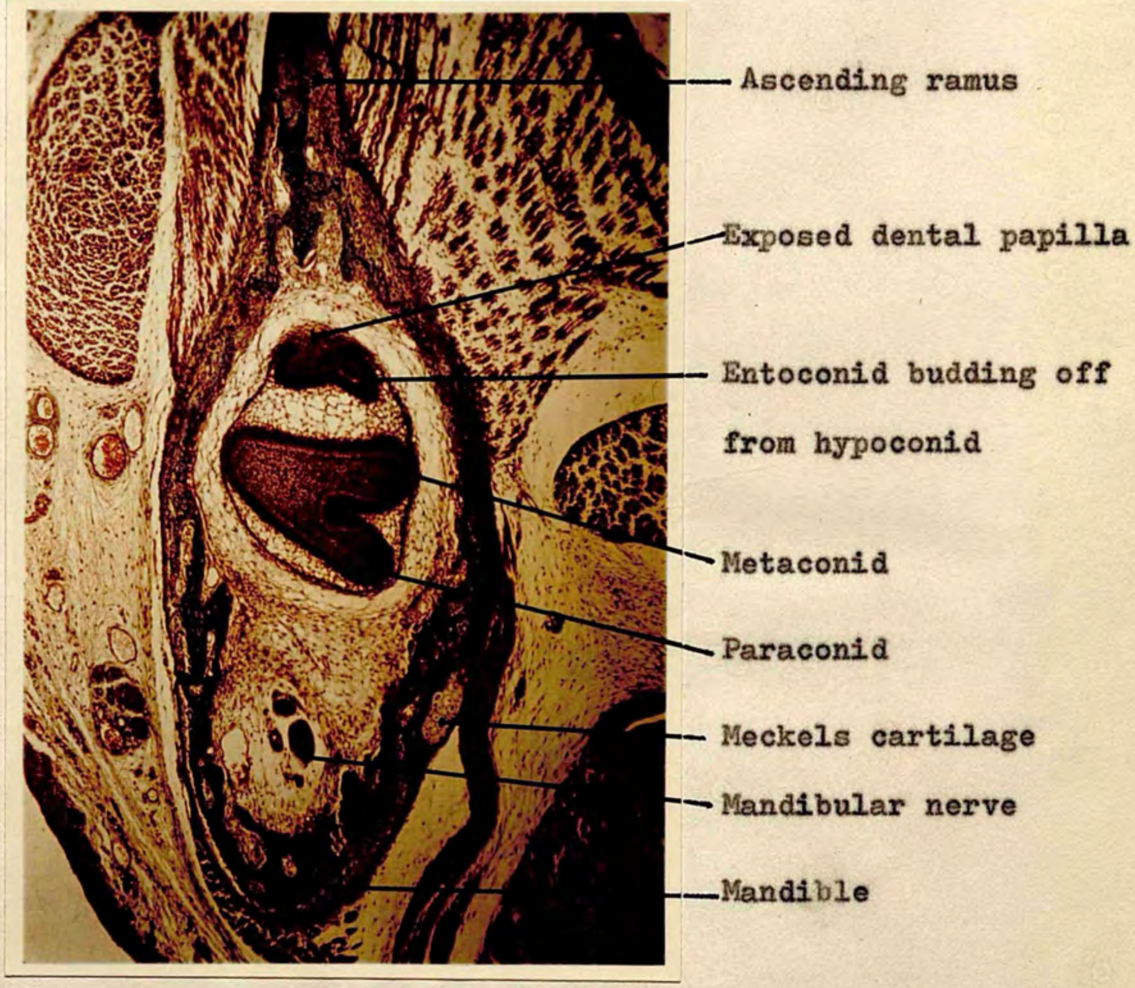
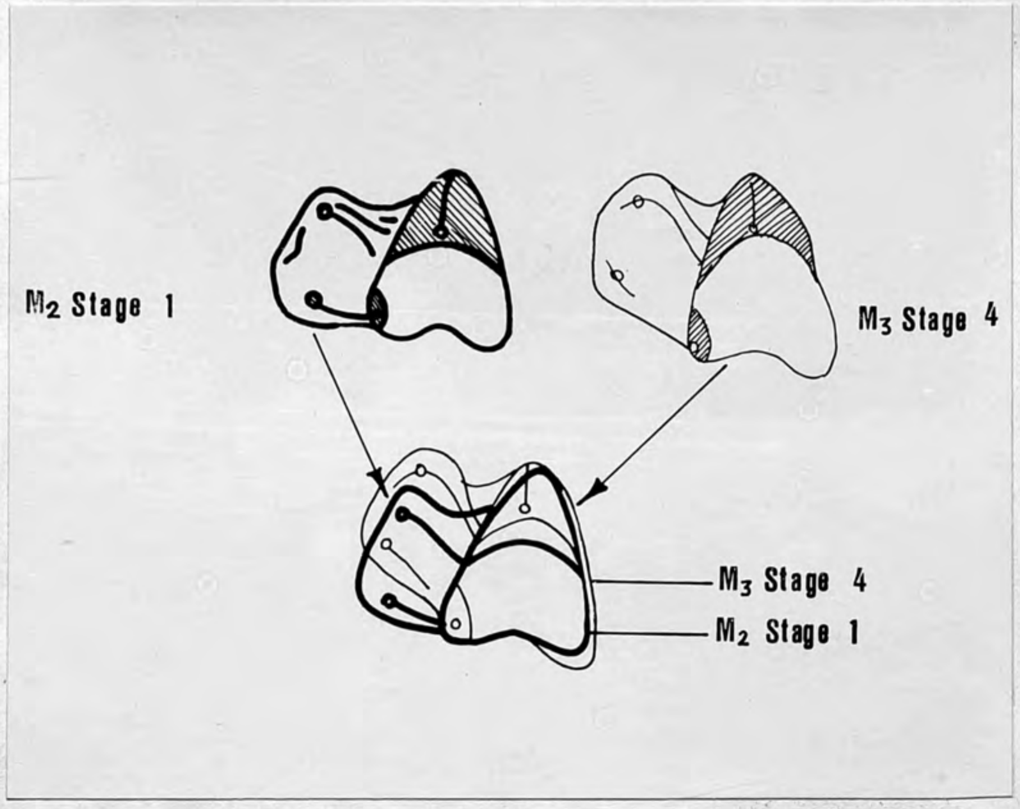


FIGURE 33 Comparative stages of M_2 and M_3.

a) Occlusal view. Shaded area = calcified region



b) Buccal view. Shaded area = exposed dental papilla

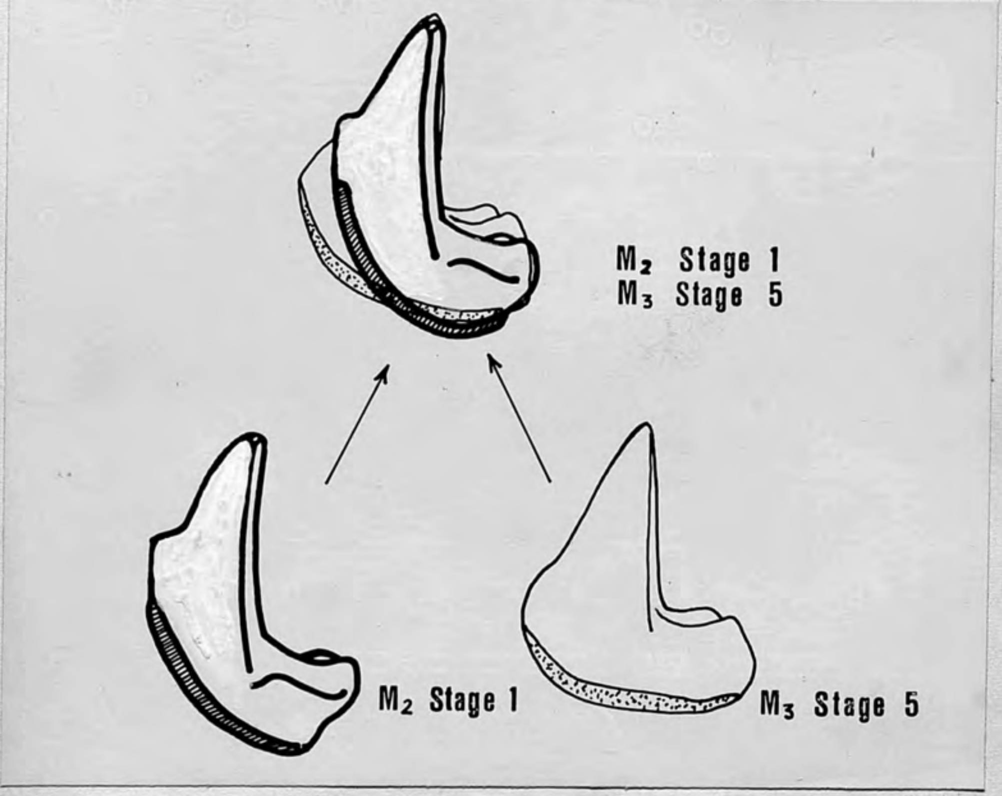
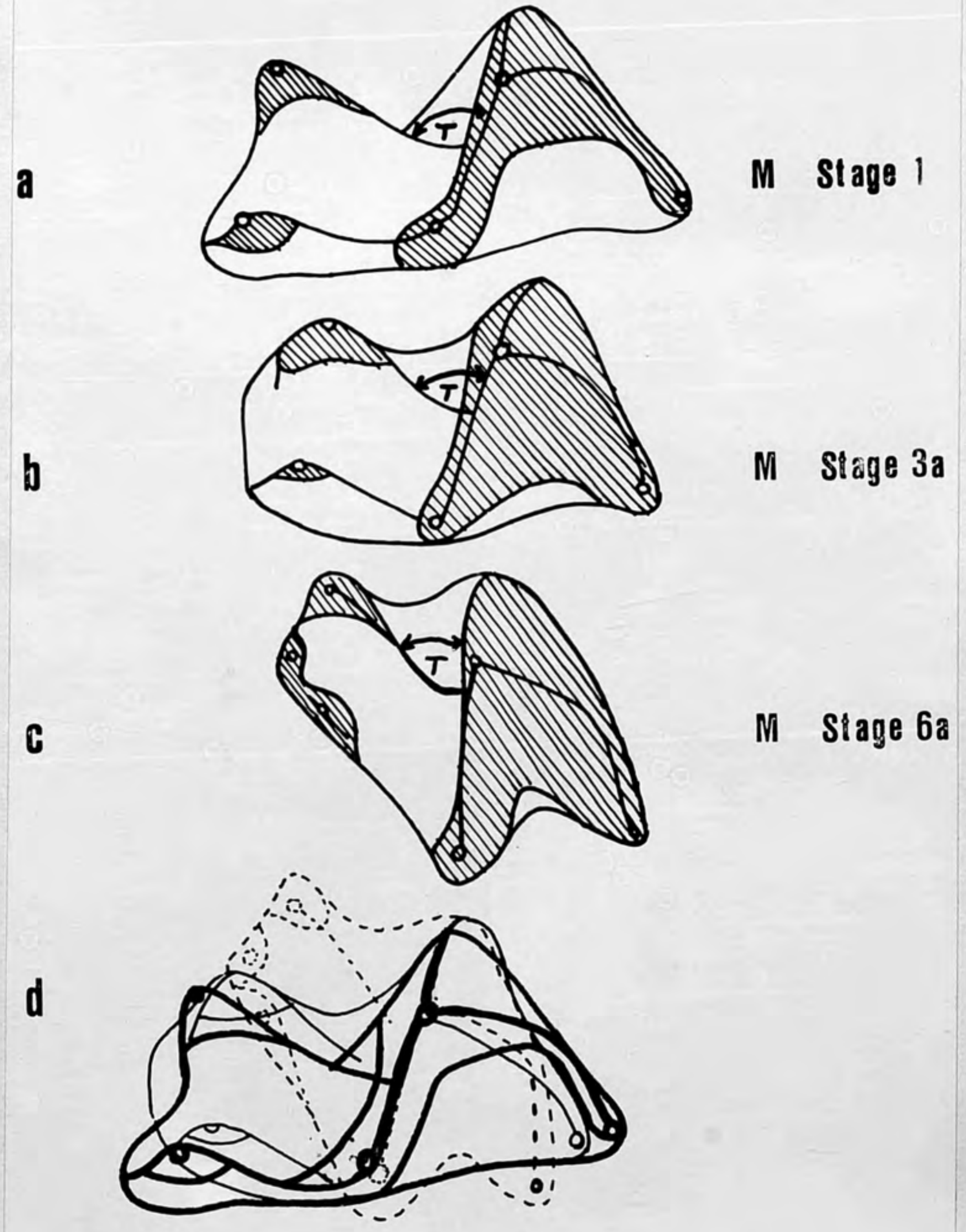


FIGURE 34 Comparitive stages of M_1 M_2 and M_3.

Occlusal view.



KEY. Shaded areas = calcified areas. These areas are marked but not shaded in diagram d.

FIGURE 35 Diagram showing cusps interdigitating side view.

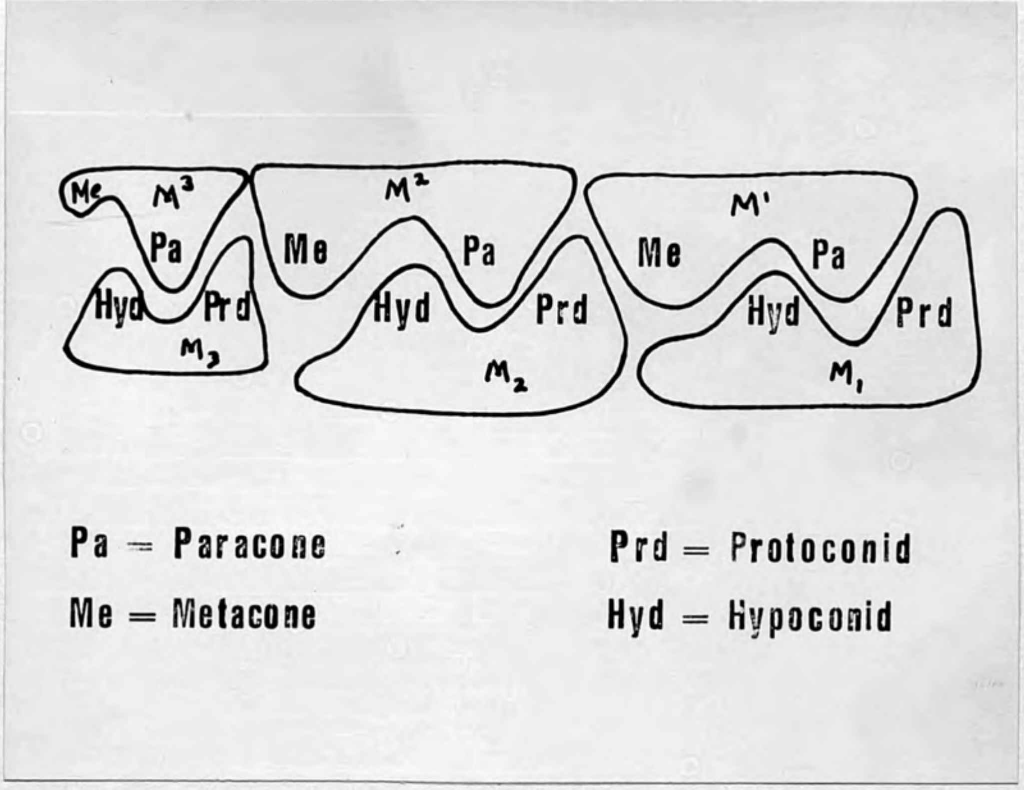
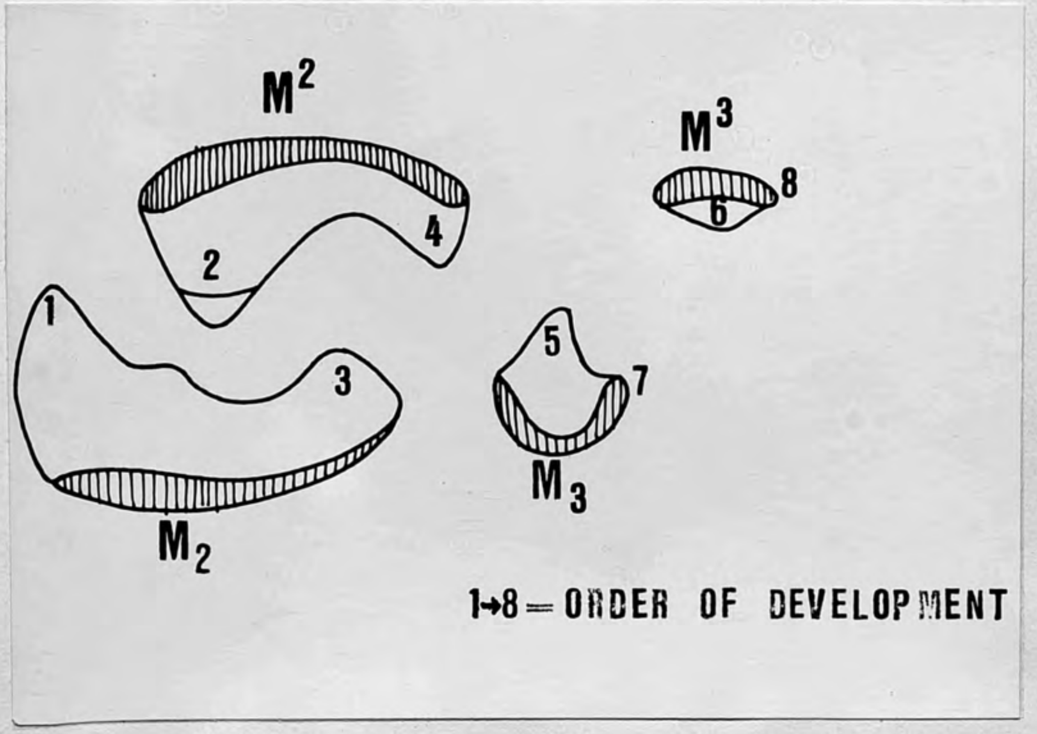


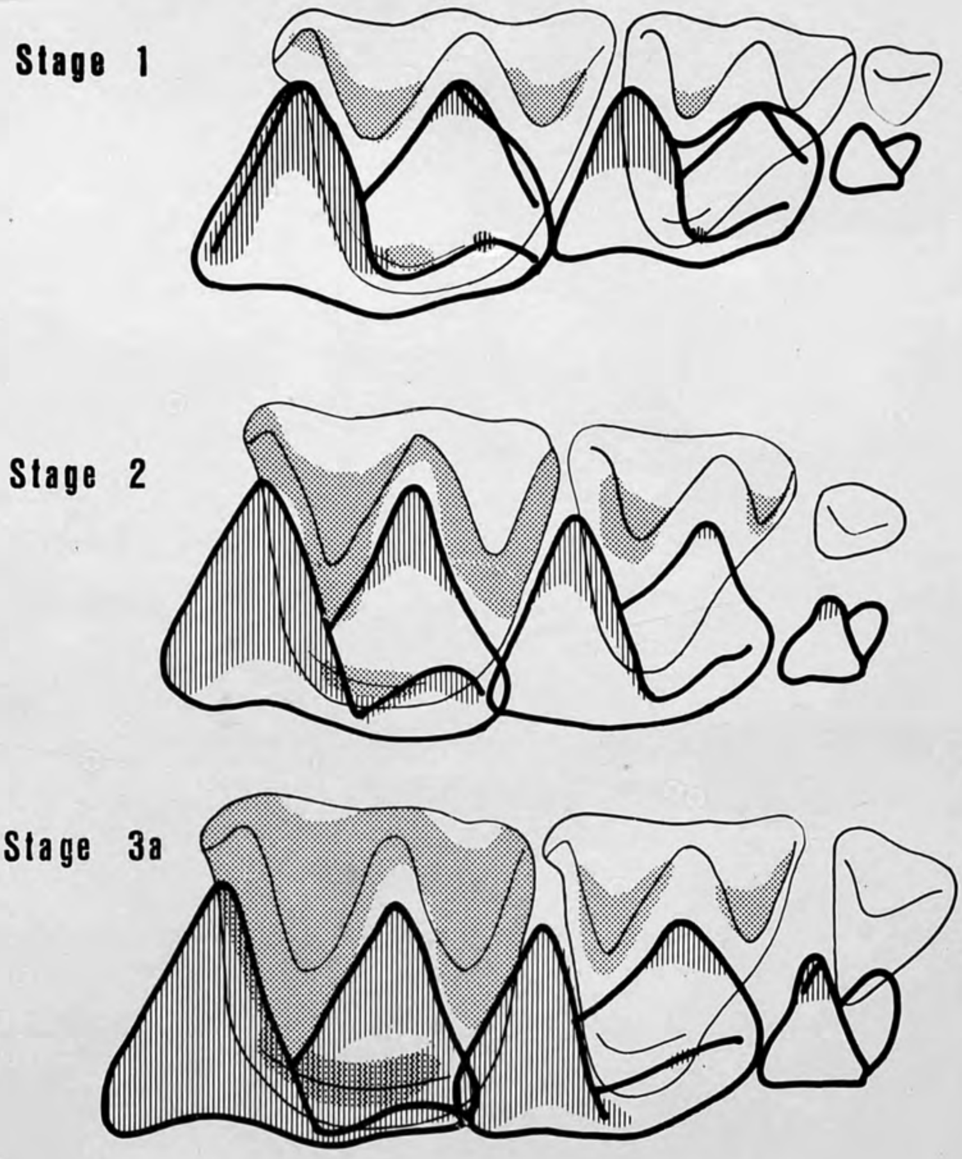
FIGURE 36 Second and third molars Stage 1



KEY ; ▥ = EXPOSED DENTAL PAPILLA

<u>FIGURE 37a</u> Diagram to show calcification during development:

a)stages 1, 2 and 3a.



KEY. Shaded areas = Calcified areas.

FIGURE 37b) Stages 4, 6a and 8.

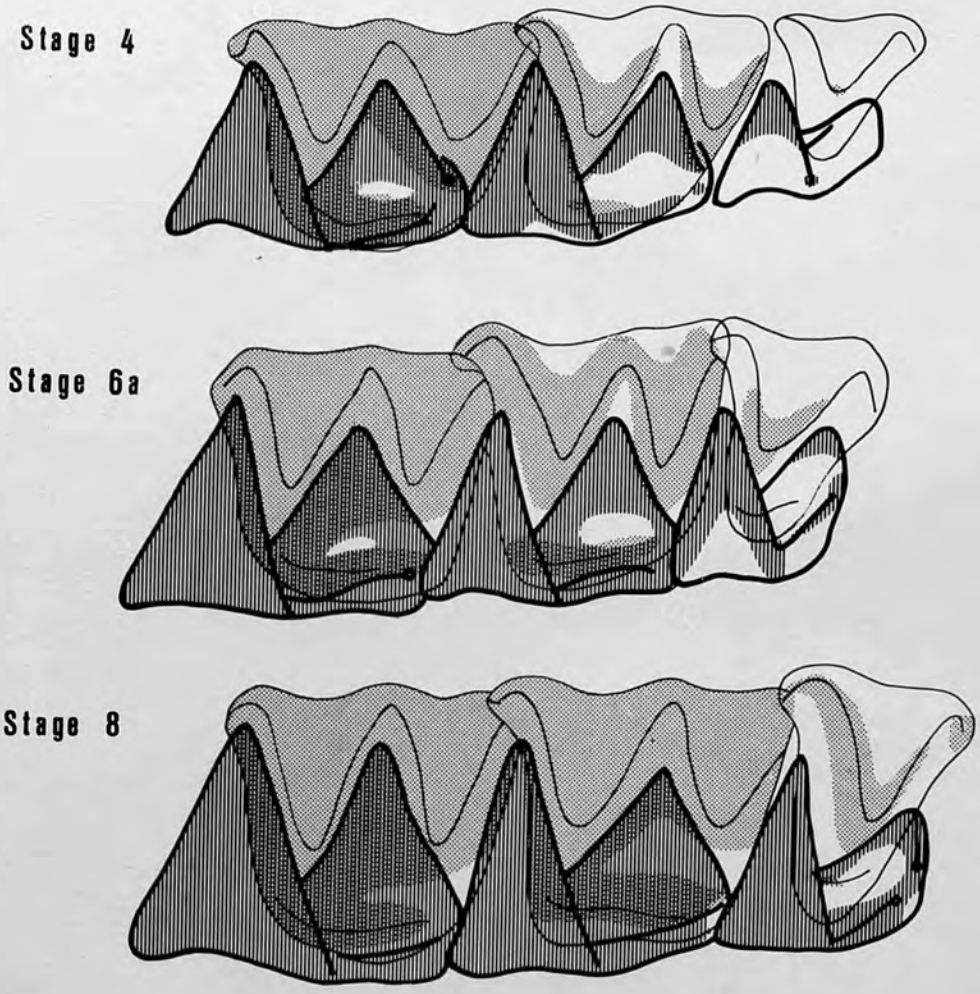


FIGURE 38 Wax models of upper and lower third molars in various stages of development.

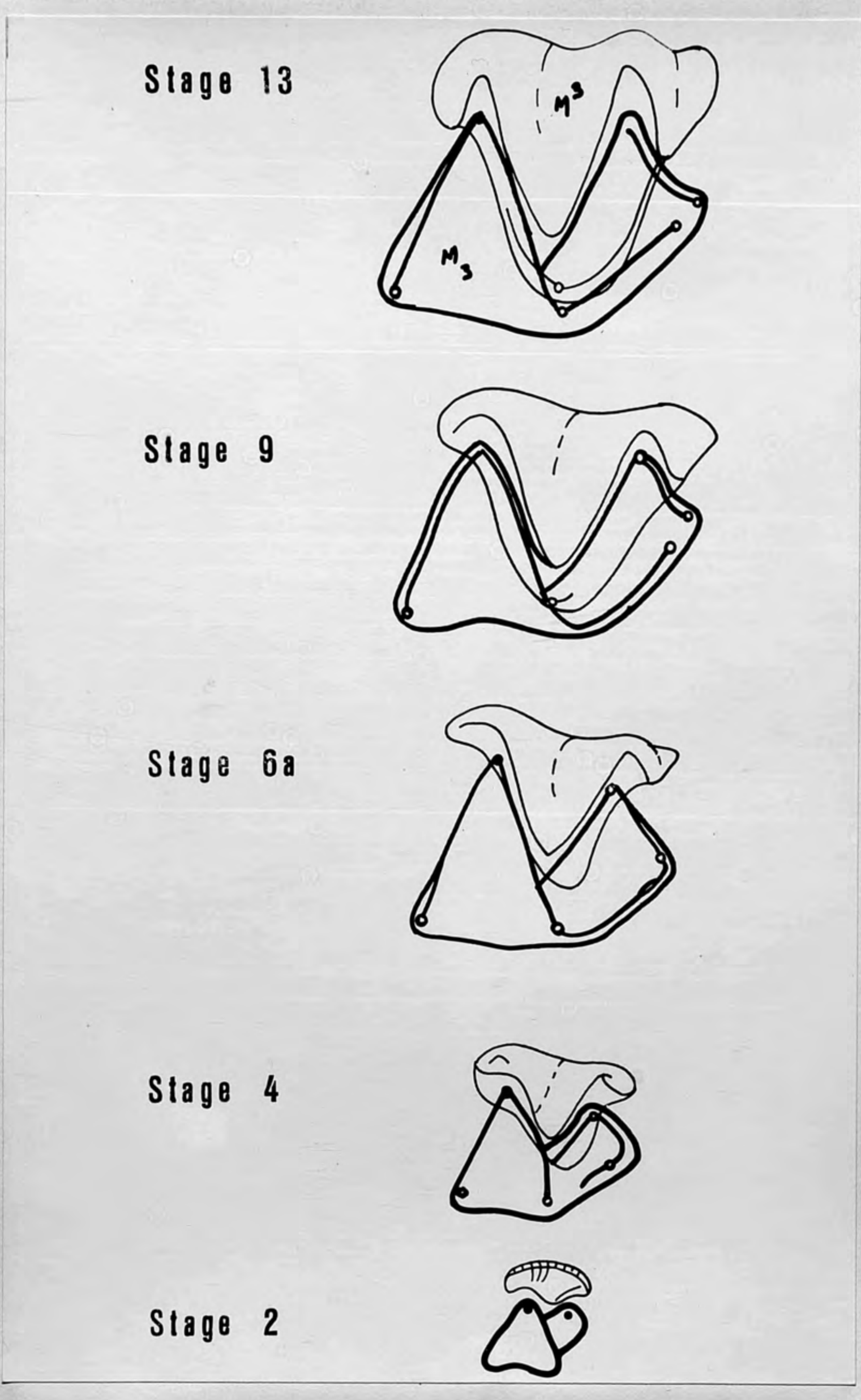


FIGURE 39 Graph to show the relationship between the length of the paracone and the distance between the protoconid and hypoconid during development.

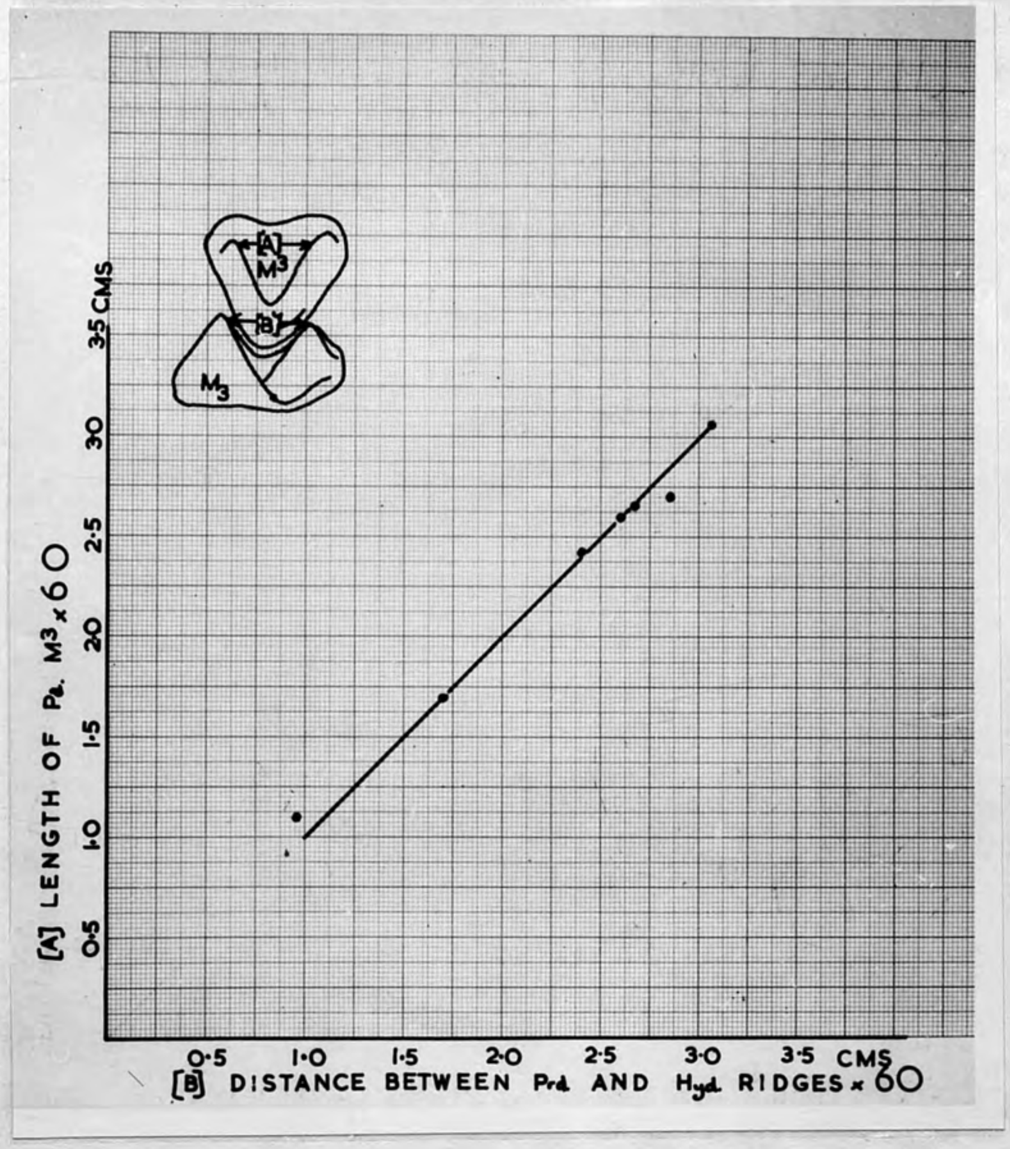


FIGURE 40 Graph to show the relationship between the lengths of commissure 4 in M^2 and commissure 1 in M_3 during development.

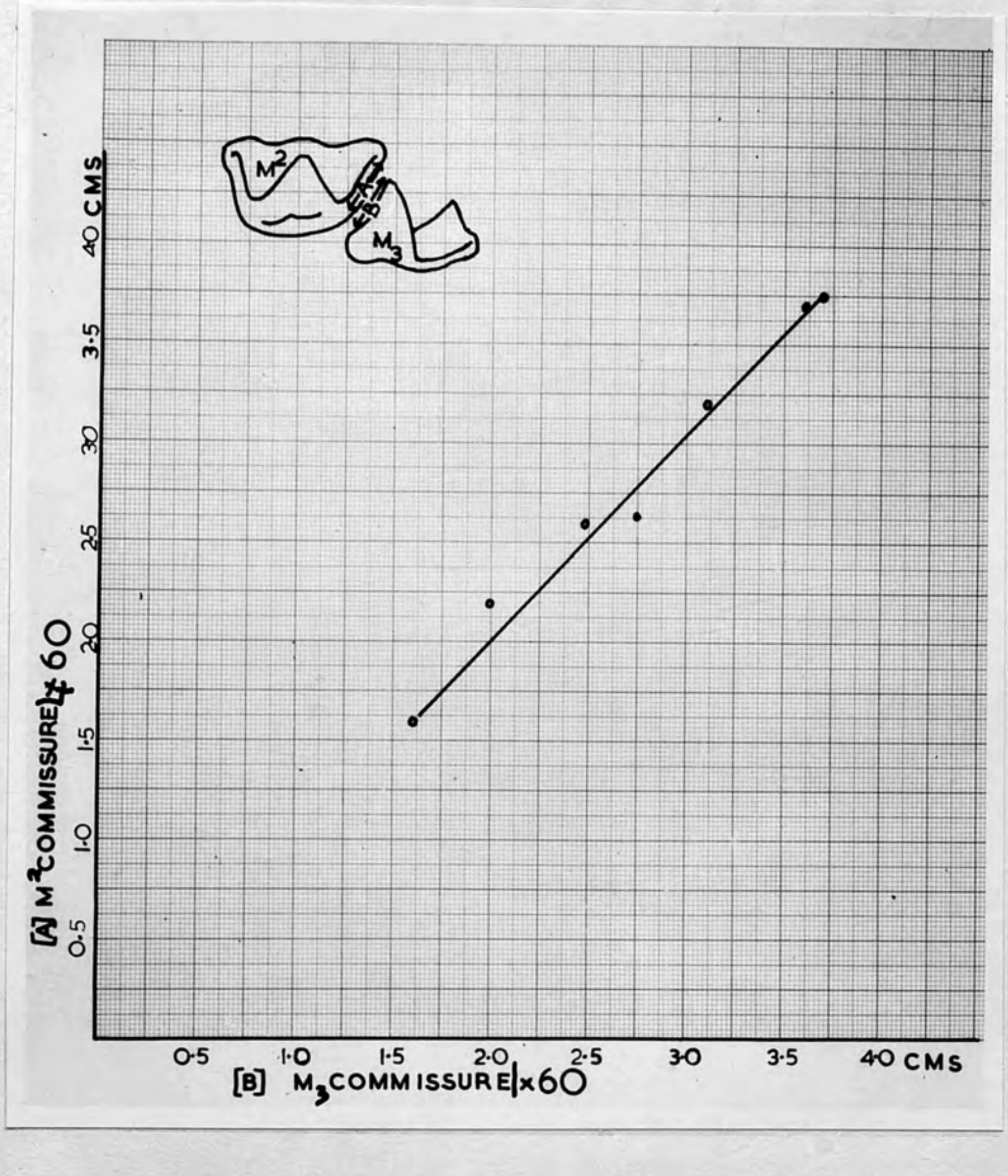


FIGURE 41 Graph to show the relationship between the lengths of commissure 3 in M^3 and commissure 4 in M_3 during development.

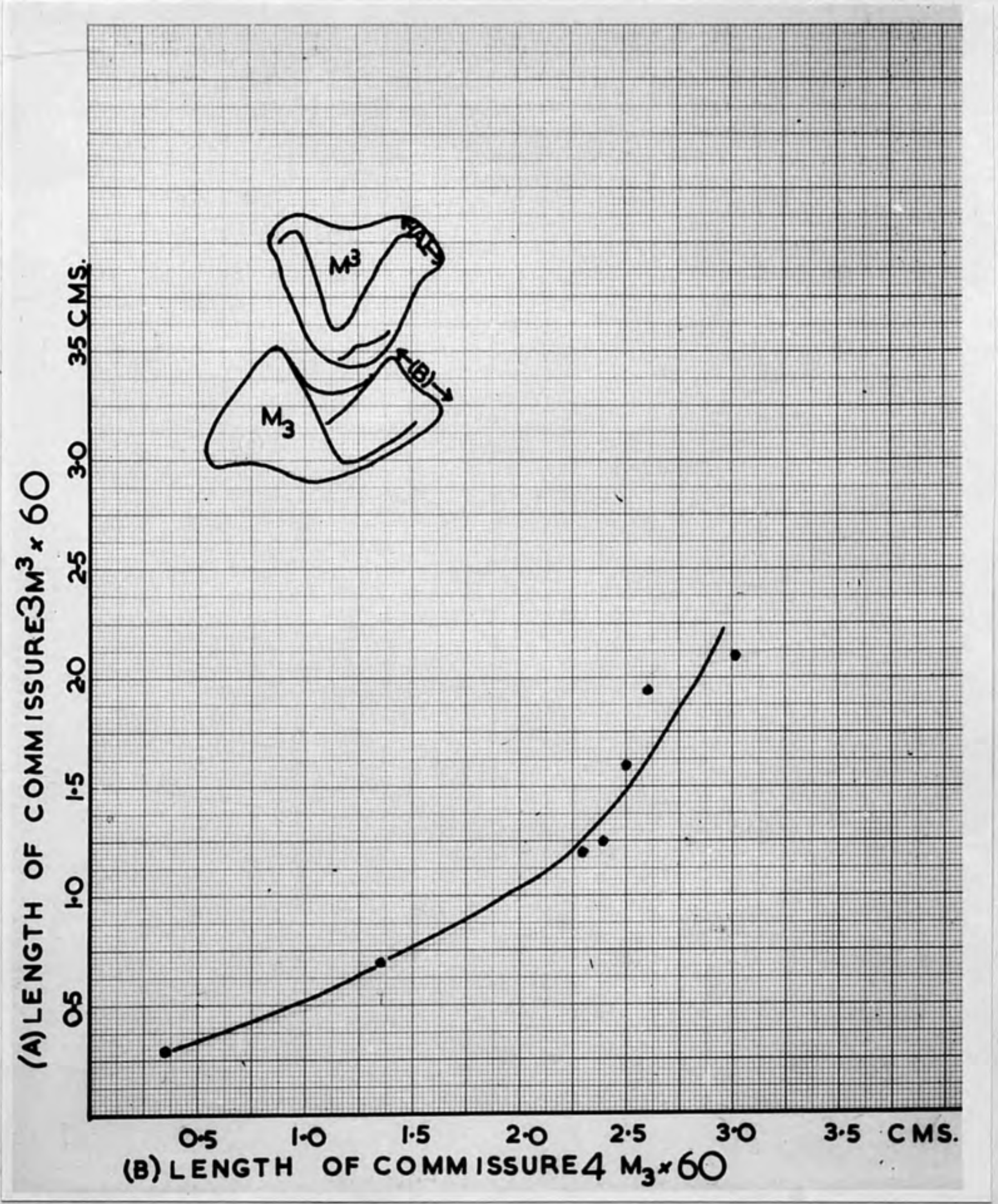
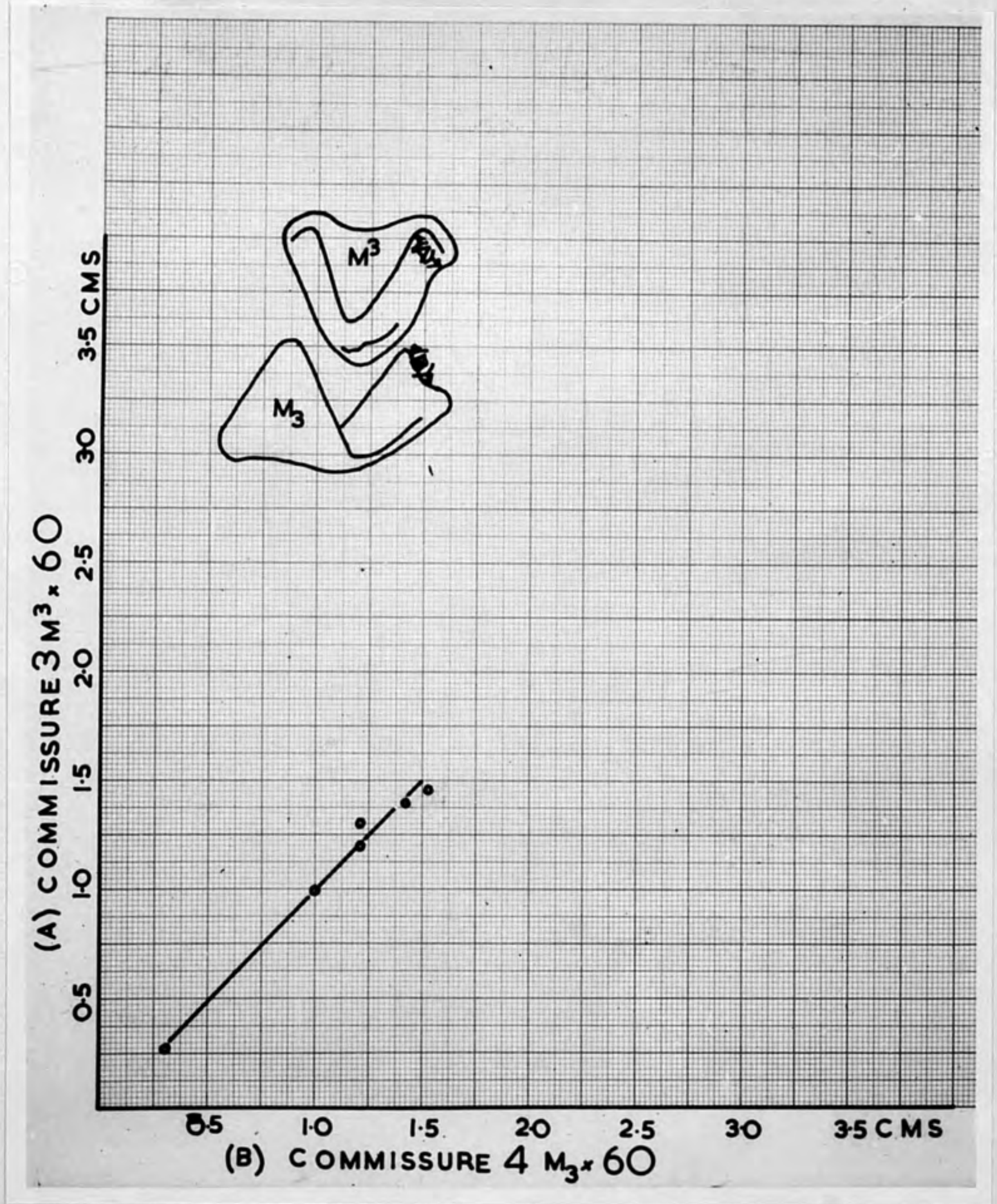


FIGURE 42 Graph to show the relationship between the length of commissure 3 in M^3 and the length of commissure 4 discounting the hypoconulid area in M_3 during development.



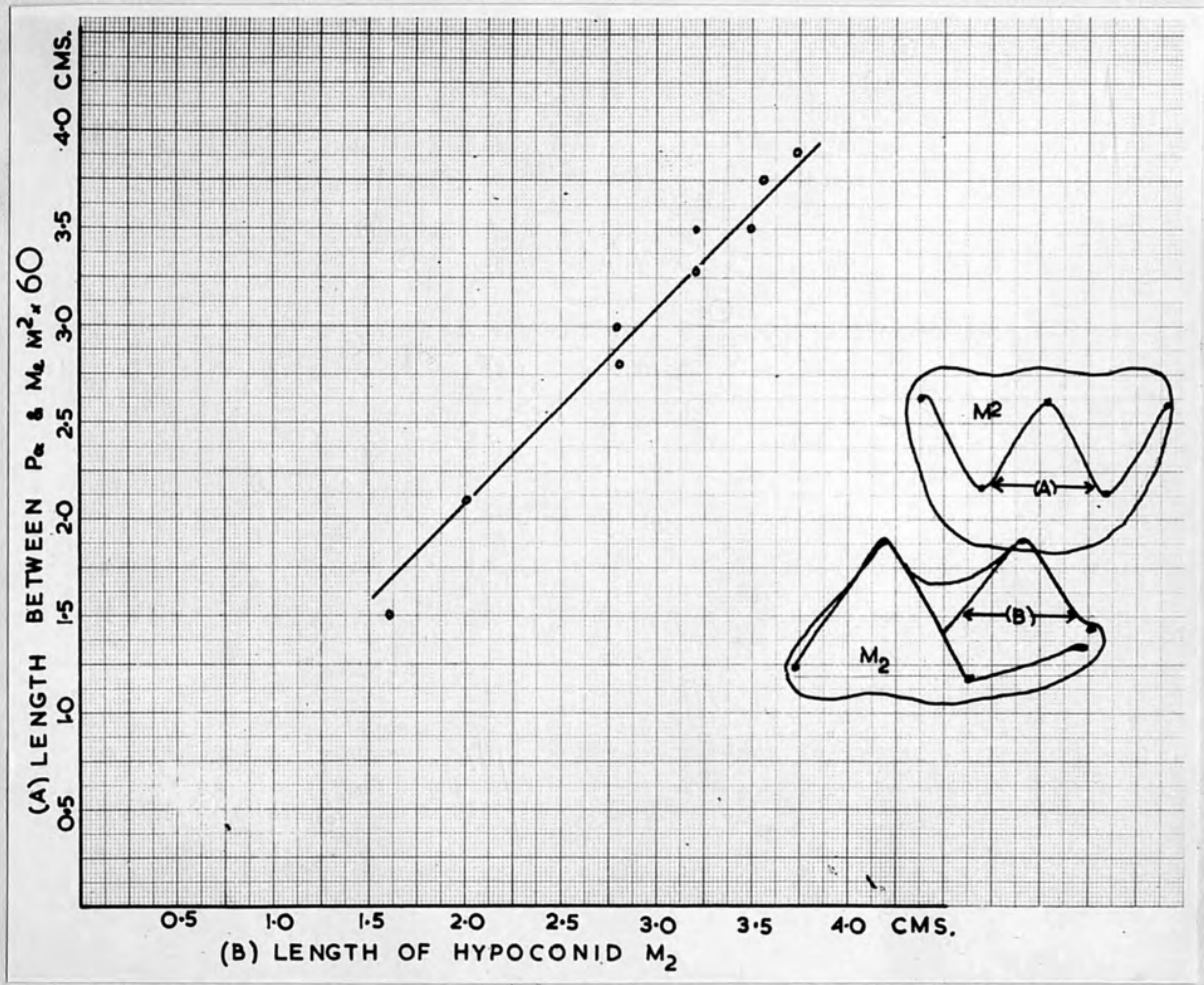


FIGURE 43 Graph to show the relationship between the length of the hypoconid in M_2 and the distance between the paracone and metacone in M^2 during development.

FIGURE 44 To show development of the mandibular toothrow.

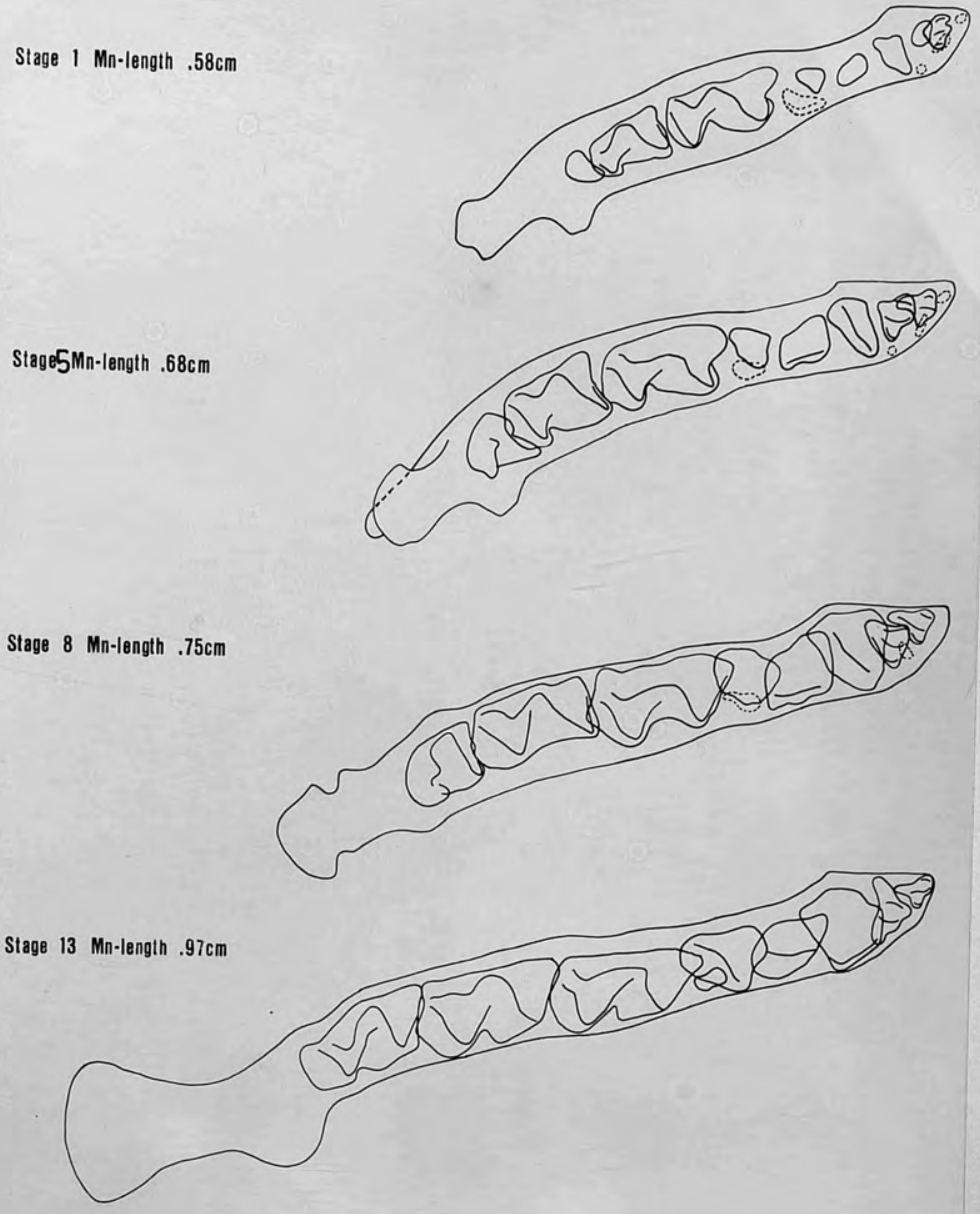


FIGURE 45 To show development of maxillary toothrow.

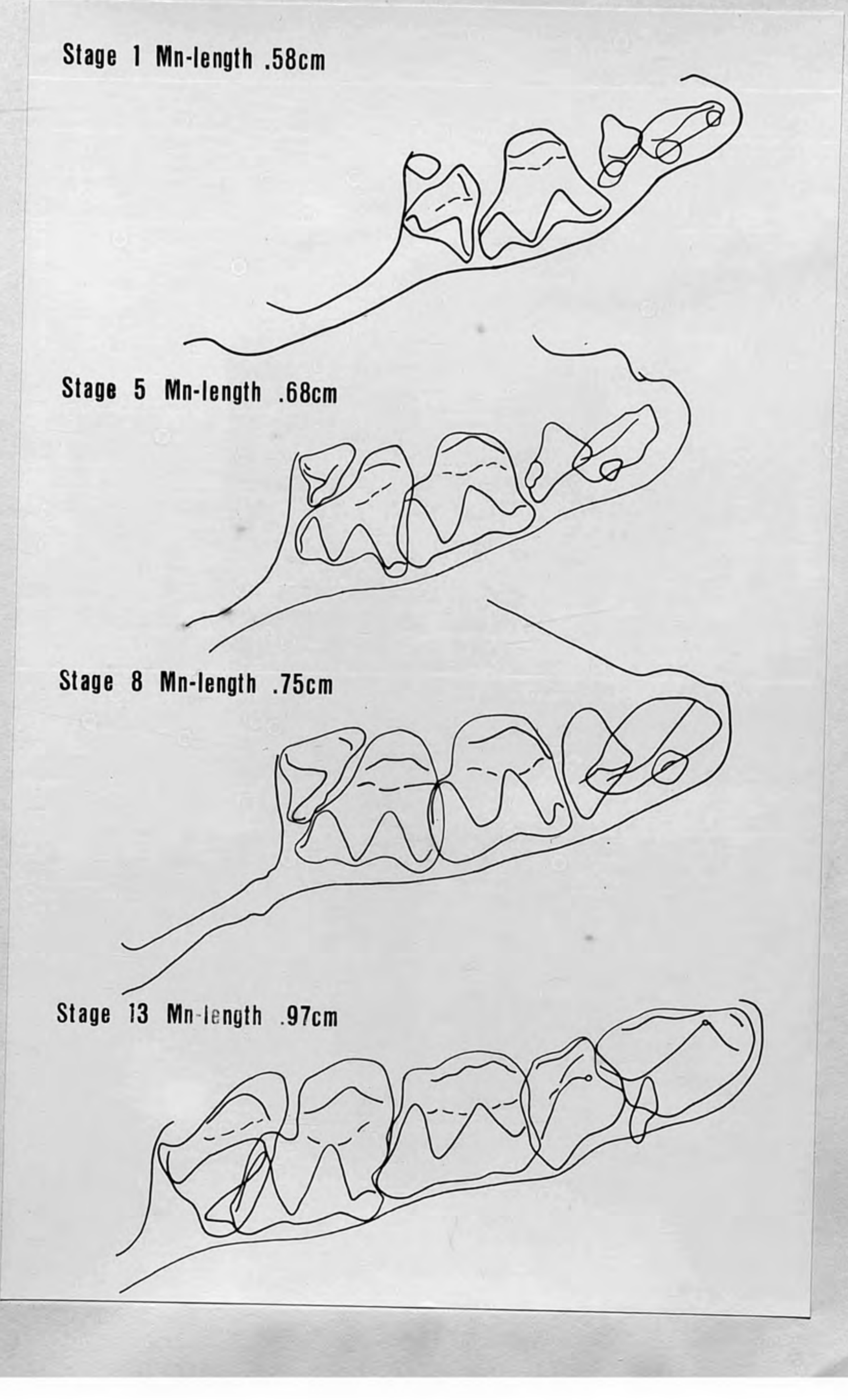


FIGURE 46 Mandible in stages 1, 4 and 13 superimposed to show growth.

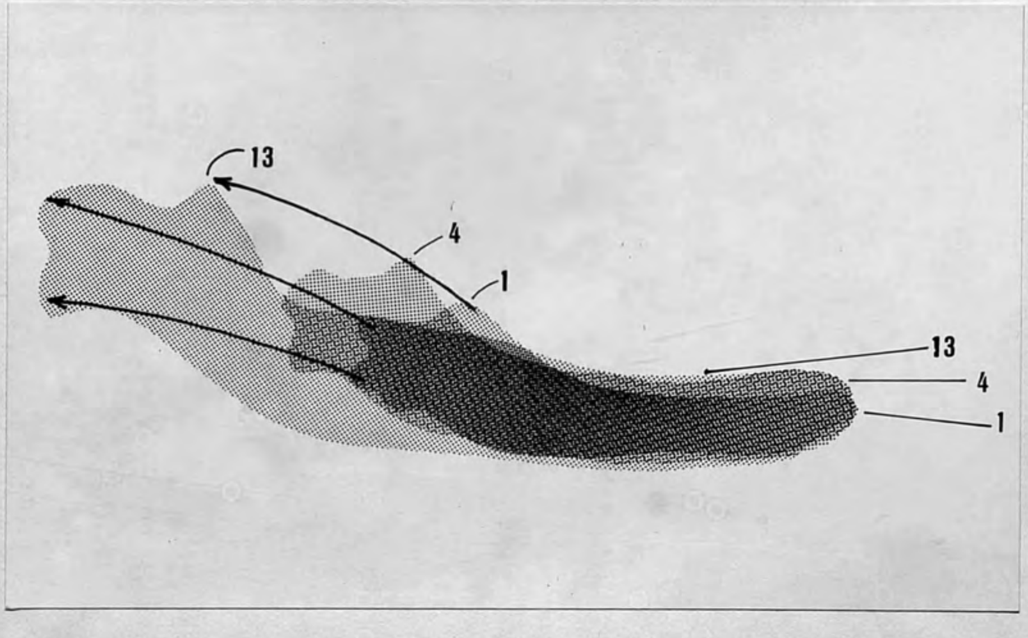


FIGURE 47 Outlines of the mandible and mandibular teeth stages 1, 5 and 13. The broken line passing posteriorly to M_3 demonstrates the differences in the position of M_3 relative to the ascending ramus in these 3 stages.

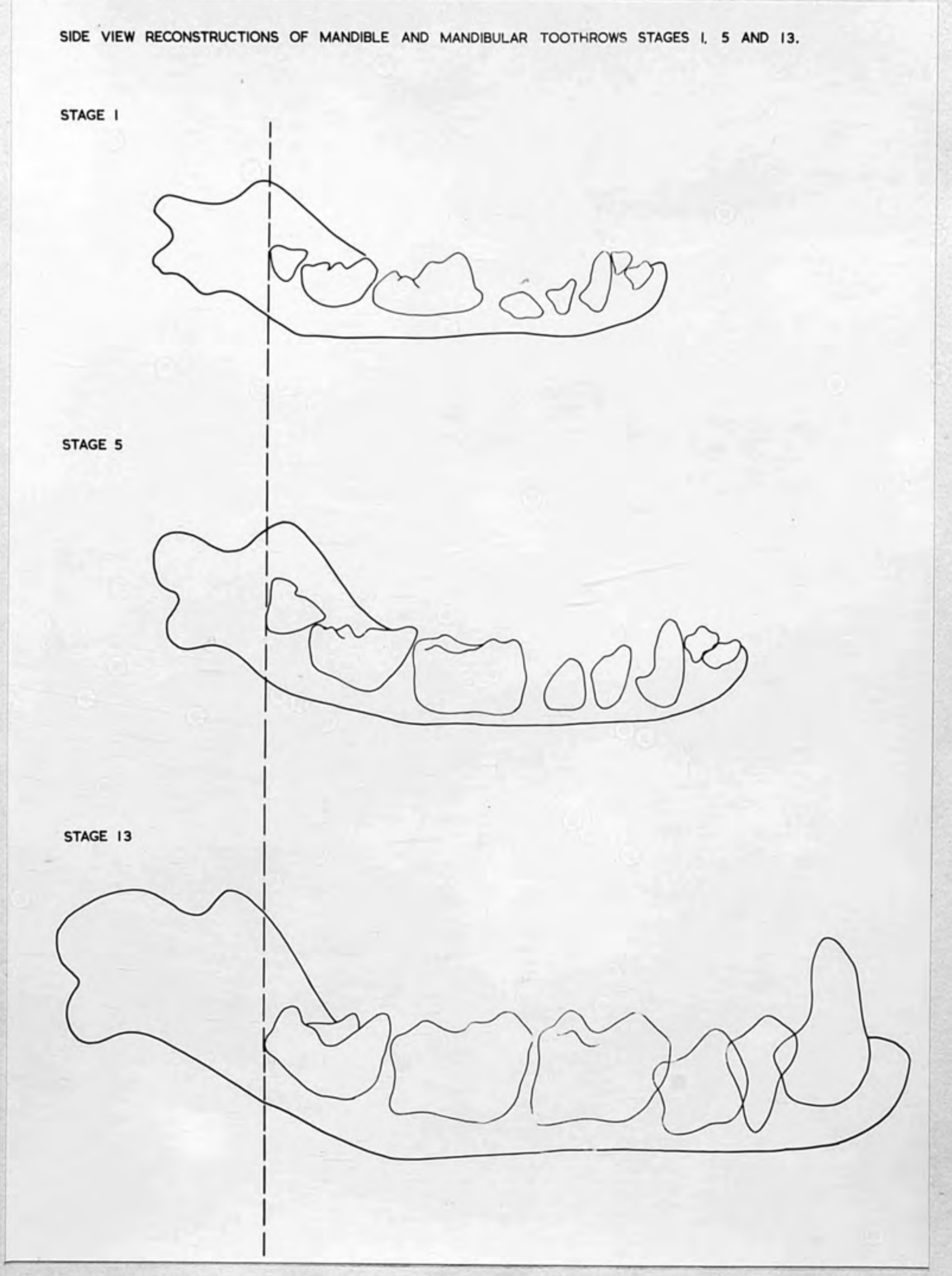
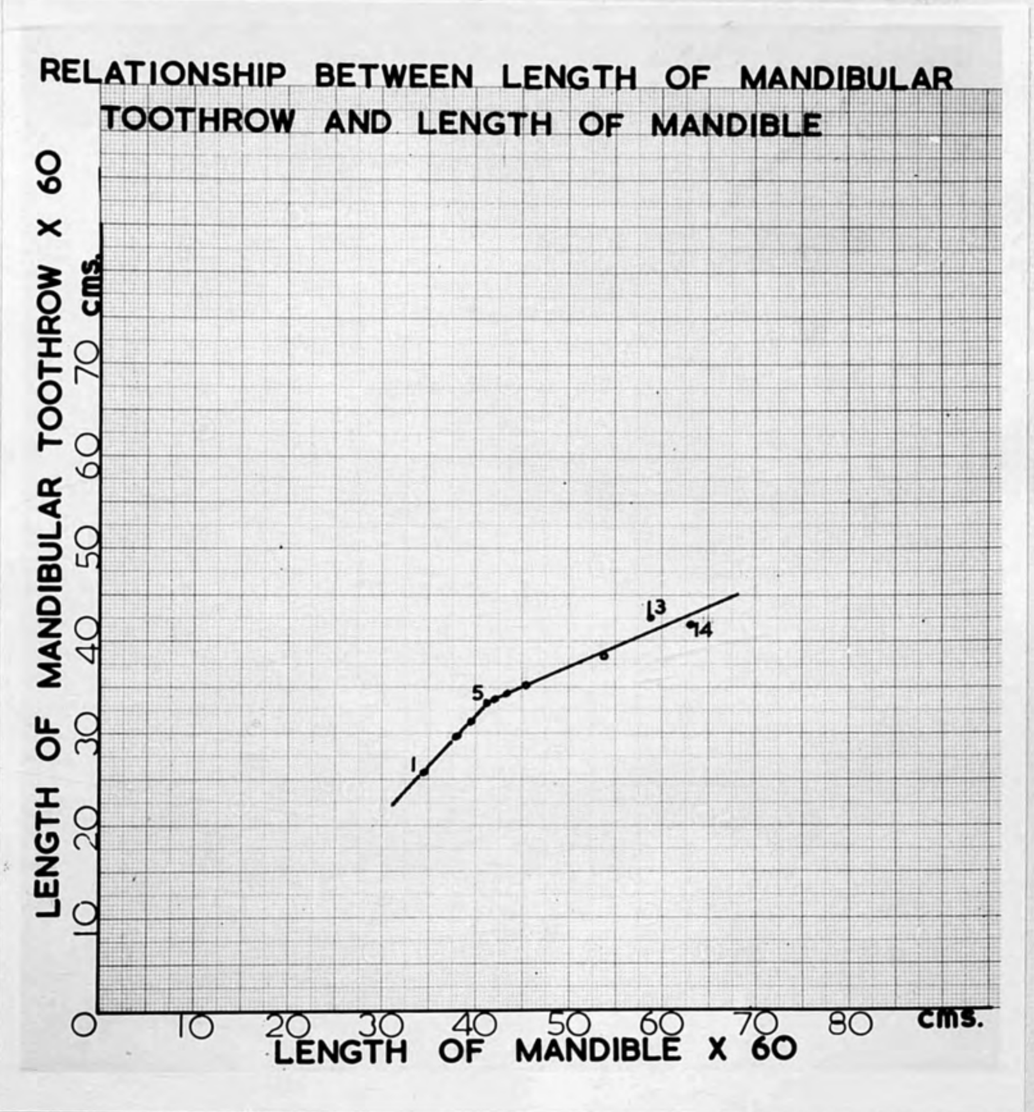


FIGURE 48



RELATIONSHIP BETWEEN LENGTH OF MANDIBULAR TOOTHROW AND LENGTH OF MANDIBLE

MANDIBULAR TOOTHROWS STAGES I, 5 AND 13 SUPERIMPOSED TO SHOW GROWTH

Side-view

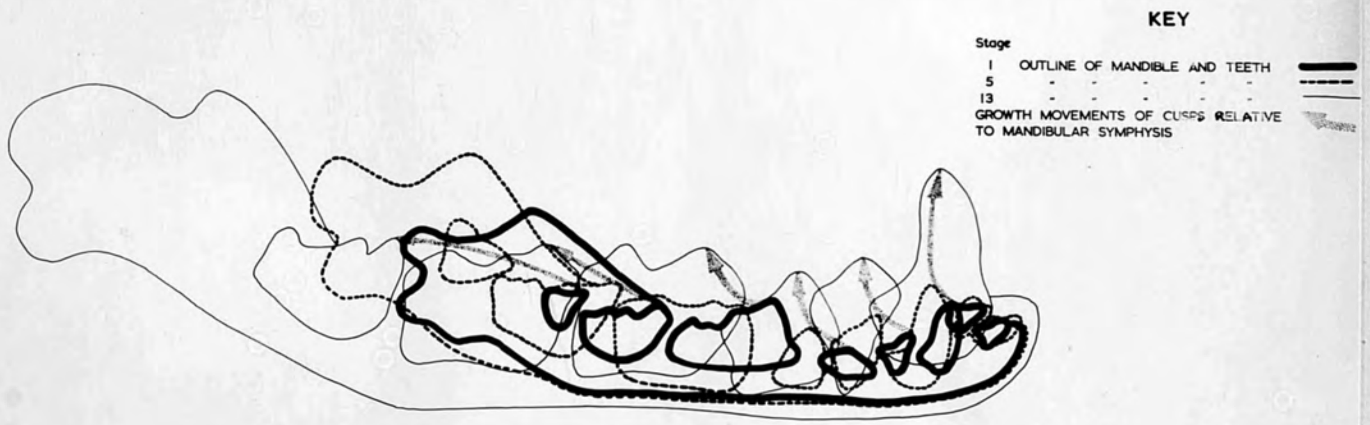


FIGURE 49

MANDIBLE AND MANDIBULAR TOOTHROWS STAGES I AND 13 SUPERIMPOSED

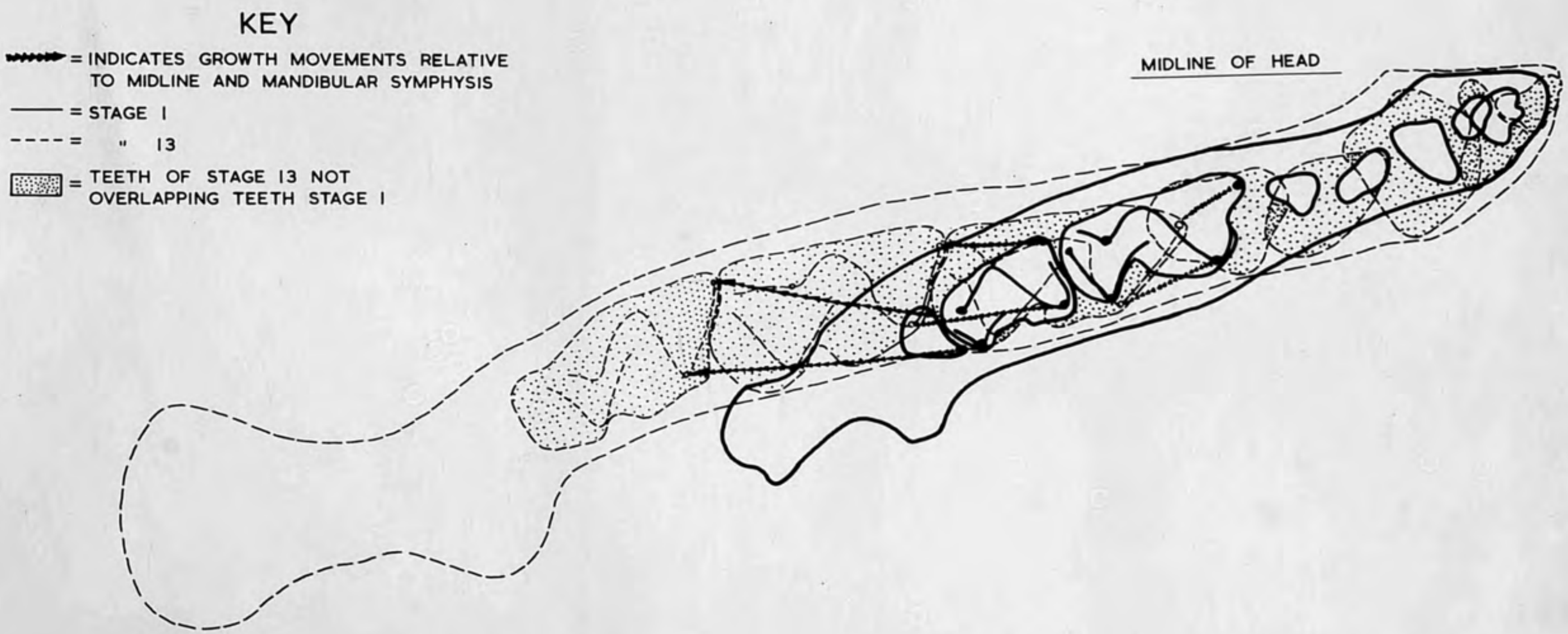
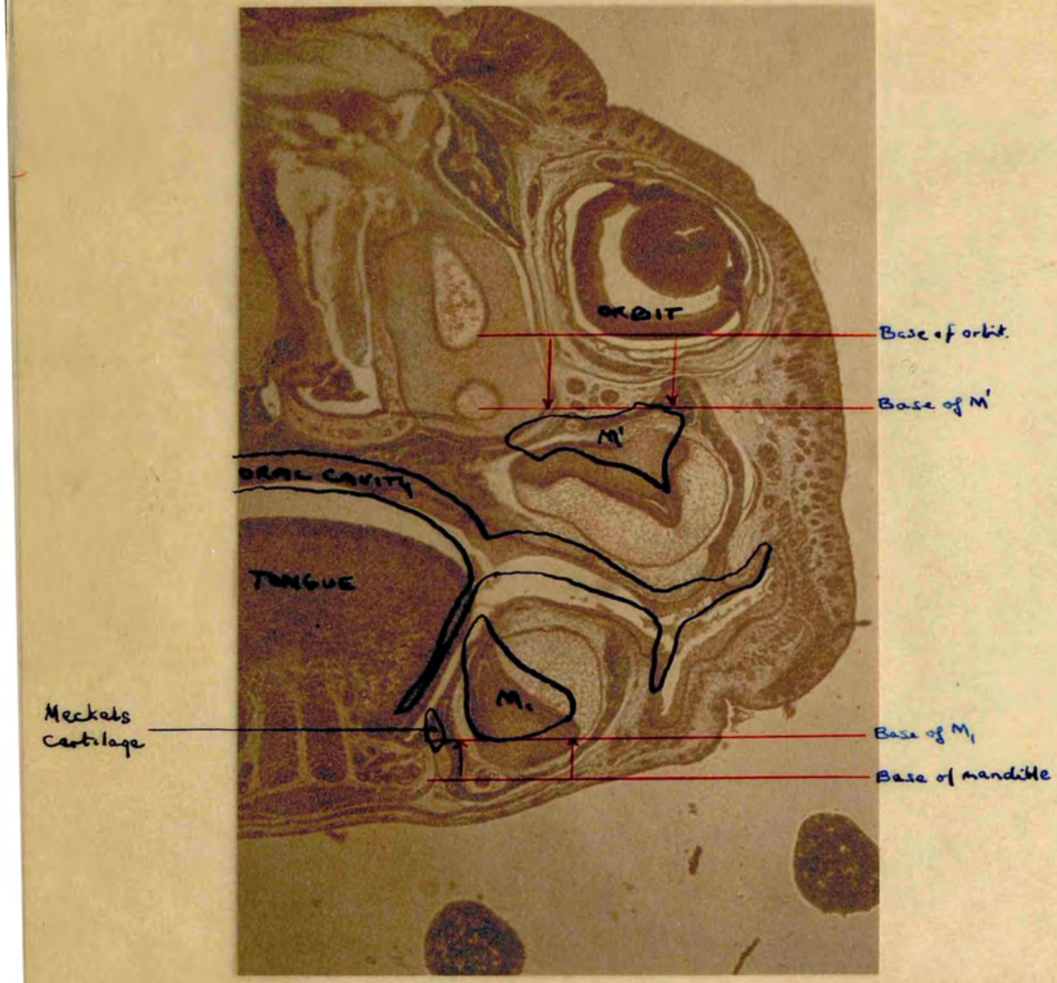
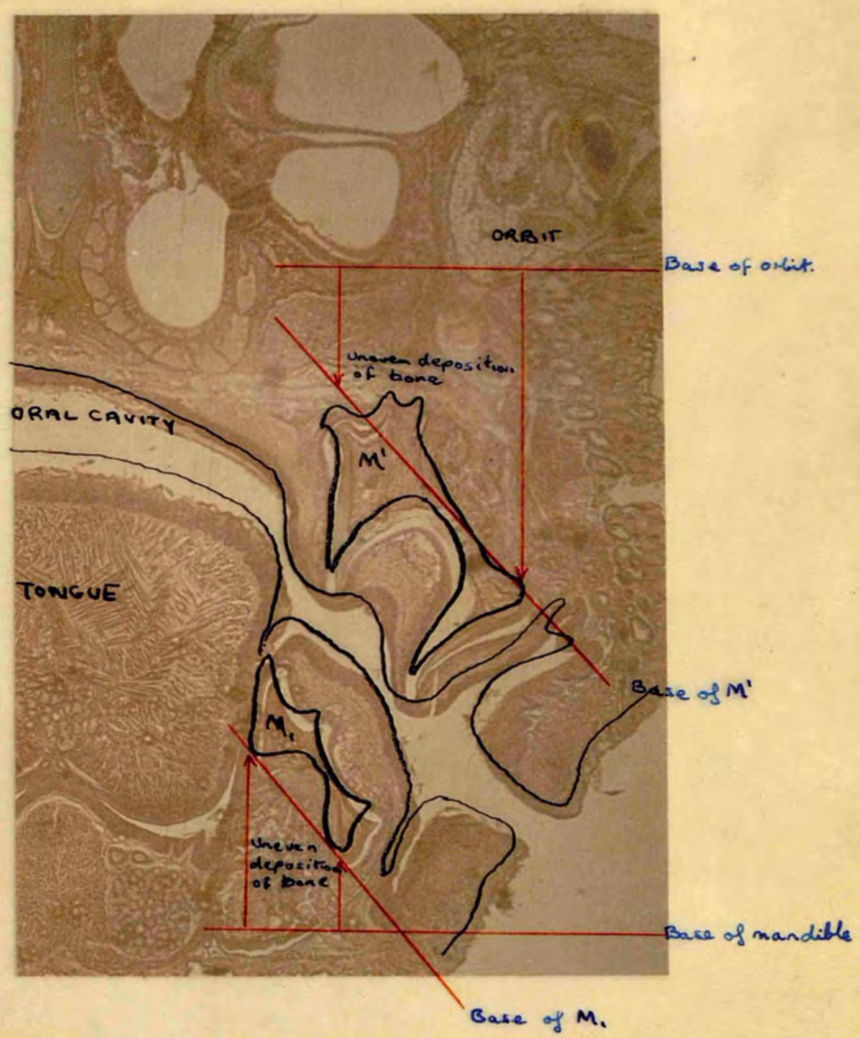


FIGURE 50



a) Transverse section through the head of <u>H. beatus</u> in the region of M^1 and M_1 Stage I.

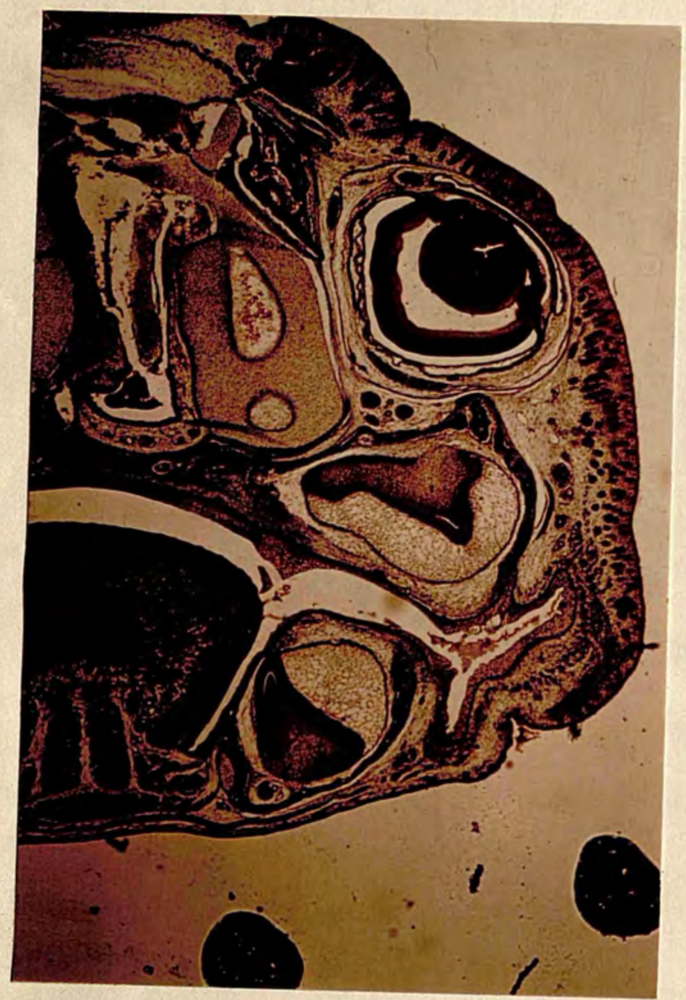
FIGURE 51 (a)



b) Transverse section through the head of <u>H. beatus</u> in the region of M^1 and M_1 Stage 13.

Degree of rotation of the tooth bases between stages I and 13 is equal but opposite in the opposing jaws

FIGURE 52 (b)



<u>FIGURE 51</u> (a)

<u>FIGURE 52</u> (b)

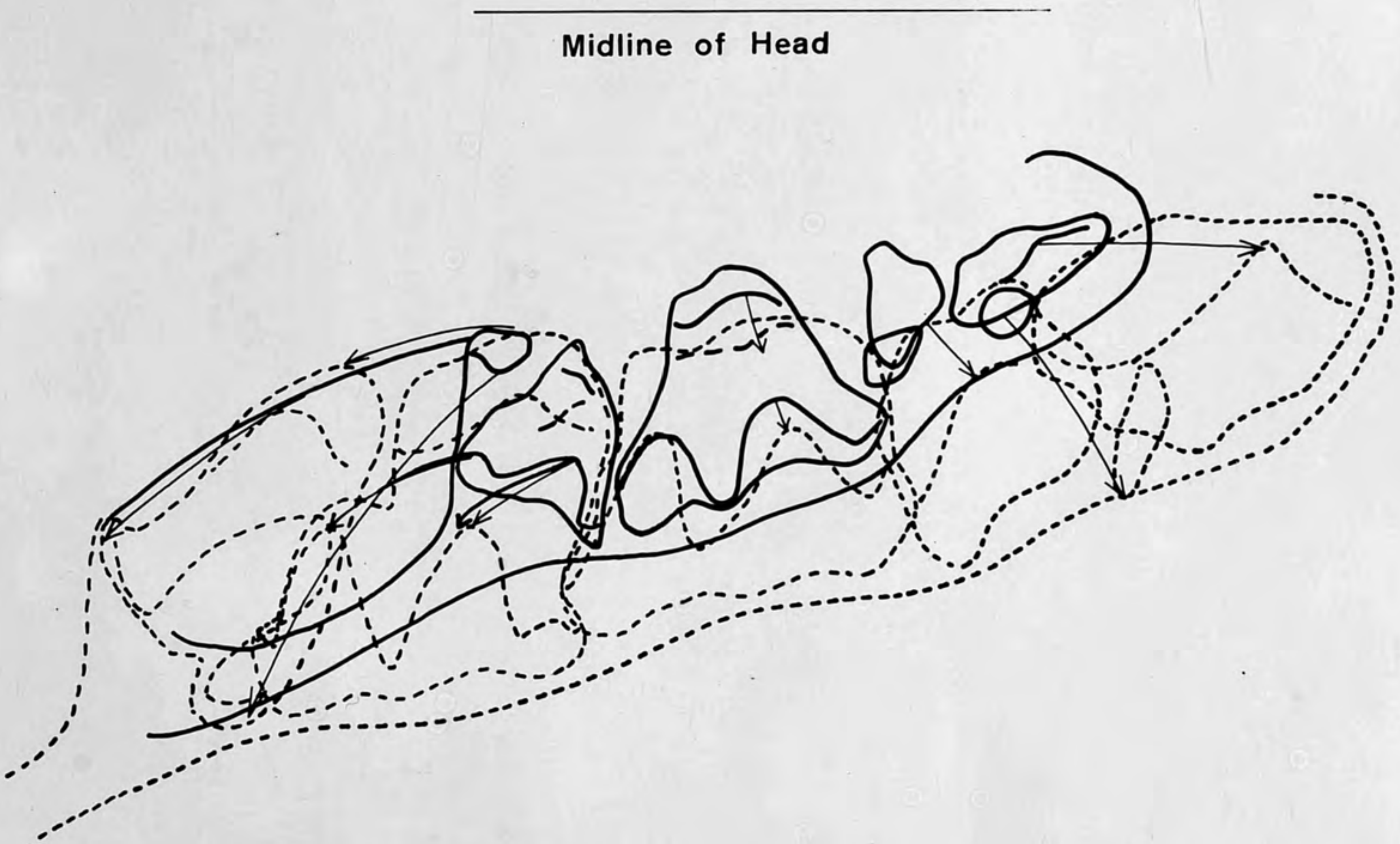


FIGURE 53 Plan-view reconstructions of the maxilla and maxillary toothrows in stage 1 (continuous line) and stage 13 (broken line) superimposed. Arrows show growth movements of the cusps relative to M^1 and the midline of the head.

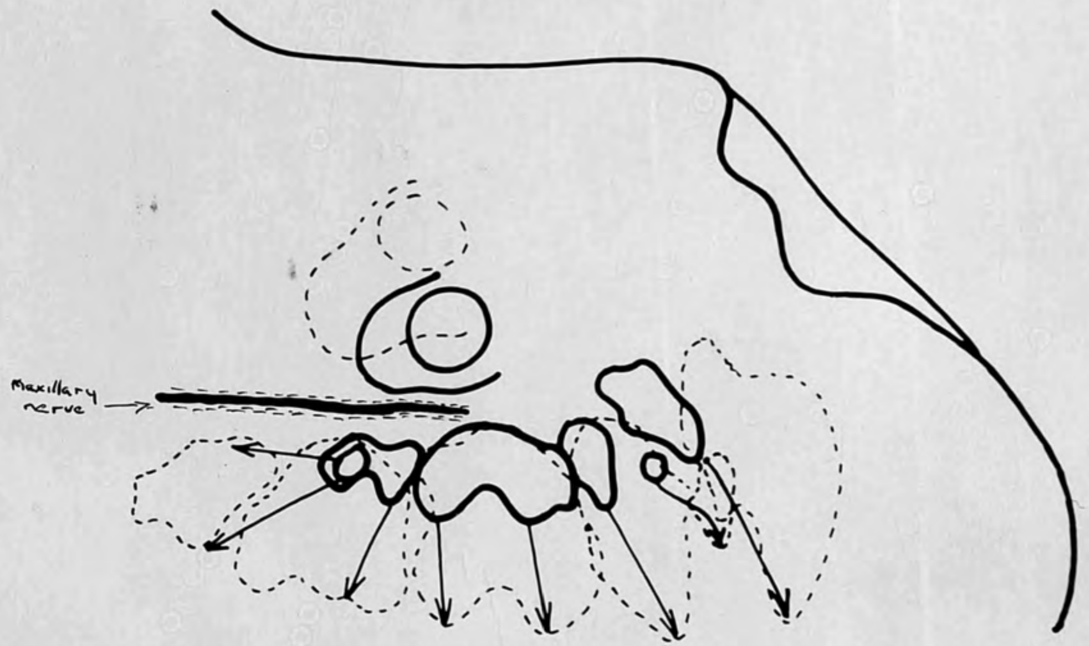
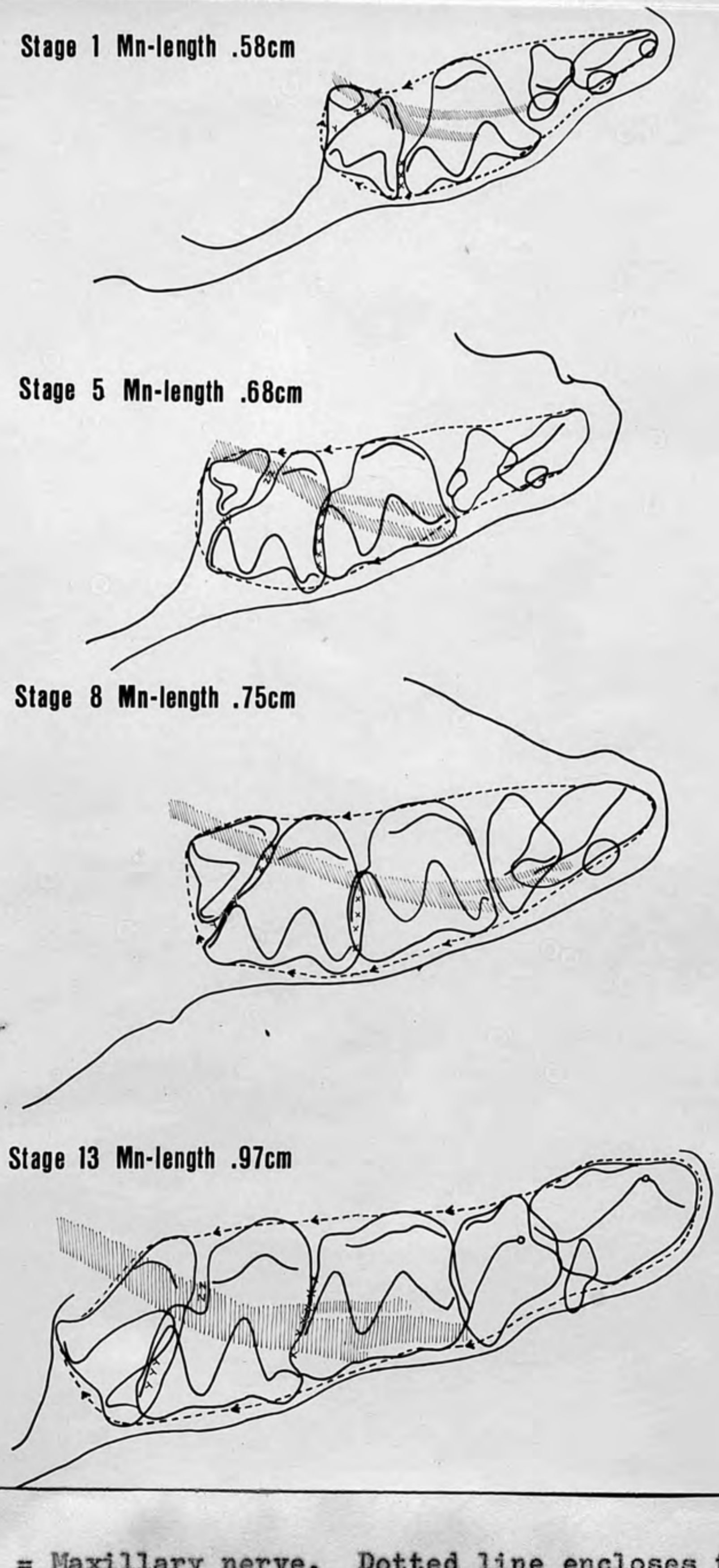


FIGURE 54 Side-view reconstructions of the maxillary teeth in stage 1 (continuous line) and stage 13 (broken line) superimposed. Arrows show growth movements of the cusps relative to M^1 and the maxillary nerve.

FIGURE 55 Unfurling of maxillary toothrow.

Plan view reconstruction.



KEY. ▨ = Maxillary nerve. Dotted line encloses toothrow.

FIGURE 56

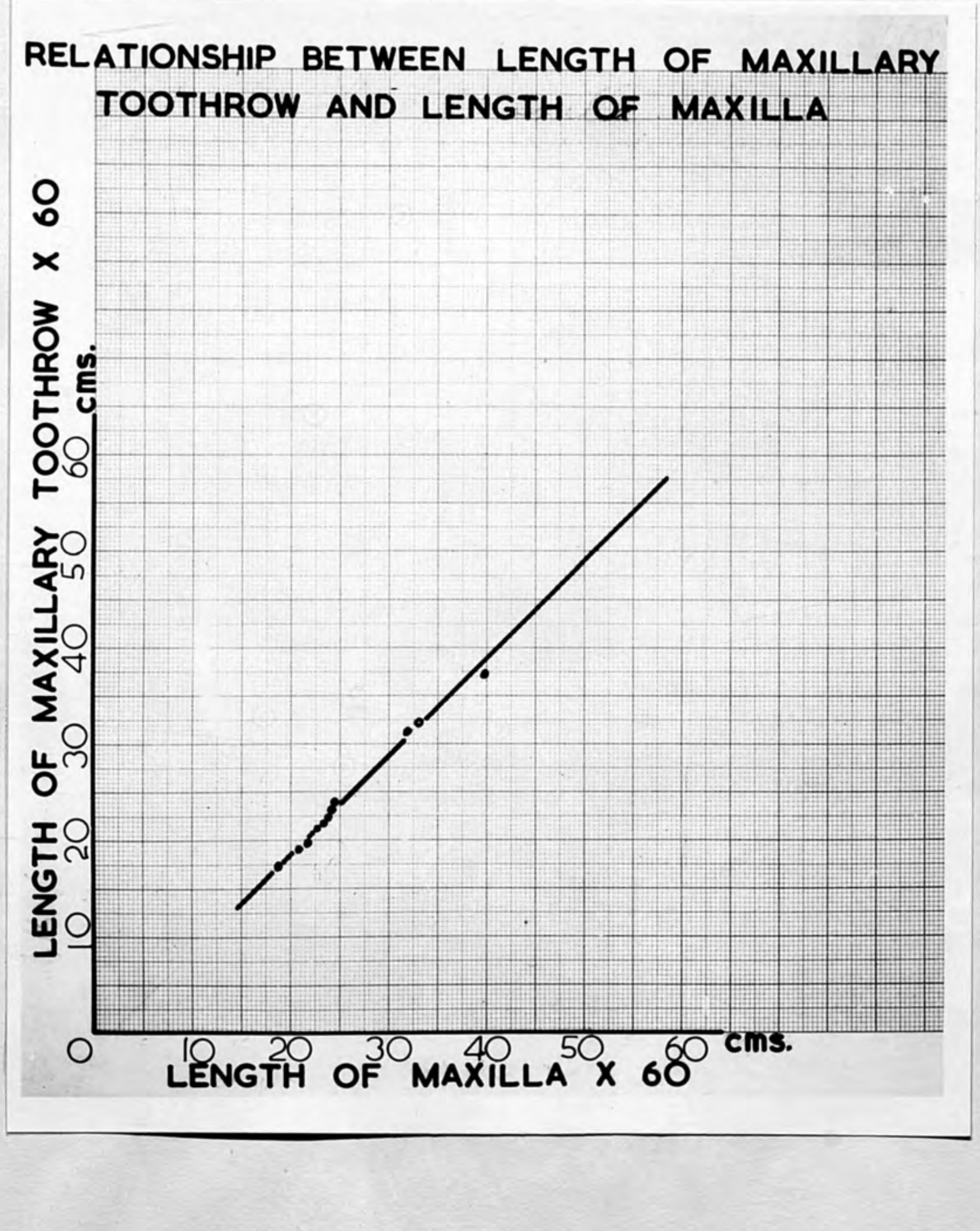
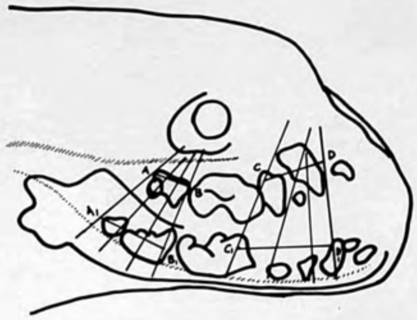
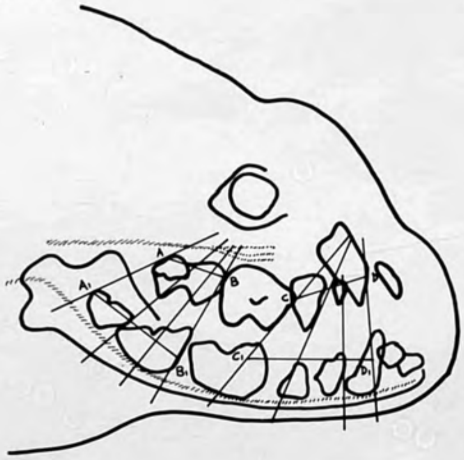

RELATIONSHIP BETWEEN LENGTH OF MAXILLARY TOOTHROW AND LENGTH OF MAXILLA
LENGTH OF MAXILLARY TOOTHROW X 60
cms.
10
20
30
40
50
60
0
10
20
30
40
50
60
cms.
LENGTH OF MAXILLA X 60

FIGURE 57 Side-view reconstructions of the teeth *in situ* in the head in stages 1, 5, 6a, 9 and 13. Stage 14 is a side-view drawing of the teeth made from a photograph of an adult skull. All to the same scale. Lines pass through points on upper and lower teeth that will later occlude.

Stage 1



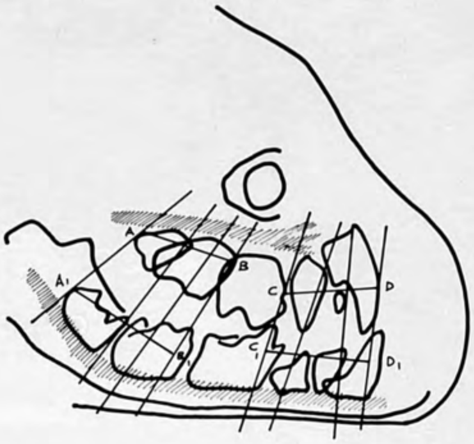
Stage 5



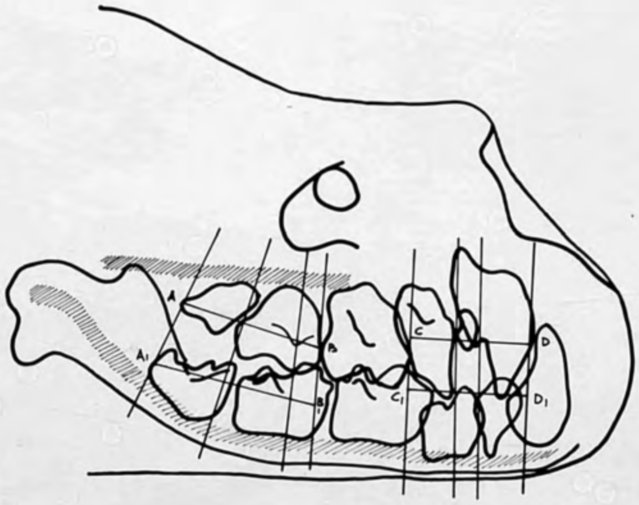
Stage 6a

FIGURE 57 continued

Stage 9



Stage 13



Stage 14 Final Stage

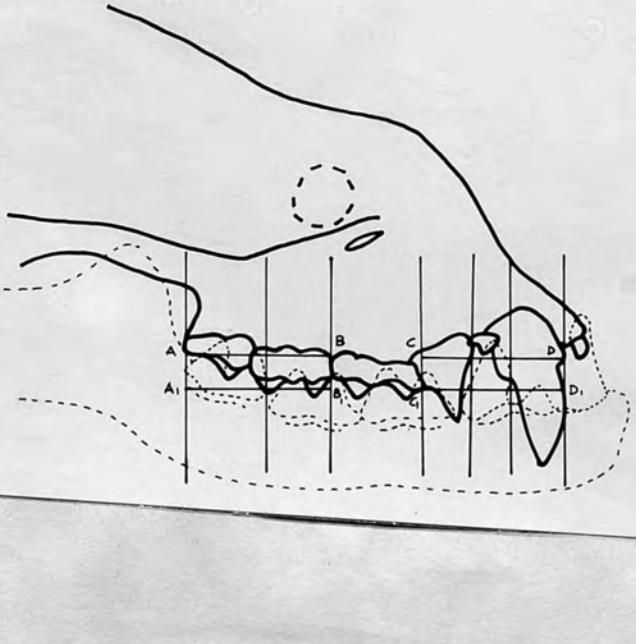


FIGURE 58 Plan-view reconstructions of upper and lower toothrows *in situ* in the head in Stages 1,5,8 and 13. Stage 14 shows upper and lower teeth *in situ* in the adult dentition, and is drawn from photographs of an adult skull. All to the same scale.

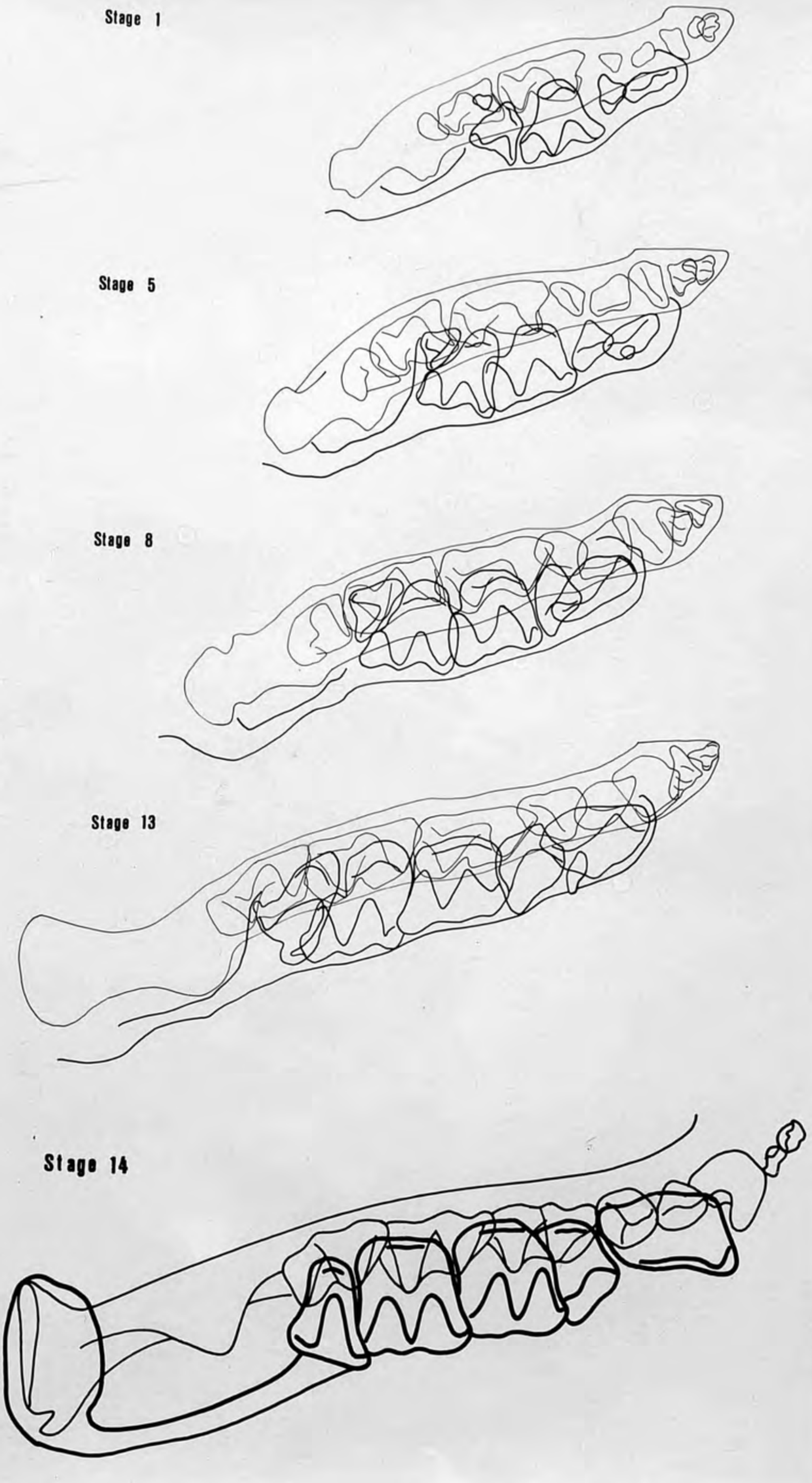
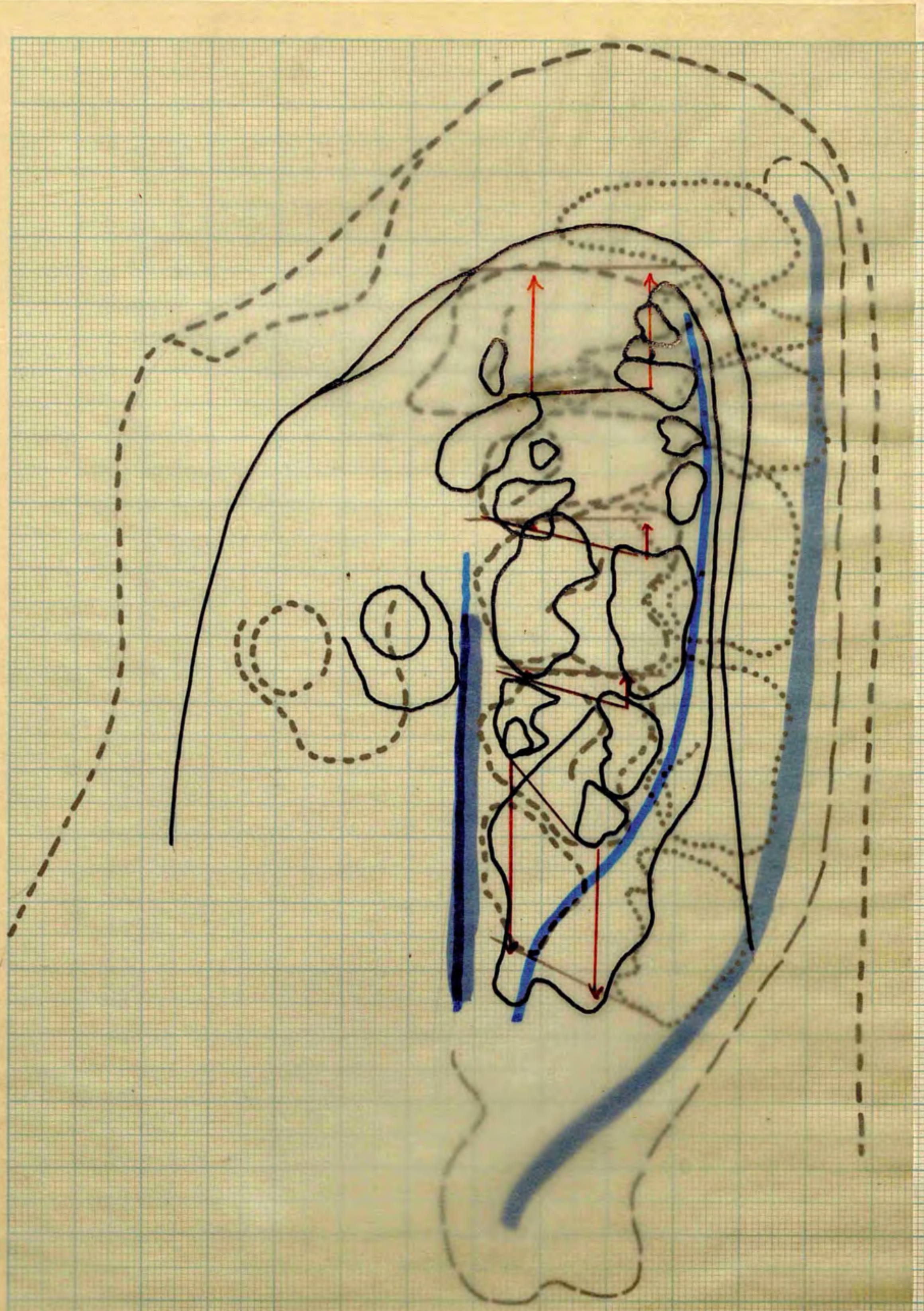


FIGURE 59 Side-view reconstruction of the teeth in Stages 1 and 13. Stage 1 (on tracing paper) is superimposed onto Stage 13 (on graph paper) so that M^1 and the maxillary nerve coincide. Brown lines join points that will later occlude, and red arrows show forward or backward movements of these points relative to M^1 and the maxillary nerve.

It can be seen that the lower molars move forwards relative to the upper molars.

FIGURE 59



▬ = Maxillary or Mandibular nerve.

FIGURE 59

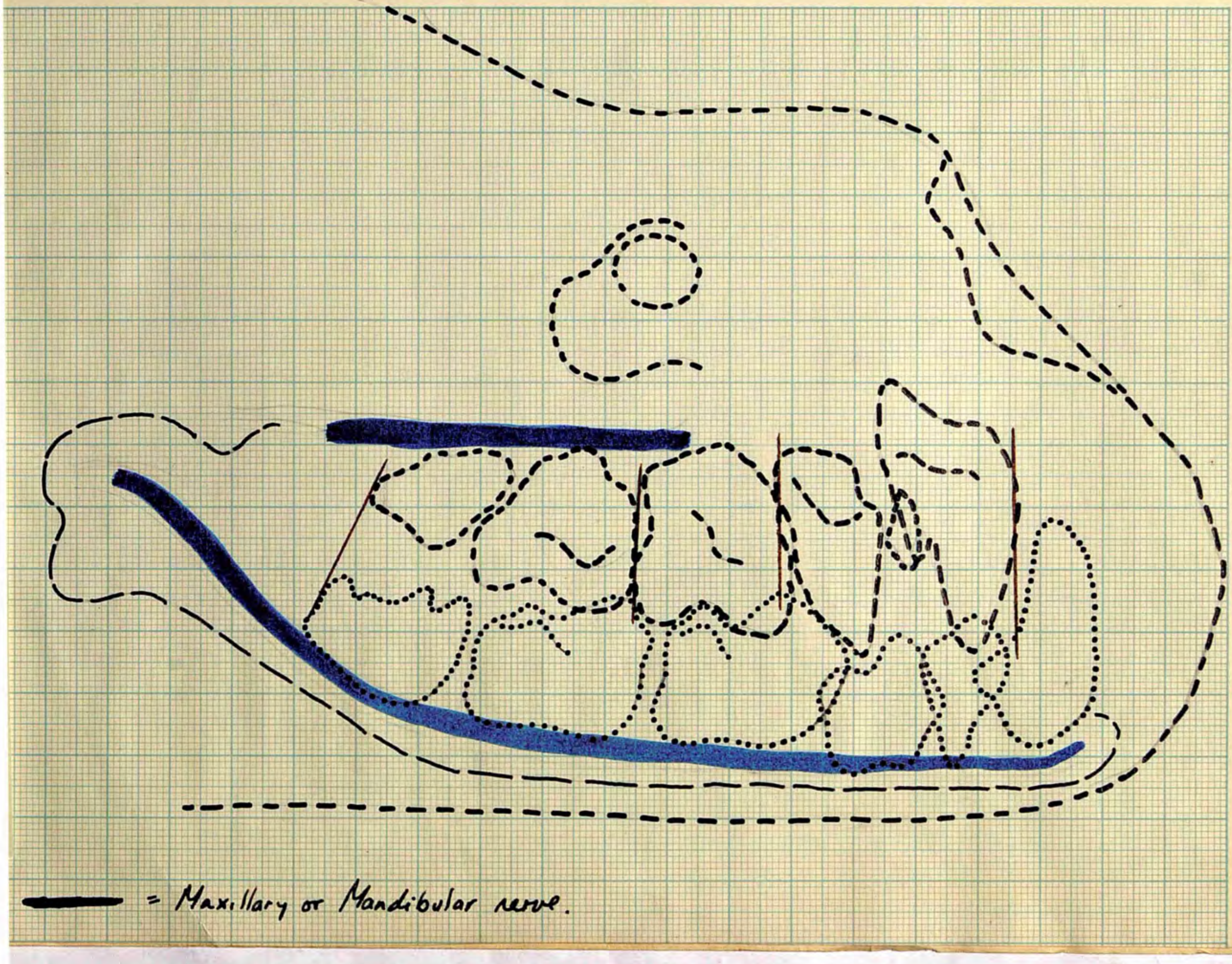


FIGURE 60

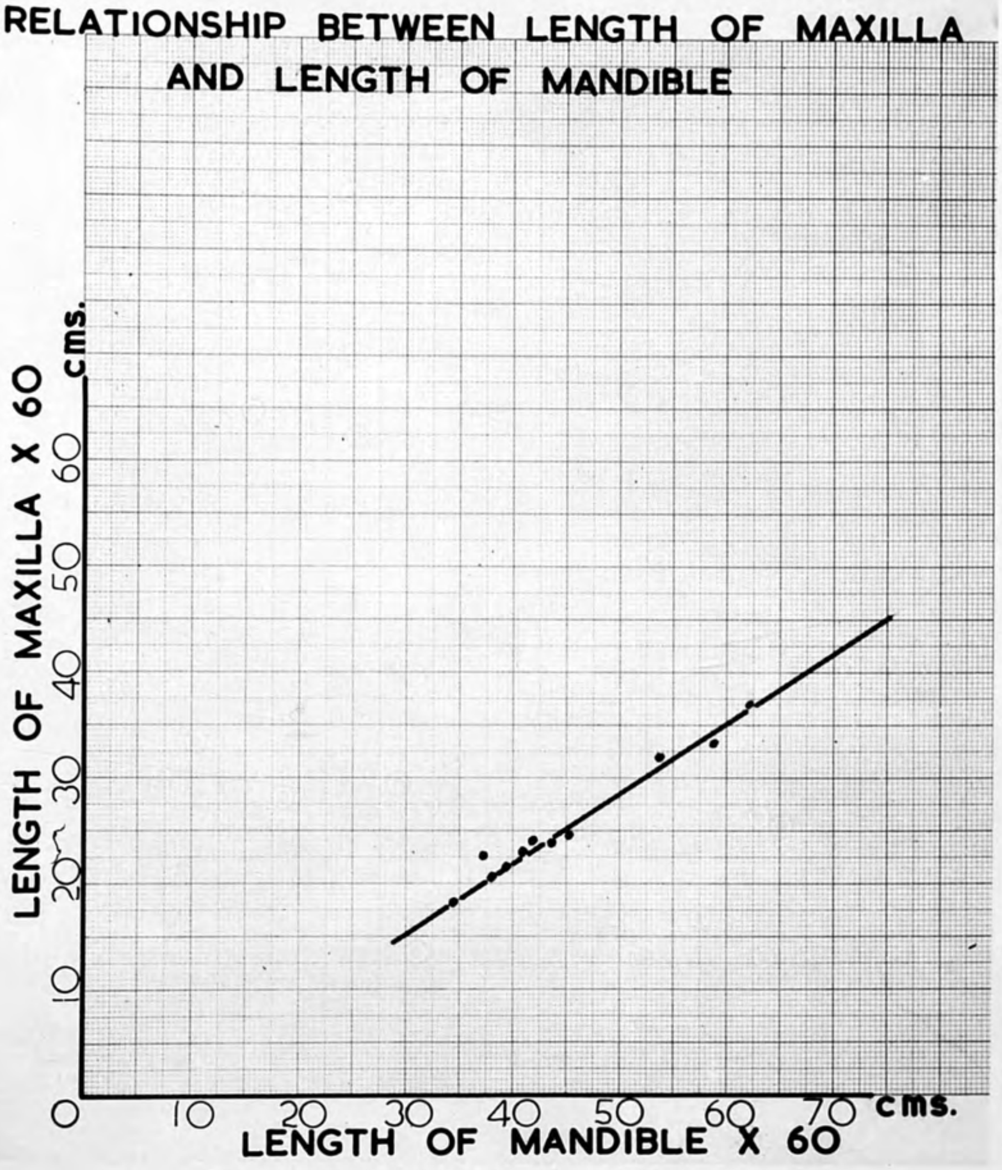

RELATIONSHIP BETWEEN LENGTH OF MAXILLA AND LENGTH OF MANDIBLE
LENGTH OF MAXILLA X 60
cms.
0
10
20
30
40
50
60
70
cms.
LENGTH OF MANDIBLE X 60

FIGURE 61 Mn-length is taken as the criterian for age.

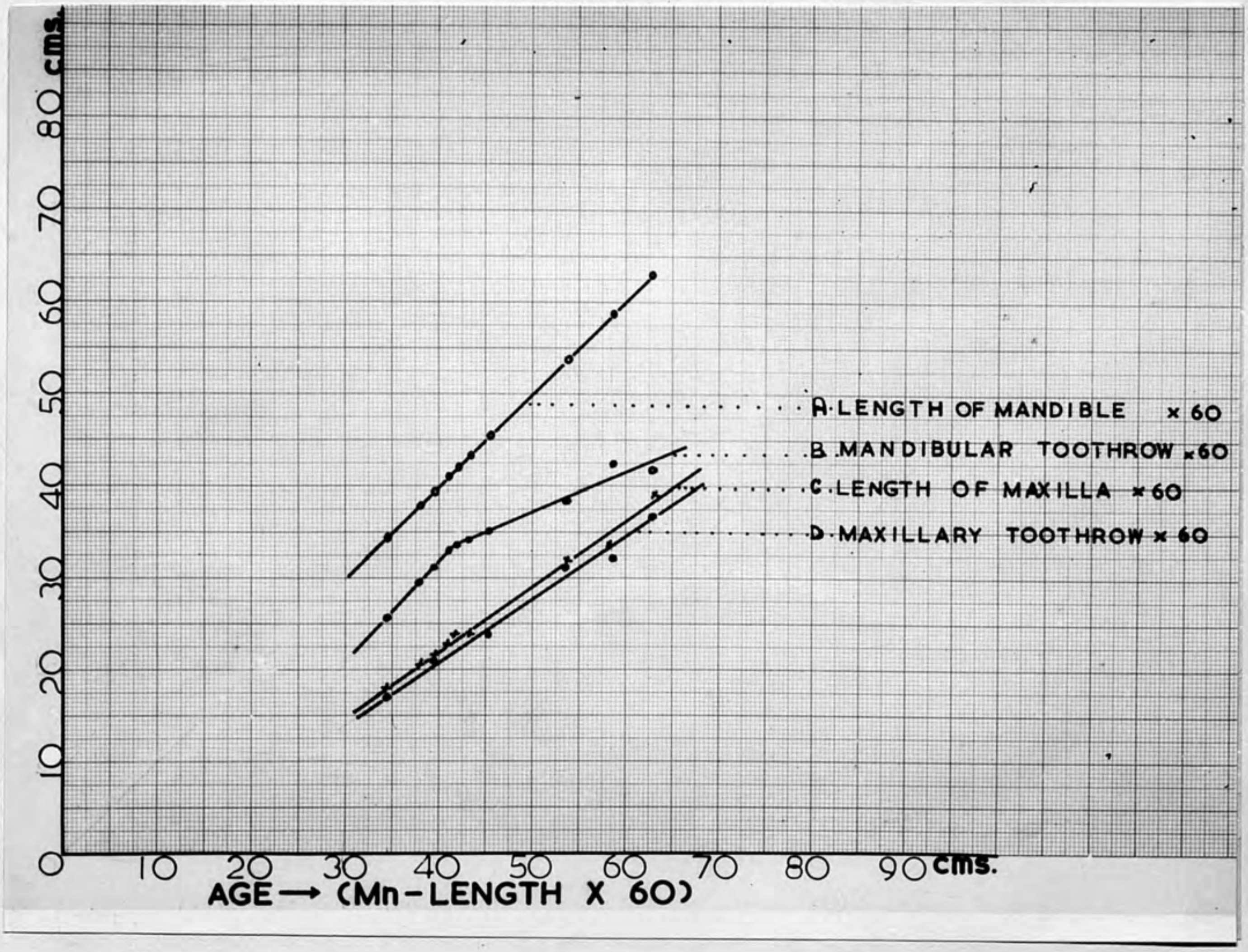
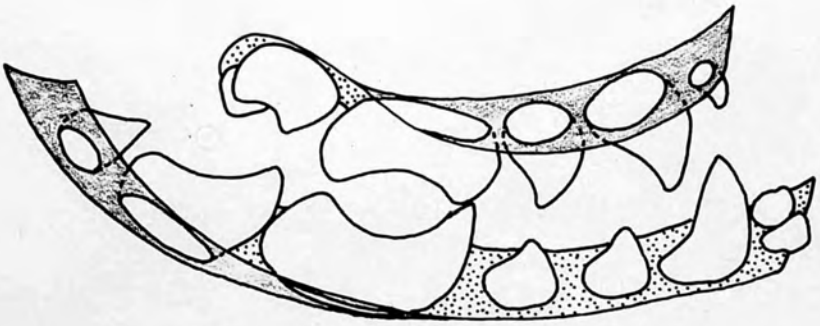


FIGURE 62

DIAGRAMMATIC REPRESENTATION OF THE TOOTHROWS IN SITU SIDE VIEW

EARLY STAGE



LATE STAGE OF DEVELOPMENT