

ODONTOGRAPHY;

OR, A

TREATISE

ON THE

COMPARATIVE ANATOMY OF THE TEETH;

THEIR PHYSIOLOGICAL RELATIONS, MODE OF DEVELOPMENT,

AND

MICROSCOPIC STRUCTURE,

IN THE

VERTEBRATE ANIMALS.

BY RICHARD OWEN, F.R.S.

CORRESPONDENT OF THE ROYAL ACADEMY OF SCIENCES OF PARIS, BERLIN, &c. &c., HUNTERIAN PROFESSOR TO THE
ROYAL COLLEGE OF SURGEONS, LONDON.

VOLUME I.

TEXT.

LONDON:

HIPPOLYTE BAILLIÈRE, PUBLISHER,

FOREIGN BOOKSELLER TO THE ROYAL COLLEGE OF SURGEONS.

219, REGENT STREET.

PARIS: J. B. BAILLIÈRE LIBRAIRE DE L'ACADÉMIE DE MÉDECINE.

LEIPZIG: T. O. WEIGEL.

1840—1845.

PART III.

DENTAL SYSTEM OF MAMMALS.

CHAPTER I.

GENERAL CHARACTERS OF THE TEETH OF MAMMALS.

124. The class *Mammalia*, like that of *Pisces* and *Reptilia*, includes a few species which are entirely devoid of teeth; these are the Ant-eaters, forming, when clothed with hair, the genus *Myrmecophaga*; when defended by scales, the genus *Manis*; and when armed with spines, the genus *Echidna*. A few Mammals have the jaws provided with horny substitutes for teeth, as the Whalebone-whales (*Balæna* and *Balænoptera*), and the Ornithorhynchus; in the rest of the class true teeth are present. In the Feline tribe the epithelium of the tongue is thickened at the fore-part of its dorsum, and invests the papillæ there with hard sheaths, like prickles, which are analogous to the lingual teeth of certain Fishes and Batrachians. The back part of the dorsum of the tongue in the *Echidna* is provided with a plate of horny denticles, which bruise its food against the hard and prickly epithelium covering the palate. Horny processes, analogous to the palatal teeth of Fishes and Reptiles, are likewise developed upon the roof of the mouth of the great Bottle-nose Dolphin, thence termed *Hyperoodon* by Lacépède.

125. *Number*.—In the last-named Cetacean, the true teeth are two in number, whence its specific name, *bidens*: the Narwhal likewise has but two teeth, both of which are concealed in the substance of the jaws in the female, whilst only one is ordinarily visible in the male: but this grows to an unusual length. The *Delphinus griseus* has five teeth on each side of the lower jaw; but they soon become reduced to two on each side. Amongst the Marsupial

animals, the genus *Tarsipes* is remarkable for the paucity as well as minuteness of its teeth. The Elephant has never more than one entire molar, or parts of two, in use on each side of the upper and lower jaws, to which are added two tusks, more or less developed in the intermaxillary bones. Some Rodents, as the Australian Water-rats, (*Hydromys*), have two grinders on each side of both jaws; which, added to the four cutting teeth in front, make twelve in all: the common number of teeth in this order is twenty; but the Hares and Rabbits have twenty-eight teeth. The Sloth has eighteen teeth. The number of teeth, thirty-two, which characterises Man, the Apes of the old world, and the true Ruminants is the average one of the Class *Mammalia*. The examples of excessive number of teeth are presented, in the order *Bruta*, by the Priodont Armadillo, which has ninety-eight teeth; and, in the Cetaceous Order, by the Cachalot, which has upwards of sixty teeth, though most of them are confined to the lower jaw,—by the common Porpoise, which has between eighty and ninety teeth,—by the Gangetic Dolphin, which has one hundred and twenty teeth, and by the true Dolphins (*Delphinus*), which have from one hundred to one hundred and ninety teeth, yielding the maximum number in the class *Mammalia*.

126. *Form*.—Where the teeth are in excessive number, as in the species above cited, they are small, equal, or sub-equal, and of a simple conical form: pointed and slightly recurved in the common Dolphin; with a broad and flattened base in the gangetic Dolphin (*Inia*); with the crown compressed, and broadest in the Porpoise; compressed, but truncate, and equal with the fang in the Priodon. The simple dentition of the smaller Armadillos, of the Orycterope, and of the three-toed Sloth presents a difference in the size, but little variety in the shape of the teeth, which are sub-cylindrical with broad triturating surfaces: in the two-toed Sloth, the two anterior teeth of the upper jaw are longer and larger than the rest, and adapted for piercing and tearing. In almost all the other *Mammalia* particular teeth have special forms for special uses; thus, the front-teeth, from being commonly adapted to effect the first coarse division of the food, have been called cutters or incisors, and

the back-teeth which complete its comminution, grinders or molars ; large conical teeth, situated behind the incisors, and adapted by being nearer the insertion of the biting-muscles to act with greater force, are called holders, tearers, laniaries, or more commonly canine teeth, from being well developed in the Dog and other Carnivora, although they are given, likewise, to many vegetable feeders, for defence or combat.

The names 'incisors,' 'laniaries,' 'molars,' are not, however, always indicative of the shape of the crowns of the teeth which occupy the relative positions above mentioned. In some Carnivora, for example, the front teeth have broad tuberculate summits adapted for nipping and bruising, while the principal back teeth are as admirably shaped for cutting, and work upon each other like the blades of shears. The front teeth in the Elephant project, from the upper jaw, in the form and direction of long pointed horns ; in the extinct Dinotherium the lower incisors had a similar form and development, but were bent down from the end of the jaw. Hence, therefore, shape alone has been found insufficient to characterize the analogous teeth in the Mammalia, and it has been necessary to consider the position, and also the mode of succession of the teeth, in order to their definition and classification.

Comparative Anatomists, by common consent, now apply the term '*incisor*,' arbitrarily, to those teeth which are implanted in the intermaxillary bones and in the corresponding part of the lower jaw. When the tooth which succeeds the incisors, or the first of the upper maxillary bone, is conical, pointed, and longer than the rest, it is called a *canine*, as is also its analogue in the lower jaw, which always passes in front of it when the mouth is closed. Of the remaining teeth, those which are shed and replaced vertically, or which have successors descending into their place in the upper, and ascending in the lower jaw, are called '*premolars*,' or false molars, and in Human Anatomy '*bicuspides*' ; the remaining teeth, which are not displaced by vertical successors, but which follow each other from behind forwards, in both jaws, are called *molars*, or true molars.

Naturalists have availed themselves of the degree of constancy

with which the foregoing kinds of teeth are recognizable in the Mammalian genera, to indicate them by an abbreviated formula of the initial letters, or first syllables of their respective denominations; thus, *I* or *in.* signifies incisor; *c* or *can.* canine; *p* or *prem.* premolar; *m* or *mol.* molar: succeeding numerals, according to their relative position to added lines, give the number of these several kinds of teeth on the right and left sides of the upper and lower jaws. For example, the dental formula of the genus *Homo* is:—

$$\text{Incisors } \frac{2-2}{2-2}; \text{ canines } \frac{1-1}{1-1}; \text{ premolars } \frac{2-2}{2-2}; \text{ molars } \frac{3-3}{3-3}: = 32.$$

which expresses that, on each side of both upper and lower jaws, there are two incisors, one canine, two premolars, and three true molars; thirty-two in all.

The last upper premolar and the first lower true molar in the Carnivora are termed, from their peculiar form, 'sectorial' or 'carnassial' teeth, 'molaires carnassières' of Cuvier. Teeth of an elongated conical form, projecting considerably beyond the rest, and of uninterrupted growth are called 'tusks;' such are the incisors of the Elephant and Dugong, the canines of the Boar and Walrus: the long and large incisors of the Rodents have been termed from the shape and structure of their cutting edge, scalpriform or chisel-teeth, 'dentes scalprarii.' The inferior incisors of the Flying Lemurs, (*Galeopithecus*), have the crown deeply notched, like a comb, and are termed 'dentes pectinati.' The canines of the Baboons are deeply grooved in front, like the poison-fangs of some serpents. The compressed conical crowns of the molar-teeth of the small-clawed Seals, (*Stenorhynchus*), are divided either like a trident, into three sharp points, or like a saw, into four or five points, 'dentes serrati.' Molar teeth, which are adapted for mastication, have either tuberculate, or transversely ridged, or flat summits, and usually are either surrounded by a ridge of enamel, or are traversed by similar ridges arranged in various patterns. Certain molars in the Dugong, the Mylodon and the Zeuglodon, are so deeply indented laterally by opposite longitudinal grooves, as to appear to be composed of two cylindrical teeth cemented together, and the transverse section of the crown is bilobed. The teeth of the Glyptodon were fluted by two analogous grooves on each side. The large molars

of the Capybara and Elephant have the crown cleft into a numerous series of compressed transverse plates, cemented together side by side.

The ordinary teeth of the Mammalia have so much more definite and complex a form, than those of Fishes and Reptiles, that three parts are usually recognized in them, viz., the fang, the neck, and the crown. The fang or root (*radix*) is the inserted part, the crown (*corona*), the exposed part, and the constriction which divides these is called the neck, or *cervix*. The term, 'fang,' is properly given only to the implanted part of a tooth of restricted growth, which gradually tapers to its extremity; those teeth which grow uninterruptedly have not their exposed part separated by a neck from their implanted part, and this generally maintains to its extremity the same shape and size as the exposed crown.

It is peculiar to the class Mammalia to have teeth implanted in sockets by two or more fangs; but this can only happen to teeth of limited growth, and generally characterizes the molars and premolars.

127. *Attachment*.—In no mammiferous animal does ankylosis of the tooth with the jaw constitute a normal mode of attachment. Each tooth has its particular socket, to which it firmly adheres by the close co-adaptation of their opposed surfaces, and by the firm adhesion of the alveolar periosteum to the organized cement, which invests the fang or fangs of the tooth: but in some of the *Cetacea*, at the posterior part of the dental series, the sockets are wide and shallow, and the teeth adhere more strongly to the gum than to the periosteum: in the Cachalot I have seen all the teeth brought away with the ligamentous gum, when it has been stript from the sockets of the lower jaw.

True teeth implanted in sockets are confined, in the present class, to the maxillary, intermaxillary, and lower maxillary bones, and to a single row in each. They may project only from the intermaxillary bones as in the Narwhal; be apparent only in the lower maxillary bone, as in the Cachalot; or be limited to the superior and inferior maxillaries, and not present in the intermaxillaries, as in the true *Pecora*, and most *Bruta* of Linnæus; in general, teeth are situated in all the bones above mentioned. In Man, where the intermaxillaries early coalesce with the maxillary bones, where the jaws

are very short, and the crowns of the teeth are of equal length, there is no interspace or 'diastema' in the dental series of either jaw, and the teeth derive some additional fixity by their close apposition and mutual pressure. No inferior Mammal now presents this character; but its importance, as associated with the peculiar attributes of human organization, has been somewhat diminished by Cuvier's discovery of a like contiguous arrangement of the teeth in the jaws of the extinct *Anoplotherium*.

128. *Substance*.—The teeth of the Mammalia usually consist of hard or unvascular dentine, defended at the crown with an investment of enamel, and everywhere surrounded by a coat of cement. The coronal cement is of extreme tenuity in Man, Quadrumana and terrestrial Carnivora; it is thicker in the Herbivora, especially in the complex grinders of the Elephant, and is thickest in the teeth of the Sloths, Megatherioids, Morse, and Cachalot. Vertical folds of enamel and cement penetrate the crown of the tooth in the Ruminants, and in most Rodents, and Pachyderms, characterizing by their various forms the genera of the two last orders: but these folds never converge from equidistant points of the circumference of the crown towards its centre. The teeth of the quadrupeds of the order *Bruta*, (*Edentata*, Cuv.), have no true enamel; this is absent, likewise, in the molars of the Dugong, the Zeuglodon and the Cachalot.(1) The tusks of the Narwhal, Walrus, Elephant, Mastodon, and Dinotherium, consist of modified dentine, which, in the large proboscidian animals, is properly called 'ivory,'(2) and is covered by cement.

The central part of the fully-formed tooth in man and most other animals contains an irregular kind of osseous substance, which is most abundant in the Cachalot,(3) and forms around foreign bodies which may gain admission to the pulp-cavity of tusks. A fifth substance which, from the number and regular position of the vascular canals

(1) M. Fr. Cuvier divides the teeth of Mammalia, according to their composition, into four classes: the first consist of ivory, (dentine), enamel and cement; the second of ivory and enamel; the third of ivory and cement; the fourth of ivory only. '*Dents des Mammifères*,' p. xxi. I have met with no Mammalian teeth, in which cement is absent, and believe that the second and fourth of the above-cited classes of teeth, have no existence in Nature.

(2) "*Hoc solum est ebur*," Plinius, Hist. Nat. lib. xi. c. 37.

(3) Pl. 89, fig. 2, c.

in it, I have termed the 'vascular dentine,' forms the body or axis of the tooth in the Sloth-tribe,(1) and is present in smaller proportion in the centre of the teeth of the Armadillos. The teeth of the *Orycteropus* consist of congeries of long and slender prismatic columnar denticles, each consisting of a body of dentine, with a coating of cement, by which they are united together to form a composite tooth, as in some of the Cartilaginous Fishes.

129. *Structure*.—In most Mammals the body of the tooth consists of a gelatinous animal basis and calcareous earth, combined and arranged according to the plan which characterizes the tissue called "unvascular dentine." (2) The compartments of the basal substance, which I have called 'calcigerous' or 'dental cells,' and which contain the hardening salts in their densest state, are sub-circular (Pl. 95), or sub-hexagonal (Pl. 70). The calcigerous and nutrient tubes varying from $\frac{1}{10,000}$ to $\frac{1}{20,000}$ th of an inch in diameter, and placed with intervals equal to from two to six of their own diameters, proceed, at first with strong, and then with gentle curves from the pulp-cavity to the outer surface of the dentine, their general direction being always more or less nearly at right angles to that surface: those tubes which proceed from the apex, and from the basal third-part of the pulp-cavity are the straightest. They are nearly parallel to one another, both in their general course and curvatures; but, as the outer surface of the tooth exceeds the inner one in extent, the tubes slightly diverge in their course and divide, decreasing in diameter to their peripheral extremities, and rapidly so near their termination where they become irregularly flexuous and often interlaced. The dichotomizing calcigerous tubes send off from their sides much more minute branches, which quickly divide and sub-divide in the interspaces of the trunks, and penetrate the dental cells. In the unvascular dentine of all Mammalian teeth the tubes present the "primary curvatures," and "secondary gyrations" described in the Introduction.(3) These curvatures are strongest and least regular in the dentine of the Elephant's grinders. In that of the tusks of the Elephant and Mastodon, the form, extent, and parallelism of the secondary curvatures of the dental tubes, cause the peculiar appearance of the decussation of curved lines, like the ornamental work called

(1) Pl. 82, fig. 1.

(2) Introduction, p. iii, & iv.

(3) P. xvi.

'engine-turning,' upon the surface of transverse or oblique sections or fractures of the tusk, which is characteristic of true 'ivory.'

In the incisors of certain Rodents, and in the molars of the Sloths and Megatherioids, or the large extinct phyllophagous *Bruta*, more or less of the dentine is modified by the persistence of certain tracts of the pulp-cavity, forming vascular or medullary canals; the characters of this "vascular dentine" will be described in the sections devoted to the dentition of the species possessing it.

The dentine of the long and slender prismatic denticles which are aggregated to form the compound tooth of the *Orycterope*(1) is unvascular, and is characterized chiefly by the frequent division and wide angles at which the branches of the bifurcating calcigerous tubes diverge, before resolving themselves into their minute wavy terminations.

The cement, which, with the dentine, is present in all teeth of mammalian animals, is characterized, except where it forms an extremely thin layer, by the radiated calcigerous cells.(2) These are usually arranged in lines or layers parallel with the surface of the cæmental coat and with each other; they average a diameter of $\frac{1}{1000}$ th of an inch in Man; they are rather smaller in the true Carnivora; proportionally larger in some of the Pachyderms; but present their most minute size in some of the Ruminants, as the Giraffe and Ox. The radiated forms of these cells arises from the numerous minute tubes continued from or opening in them, and which are analogous to the more parallel calcigerous tubes of the dentine, with which they communicate.

In the thick radical cement of the Seal's teeth, and in both the radical and coronal cement of the teeth of most Herbivora, very conspicuous vascular canals are present in addition to the calcigerous tubes and cells. These canals in the cement of the molars of the *Megatherium* are numerous and constant, take a course parallel with each other and transverse to the outer plane of the cement, and anastomose by loops close to the dentine, towards which the convexity of the loops is directed.(3)

(1) Pl. 78.

(2) *Corpuscula Purkingii*.

(3) Pl. 84, b, b.

The structure of the enamel presents fewer varieties than in the lower classes of Vertebrata, and in all the Mammalian genera in which it exists, it manifests its most distinctive and elaborate condition. It consists of more or less curved or wavy prismatic fibres, averaging about $\frac{1}{4000}$ th of an inch in diameter, and having a general direction vertical to the plane of the dentine; some of the fibres extend through the thickness of the enamel, others are shorter and are wedged in their interspaces; the fibres of the thick enamel of the molars of the large Pachyderms are most curved and interwoven; they are so arranged, however, as always to have one end directed towards the outer surface of the tooth, and the other end to that by which the enamel is attached to the dentine: the outer, or peripheral end of the fibre is sensibly larger than the inner one. In Man and Quadrumana the fibres are transversely striated: I have not detected this character in the Herbivorous Quadrupeds. The fine horizontal lines on the exterior surface of the enamel(1) are usually most conspicuous in the teeth of Mammals.

130. *Development*.—The teeth in this, as in the foregoing classes, are formed by superaddition of the hardening salts to pre-existing moulds of animal pulp or membrane, organized so as to insure the arrangement of the earthly particles according to that pattern which characterizes each constituent texture of the tooth. The complexity of the primordial basis, or matrix, corresponds, therefore, with that of the fully-formed tooth, and is least remarkable in those conical teeth which consist only of dentine and cement. The primary pulp, which first appears as a papilla rising from the free surface of the alveolar gum, is the part of the matrix which by its calcification constitutes the dentine; it sinks into a cell and becomes surrounded by a closed capsule, in every Mammiferous species, at an early stage of the formation of the tooth; and, as the cement is the result of the ossification of the capsule, every tooth must be covered by a layer of that substance. In those teeth which possess enamel, the mould or pulp of that constituent is developed

(1) Introduction, p. xxvi.

211. *Microscopic Structure*.—The body of the long molar teeth of the Horse consists of columns of fine-tubed unvascular dentine (Pl. 137, *a*), coated by enamel (*b*) which descends in deep folds into the substance of these teeth; the enamel is covered by cement (*c*), thickest in the interspaces of the inflected enamel-folds and upon the crowns of the molars, where it is permeated by vascular canals, thinnest on the crowns of the canines and incisors. At the roots of these teeth, and on those developed from the worn down molars, the dentine is immediately invested by cement.

In a vertical section of the incisor, as in Pl. 136, fig. 11, the pulp-cavity, contracting as it approaches the vertical enamel-fold, divides near the end of that fold, and extends a little way between it and the periphery of the incisor, or leaves a few medullary canals and a modified thin tract of irregularly formed dentine, between the reflected and the outer coat of enamel but rather nearer the former. Above this tract, near the summit of the crown, the dentinal tubes proceed in a nearly vertical direction, with a gentle sigmoid primary flexure, where they diverge from the perpendicular; lower down the dentinal tubes diverge in opposite directions, curving from the remains of the pulp-fissure towards the outer and the inner enamel; and are described by Retzius as being bent in the form of the Greek ϵ (1); but the course of two distinct series of dentinal tubes, and not that of a single tube is illustrated by this comparison; when the pulp-cavity becomes single and central, as at the lower half of the tooth, the tubes diverge to the periphery, with one principal primary curve, convex towards the crown. Each tube is bent in minute secondary gyrations to within a short distance of its peripheral termination, where it is much diminished in size, and is dichotomously branched. The tubes at their commencement from the upper calcified tracts of the pulp-cavity, which usually retain some remnants of that vascular receptacle in the form of medullary canals, are strongly and irregularly flexuous, before they fall into the ordinary primary curves. Those tubes proceeding towards the inner reflected fold of enamel, are more vertical than the tubes going to the periphery.

(1) Loc. cit. p. 27.

A transverse section of the incisor of a young Horse or Ass taken across the part marked *a* in fig. 11, shows a long oval island of vascular cement in the centre, bounded by a border of enamel, with an irregular crenate edge next the cement, and an even edge next the dentine; which is here clearly seen to be divided into an inner and an outer tract by an irregular series of the vascular canals continued from the summit of the pulp-cavity, and by the irregularly tortuous dentinal tubes which, with the canals, indicate the last converted remnant of the pulp in this part of the crown. The inner tract of dentine next the island of enamel is well defined, and a little broader than the section of the enamel itself, and shows the extremities of the tubes cut transversely across, which tubes, as before observed, were at this part directed chiefly in the axis of the incisor towards the working surface of the crown. The tubes in the outer tract of dentine, inclining more towards the sides of the tooth, are more obliquely divided and at the ends of the section they are seen lengthwise elegantly diverging towards the sides of the section. This tract of dentine is bounded externally by a layer of enamel, one sixth part thicker than that forming the central island; and the enamel is coated by an outer layer of cement, of its own thickness at the sides, but thinning off at the two ends of the section. The dentinal tubes proceeding from the residuary pulp-tract make strong and irregular curvatures, diverging to include the divided area of the vascular canals, and in the outer layer at one side of the section, they describe strong zig-zag curves at the middle of the outer division of the dentine.

The diameter of the dentinal tubes at their central and larger ends is pretty regularly, about $\frac{1}{6000}$ th of an inch; at the middle of their course $\frac{1}{8000}$ th of an inch; thence decreasing, and very rapidly after the terminal bifurcations commence.

The dentinal tubes are separated from one another by intervals varying between once and twice the thickness of the tubes; in some parts of the dentine of the incisor they are more closely crowded together, especially near their origin from the pulp-cavity. The secondary gyrations of the dentinal tubes describe a curve about $\frac{1}{1500}$ th of an inch in length; these subside in the slender terminations

of the tubes, which bifurcate dichotomously once or twice, and send off small lateral branches near the enamel. The small lateral branches are chiefly visible in the peripheral third part of the tubes, and are sent off at very acute angles, except in the strongly and irregularly bent origins from the pulp-tract. I have never seen these small branches of the dentinal tubes terminating in radiated cells like those of cement and bone, as Retzius describes, (*loc. cit.* p. 27), and figures (Tab. V, fig. 3); but the peripheral smallest branches near the enamel occasionally dilate into corpuscles much more minute than the radiated cells, as they do in the teeth of most quadrupeds. The dentine, as seen in a longitudinal section of the crown of a molar, by a magnifying power of three hundred linear dimensions is figured at *a*, Pl. 137. The tubes are here separated by rather wider interspaces than those of the incisor, and do not decrease in size so rapidly: the convexity of the terminal bend of the tubes is turned towards the summit of the crown.

The clear dentinal cells are very small near the peripheral part of the dentine in the incisor, but increase in size as they approach the pulp-cavity: they are of a sub-circular figure, with bright transparent outlines.

The central cement in the crown of the incisor is permeated by vascular canals, separated by intervals of from two to three times their own diameter, directed in the middle of the substance in the axis of the tooth, but diverging like rays obliquely towards its periphery: the clear substance forming the walls of the canals is arranged in concentric layers; the thickness of the wall being about equal or rather less than the area of the canal. The radiated cells, generally of a full oval, sometimes of an angular form, are chiefly dispersed in the interspaces of the vascular canals, and with their long axis parallel with the plane of the layers of the coats. The finer system of tubes radiating from the cells, and corresponding by minute branches from the vascular canals, freely intercommunicate. In the peripheral cement of the incisors examined by me, I found no vascular canals, but only the radiated cells, and the fine tubuli which I have called 'cemental', and which traverse the cement at right angles to its plane, and communicate with the

tubes radiating from the cells. These are more usually elliptical than in the thicker central cement, their long axis being parallel with the borders of the cement; they are most abundant next the enamel and rarely encroach upon the clear peripheral border of the cement. The exterior coronal cement of the molars (Pl. 137, c,) is as richly permeated by vascular canals (*v*) as is the central cement of the incisor.

The enamel-fibres of the Horse's incisor are very slender, not exceeding twice the diameter of the dentinal tubes: they extend with a gentle sigmoid curve through the entire thickness of the layer; contiguous fibres curving in opposite directions. The peripheral border, or that next the cement, is everywhere indented with hemispherical pits from $\frac{1}{500}$ th to $\frac{1}{2000}$ th of an inch in diameter, four to six of the radiated cells of the cement being often clustered together in the larger depressions. The inner or dentinal border of enamel is nearly even and straight; here are seen the short cracks or fissures extending into the enamel. The fibres are rather more wavy in the thicker enamel of the molar teeth (Pl. 137, b)

If the enamel is viewed in sufficiently thin sections, it is free from those wavy dusky markings which are produced by the more tortuous fibres of the human enamel; and I have been unable to distinguish any transverse striæ in the fine fibres of that tissue in the Horse: the appearance of such is given by thicker sections of the enamel-fibres taken obliquely across them, and is produced by the cut ends of the fibres.

I may here briefly describe a very rare diseased state, which I have met with in a fossil molar tooth of a large-sized Horse, from the tertiary formations near Cromer. The tooth, which was from the lower jaw, with a grinding surface measuring one inch five lines in long (antero posterior) diameter, and eight lines in short (transverse) diameter, presented a swelling of one lobe, near the base of the implanted part of the tooth. To ascertain the nature and cause of this enlargement, I divided it transversely, and exposed a nearly spherical cavity, large enough to contain a pistol-ball, with a smooth inner surface. The parieties of this cavity, composed of dentine and enamel of the natural structure, were from one to

two lines and a half thick and were entire and imperforate. The water percolating the stratum in which this tooth had lain, had found access to the cavity through the porous texture of its walls, and had deposited on its interior a thin ferruginous crust, but the cavity had evidently been the result of some inflammatory and ulcerative process in the original formative pulp of the tooth, very analogous to the disease called 'spina ventosa' in bone. I have given two figures of this singular case of primæval disease in my "History of British Fossil Mammalia."

212. *Succession*.—The practical inducements to pay attention to the times of cutting and shedding the teeth have operated more strongly in the case of the Horse than in that of the domestic Ruminants, and have led to more numerous and persevering researches on the development and succession of the teeth. The deciduous formula of the genus *Equus* is:—

$$in. \frac{3-3}{3-3}; c. \frac{1-1}{1-1}; m. \frac{4-4}{4-4}: 32.$$

The second molar ('first grinder' of Veterinary Authors, *d m*, fig. 4, Pl. 136) is the first to pierce the gum: the white summits of the ridges of the crown are usually apparent at birth, but sometimes the gums do not yield until from the second to the fifth day; the third molar ('second grinder', fig. 5, *d 3*) rises a day or two later, often simultaneously with the proceeding: their appearance is speedily followed by that of the first incisor ('centre nipper', fig. 4, *di 1*), which usually cuts the gum between the third and sixth days. The second incisor (*di 2*) appears between the twentieth and fortieth days, and about this time the first small deciduous premolar (fig. 4, *p. 1*) takes its place, and the fourth deciduous molar ('third grinder', fig. 5, *d 4*) also begins to cut the gum. About the sixth month the inferior lateral or third incisors, (fig. 4, *di 3*) make their appearance together with the small deciduous canine (fig. 4, *d c.*) This minute tooth is shed, in the lower jaw at least, almost as soon as the crown of the contiguous incisor is in full place, being carried out by the same movement; whence the small canine had almost escaped notice until Bojanus drew the attention of veterinary authors to it by his memoir, 'De dentibus caninis

caducis', &c.(1) Bojanus never found the lower deciduous canine retained beyond the first year. The deciduous canine of the upper jaw, being developed at a short distance behind the incisors, in the maxillary bone, is less disturbed by the eruption of the outer incisor, but is nevertheless shed in the course of the second year. The deciduous canines appear from Camper's observations, to retain their place longer in the Zebra than in the Horse.(2)

M. Rousseau, who describes the first dentition as being terminated by the appearance of the lateral incisors, assigns from the seventh to the tenth month as the period of its completion.(3) The deciduous incisors have thinner and more trenchant, normally-shaped crowns than those of their permanent successors. The first true permanent molar (fig. 5, *m* 1) appears between the eleventh and thirteenth months. The second true molar (ib. *m* 2) follows between the fourteenth and twentieth month. The crowns of the premolars and the last true molar are now advancing in the closed sockets of reserve, as shown in Pl. 136, fig. 5. The first premolar (*p* 2) (essentially answering, as in the Ruminants, to the second of the Anoplothere), displaces the second (*d* 2) and, usually at the same time, the first very small deciduous molar, at from two years to two years and a half old. The first permanent incisor (fig. 6, *i* 1) rises above the gum between two years and a half and three years. At the same period the second premolar (ib. & fig. 5, *p*. 3) pushes out the third deciduous molar (*d* 3). The last premolar (ib. *p*. 4) displaces the last deciduous molar (ib. *d* 4) about the completion of the fourth year, and the appearance above the gum of the last true molar (ib. *m* 3) is usually anterior to this. Figure 6 shows the state of the dentition about this period, and should the last deciduous molar (*d* 4) have been prematurely drawn, the position of the crown of its

(1) Nova Acta Nat. Cur., tom. XII, pt. ii, 1825. p. 697. The tooth which M. Rousseau figures in his 'Anatomie Comparée du Système Dentaire,' Pl. xxv, fig. 2, as the "crochet caduc de lait," in a Horse about three years old, appears rather to be the small canine of a Mare. Compare with fig. 8, Pl. 26, of the same work, where no trace of the 'crochets caducs,' appears in a Horse of two years old.

(2) Œuvres de Pierre Camper, Paris, 1805.

(3) The appearance of the third deciduous incisors, or 'corner nippers', completes the stage of dentition called the 'colt's mouth' by Veterinary Authors.

successor below the level of the second and fourth of the large grinders, and especially the non-development of the last grinder will betray the fact that the young Horse has not passed his third year. The incisors give evidence with which it is still more difficult to tamper without detection. The first permanent incisor as above stated, takes its place before the end of the third year; and should its growth have been accelerated by extraction of its predecessor the strong 'mark' on the third deciduous incisor will indicate the deception. The second incisor (fig. 6, i 2) pushes out its predecessor between three and a half and four years. The small persistent canine, or 'tusk' contrary to the usual rule, next follows, its development having received no check by the retention of its rudimental predecessor: its appearance indicates the age of four years; but it sometimes makes its appearance earlier, rarely later. The third incisor pushes out the deciduous one about the fifth year, but is seldom completely in place before the Horse is five years and a half old.(1) The third premolar is then usually on a level with the other grinders.

213. *Toxodon*.—This extinct genus of large pachydermal Quadrupeds is represented by two species, both equalling the Hippopotamus in size, whose remains have been discovered by Mr. Darwin and M. de Angelis in the recent tertiary deposits of South America. In both, the teeth consist of molars and incisors, separated by a long diastema, or toothless space. In the upper jaw the molars are *fourteen* in number, there being *seven* on each side; the incisors *four*, which differ in their proportions in the two species. In the *Toxodon platensis* the outer or second incisor is very large, and the inner one small, in each intermaxillary bone. In the lower jaw there are *six* incisors and *twelve* molars.

The general form and nature of the teeth are indicated by the sockets, and the structure of the grinders is exhibited in a broken molar, the last in the series on the left side of the skull of the *Toxodon platensis*, discovered by Mr. Darwin; and by another perfect

(1) Upon the rising of the third permanent incisors or 'corner nippers' the 'colt' becomes a 'horse', and the 'filly' a 'mare', in the language of the dealers. For the subsequent changes in the character of the teeth, see the descriptions of the Plate 136.

molar, the last but one on the right side of the upper jaw. This tooth is curved, with the convexity turned outwards when lodged in the socket, contrary to the position of the superior curved molars in the Guinea-pig and Wombat. The outer surface of the tooth is traversed by two slight convex longitudinal risings: the inner side presents, anteriorly, a slightly concave surface, and posteriorly two prominent longitudinal convex ridges separated by a deep channel, which is flat at the bottom: a fold of enamel is continued from the anterior angle of this channel obliquely forwards half-way across the body of the tooth. The outer coat of enamel is interrupted at the anterior and posterior margins of the grinder. The form of the grinding surface of this molar is shewn in Pl. 86, fig. 4.

All the molar teeth are long and curved, and without fangs, as in the Wombat and most of the herbivorous species of the Rodent order: in those, however, with curved grinders, as the *Aperea*, or Guinea-pig, the concavity of the upper grinders is directed outward, the fangs of the teeth of the opposite sides diverging as they ascend in the sockets; but in the *Toxodon* the convexity of the upper grinders is outward, as in the Horse, but with so much greater curvature that the fangs converge and almost meet at the middle line of the palate, forming a series of arches, capable of resisting great pressure. It is this structure which suggested to me the generic term proposed for this most remarkable extinct Mammal.(1)

Of the upper incisors, the two small ones are situated in the middle of the front of the intermaxillaries, and the two large ones in close contiguity with the small incisors, which they greatly exceed in size. The sockets of the two large incisors extend backwards, in an arched form, preserving a uniform diameter, as far as the commencement of the alveoli of the molar teeth; the curve which they describe is the segment of a circle; the position, form, and extent of the sockets are such as are only found in those of the corresponding teeth of the Rodentia among existing Mammalia. The matrix, or formative pulp of the large incisors was lodged, as in the Rodentia, in close contiguity with the sockets of the anterior molars; and we are enabled to infer, from the form of the socket, notwithstanding the absence of

(1) Τόξον, *arcus*; ὀδούς, *Jens.* 'Zoology of the Beagle, Fossil Mammalia,' 4to. 1839, p. 16.

the teeth themselves, that the pulp was persistent, and that the growth of these incisors, like those of the Rodentia, continued throughout life. This condition, joined with the curvature of the socket, necessarily implies a constant wearing away of the crown of the tooth, by attrition against opposing incisors of a corresponding structure in the lower jaw : and as a corollary, we infer that the teeth in question had a partial coating of enamel, to produce a cutting edge, and were in fact, true *dentes scalprarii*. The number of incisors in the upper jaw of *Toxodon*,—four, instead of two—is not without its parallel in the Rodent order, the genus *Lepus* being characterized by a similar number of incisors, and of a similar relative size, but with a different relative position, the small incisors in the Hare and Rabbit being so placed immediately behind the large pair, as to receive the appulse of the single pair of incisors in the lower jaw. Since the sockets of the small mesial incisors of *Toxodon* gradually diminish in size as they penetrate the intermaxillary bones, we may infer that, like ordinary incisors, their growth was of limited duration, and their lodgment in the jaw effected by a single conical fang. The lower jaw of the *Toxodon platensis*, which was discovered at Bahia Blanca, in latitude 39°, on the east coast of South America, was remarkably compressed or narrow from side to side ; while the rami were of considerable depth, in order to give lodgment to the matrices and bases of grinders enjoying uninterrupted growth. The pulps of the six incisors of the lower jaw are arranged in a pretty regular semicircle, whose convexity is downwards ; the teeth themselves are directed forwards and curved upwards like the inferior incisors of the Rodentia. These incisors are nearly equal in size : they are all hollow at their base, and the indurated mineral substance impacted in their basal cavities well exhibits the form of the vascular pulps which originally occupied them : they have, likewise, a partial investment of enamel ; but though, in this respect, as well as in the curvature and perpetual growth, they resemble the ‘*dentes scalprarii*,’ of the Rodentia, they differ in having a prismatic figure, like the inferior incisors of the Sumatran Rhinoceros or the tusks of the Boar. Two of the sides, viz., those forming the anterior convex and mesial surfaces of the incisor, have a coating of

enamel about half a line in thickness, which terminates at the angles between these and the posterior or concave surface. From the relative position of the bases or roots, we may infer that they diverged from each other, like the incisors of the Horse, as they advanced forwards in order to bring their broadest cutting surface into line. That they were opposed to teeth of a corresponding structure in the upper jaw, is proved by their oblique chisel-like cutting edge.

The molar teeth in this mutilated lower jaw, like those in the upper jaw of the *Toxodon platensis*, had persistent pulps, as is proved by the conical cavity at their base: they consequently required a deep socket and a corresponding extent of jaw to form the sockets and protect the pulps. In order to economize space and to increase the power of resistance in the tooth, and perhaps also to diminish the effects of direct pressure on the highly vascular and sensible matrix, the molars and their sockets are curved, but in a less degree than those of the upper jaw. They correspond with the superior molars in the long antero-posterior diameter, in being small and simple at the anterior part of the jaw, and by increasing in magnitude and complexity as they are situated more posteriorly. They are, however, narrower from side to side, the *Toxodon* agreeing in this respect with most other large herbivorous Mammalia, the fixed surface for attrition in the upper jaw being from obvious principles more extensive than the opposed moveable surface in the lower jaw. In the first three teeth, which are premolars, the enamel is confined to the outer surface: in the last three or true molars a plate of enamel is also laid upon the middle of the inner surface, and sends one or two simple folds obliquely forwards into the substance of the tooth. (Pl. 145, fig. 3).

The first grinder in the lower jaw is of small size and simple structure. It is more curved than any of the other molars, and appears to have differed from the external incisor only in its more compressed form and vertical direction of growth: it is interesting, indeed, to find so gradual a transition, in structure, from molar to incisive teeth as this jaw presents; for the robust incisors may here be regarded as representing molars simplified by the greater deficiency of enamel,

and with a change in their direction. The second molar presents an increase in antero-posterior diameter and in length, and the enamel of the middle of the outer side makes a fold which penetrates a little way into the tooth; the cement covering the inner side is slightly concave and unbroken. The third molar presents an increase of dimensions in the same directions as the second; the enamel on the outer side of the tooth presents a similar fold. In the fourth, or first molar, besides a further increase of size and a corresponding but deeper fold of enamel on the external side and nearer the anterior part of the tooth, the grinding surface is rendered more complicated by the two folds of enamel entering the substance of the tooth from the distinct plate on the middle of the inner side: these folds divide the antero-posterior extent of the tooth into three nearly equal parts; they are both directed obliquely forwards, the hinder one goes half-way across the substance of the dentine. The fifth molar presents the same structure as the fourth, which it exceeds only slightly in size. The sixth molar has a much longer antero-posterior diameter, which measures two inches; but the lateral diameter is but slightly augmented; its structure resembles that of the fifth. The outer coat of enamel extends over half the anterior and posterior ends of the tooth.

The partial disposition of the enamel upon the molars of the *Toxodon* is peculiar to that genus; but the enamel is continued, as in other rootless teeth, to the open end of the implanted base; it is thinner than in the *Rhinoceros*. The unenamelled parts of the tooth are coated by a thin layer of cement. The entire body of the tooth is composed of compact dentine, the pulp-fissure which penetrates the middle of the lobes defined by the inflected folds of the enamel, extends from the apex of the open basal pulp-cavity to the grinding surface. The dentinal tubes are $\frac{1}{500}$ th of a line at their origin, and radiate in directions vertical to the superficies of the tooth, and of the inflected enamel-folds, and are but little inclined upwards from the horizontal plane. They maintain their original diameter, and their relative distance from each other, viz. $\frac{1}{200}$ th of a line, to near their peripheral ends. The dentinal cells are sub-hexagonal, and about $\frac{1}{900}$ th of an inch in diameter in the peripheral part of the substance.

In the discontinuity of the enamel covering the molars, the *Toxodon* differs from all known Pachyderms, and manifests a slight approach to the *Bruta*.

214. *Elasmotherium*(1).—This name has been given to an extinct Pachyderm with rootless molars, surpassing the *Toxodon* in size, and of which only the lower jaw and its dentition are as yet known; but the characters of the teeth are sufficiently remarkable to call for notice here. The molar teeth of the *Elasmotherium* are five in number in each ramus of the jaw, the anterior one being very small; the penultimate one is the largest, measuring three inches in the antero-posterior diameter, and two inches in the transverse diameter of the crown. The enamel is remarkable for its beautiful undulating folds; but its general disposition most resembles that in the inferior molars of the Rhinoceros(2). The teeth of the *Elasmotherium* differ from those of the Rhinoceros, and resemble those of the Horse in the great depth to which they are implanted in the jaw, before being divided into roots: the socket of the penultimate grinder extends, in fact, to the lower margin of the jaw without any indication of partitions for the lodgment of fangs: there is no trace of incisive teeth in the portion of symphysis which is preserved, and which extends a little more than three inches in advance of the first small molar. The above account is taken from a cast and the description by Cuvier, in the 'Ossements Fossiles', 4to. tom. II. pt. i, p. 96. The original is preserved in the Museum of Moscow, and is unique; it was discovered in the frozen drift or diluvium of Siberia.

215. *Rhinocerotidæ*.—The present family of anisodactyle Pachyderms includes the typical *Rhinoceros*, the extinct *Acerotherium* which had no horn, and the equally hornless small existing genus *Hyrax*. The essential characteristics of the dentition of the genus *Rhinoceros* are to be found in the form and structure of the molar teeth. In the first place, they differ essentially from those of the Horse or *Elasmotherium* by being implanted by distinct roots. In the upper jaw the crown is

(1) ἔλασμα a plate, θηρίον beast: in allusion to the plicated plates of enamel in the substance of the molar teeth.

(2) Compare figure 12 in Plate 136, with p. 3, fig. 11 in Plate 138.

subcubical, and the grinding surface, when moderately worn, subquadrate, and penetrated by two folds or valleys of enamel: the principal valley (Pl. 138, fig. 5, *b*) commences at the middle of the inner side, and extends obliquely outwards and forwards towards the antero-external angle of the crown about two-thirds across, where it terminates, according to the species, in a more or less expanded, sometimes bilobed, cul de sac, (*e*): the second and shorter valley (*ib.* *c*) is usually of a triangular form, and indents more or less deeply the posterior border of the crown: in most Rhinoceroses this is wanting in the last molar, which has a trihedral conical crown: both valleys are usually deepest at their blind terminations: the outer surface of the crown is gently undulated by one of the convexities (*ib.* *o'*) being sometimes produced into a longitudinal ridge. In the lower jaw the molars (*ib.* fig. 9) have an oblong, laterally compressed crown, divided into two crescentic lobes, placed obliquely, with their convexities (*o o*) outwards and a little backwards; the anterior horn of the hinder crescent, before it is worn down, abuts against the middle of the convexity and below the upper margin of the crescent in front.

The normal formula of the molar series is:— $p. \frac{4-4}{4-4}, m. \frac{3-3}{3-3}: = 28$. There are no canines. As to the incisors, the species vary not only in regard to their form and proportions but also their existence; and in the varieties of these teeth we may discern the same inverse relation to the development of the horns which is manifested by the canines of the Ruminants. Thus, the two-horned Rhinoceroses of Africa, which are remarkable for the great length of one(1) or both(2) of the nasal weapons, have no incisors in their adult dentition (Pl. 138, fig. 2); neither had that great extinct two-horned species (*Rh. tichorhinus*), the prodigious development of whose horns is indicated by the singular modifications of the vomerine, nasal, and intermaxillary bones in relation to the firm support of those weapons.(3)

The Sumatran bicorn Rhinoceros, combines with comparatively

(1) *Rhinoceros bicornis*, *Rh. sinus*.

(2) *Rb. Keitloa*, Smith.

(3) These bones in the fossil skull of the species cited are confluent with each other, forming a solid obtuse termination to the upper jaw, and are ankylosed to a strong bony partition wall extending from the vomer to the anterior outlet of the nasal passages, and thus

small horns, moderately developed incisors in both jaws; and the same teeth are present in the nearly allied extinct two-horned *Rhinoceros* called after its discoverer Schleiermacher. The incisors are well developed in both the existing unicorn Rhinoceroses, *Rh. indicus* and *Rh. sondaicus*; but they attain their largest dimensions in the singular extinct hornless species, the *Rhinoceros incisivus* of Cuvier, which makes the transition to the extinct genus *Palæotherium*, and forms the type of the aberrant subgenus *Acerotherium* of Dr. Kaup: (Pl. 138, fig. 1). The normal incisive formula is:— $\frac{2}{2} \frac{1}{1} = 8$: the median pair being the largest above and the smallest below: in the existing species the smaller incisors are disproportionally minute, and usually have no permanent successors, or are soon shed: the larger incisors are preceded by deciduous teeth which they succeed and replace. In the under jaw of a Sumatran *Rhinoceros*, now before me, the extremity of which is figured in Plate 138, fig. 15, the tips of the large permanent outer pair of incisors (*i* 2) are visible, but have not pushed out their deciduous predecessors (*d* 2); and the sockets (*d* 1) of those of the two small median incisors (*i* 1) are also retained. In one of the extinct species of *Rhinoceros* from the Himalayan tertiary beds Dr. Falconer informs me that there are six incisors in both jaws: the typical number was, therefore, retained in this ancient species, as in the contemporary Hippopotamus of the same formations. Cuvier believed that the ex-incisive character of the two-horned *Rhinoceros* of Africa was absolute. "Not only," he observes, "is its hide without folds, not only has it constantly two horns, but it has never more than twenty-eight teeth, all molars; and never possesses incisors, nor even a place for them at the anterior extremity of its jaws." (1)

affording extra support to the horn-bearing bones of the face whence the name *tichorhinus* given by Cuvier to this most common of the extinct Rhinoceroses of our Northern Hemisphere.

(1) "Non-seulement sa peau n'a point de plis; non-seulement il a constamment deux cornes, mais il n'a jamais que vingt-huit dents, toutes molaires; il manque toujours d'incisives, et n'a même point de place pour elles à l'extrémité antérieure de ses mâchoires." 'Ossements Fossiles,' 4to. 1822, tom. ii. pt. 1, p. 27. The otherwise excellent zoological descriptions of the two-horned Rhinoceroses in Dr. Smith's 'Illustrations of the Zoology of South Africa, do not

I have shown in many parts of this Treatise how strikingly the duly defined law of Unity of Organization is exemplified by the dental system; and, anticipating that this system would adhere to the typical formula by transitory representatives of the defective teeth in the adult, I made search for the germs of incisors in the dried jaws of a foetal *Rhinoceros bicornis* of South Africa. The alveolar border of the short symphysis of the lower jaw was apparently edentulous, and thickly coated with the dried gum; after soaking this for some hours in warm water, and cutting down into its substance, I detected the germs of the four lower incisors, which are figured, of half the natural size, in Pl. 138, fig. 14, *i* 1, *i* 2. Although these teeth are destined to be absorbed and never to make their appearance above the gum in the living animal, they manifest the typical relative proportions to one another, the outer pair (*i* 2) being more than double the size of the inner pair (*i* 1). The outer incisor is six lines in length, and in great part lodged in the socket; the crown is one line and a half in breadth, convex anteriorly, flattened behind; it protrudes from the jaw about five lines in advance of the alveolus of the first molar, and close to the anterior border of the jaw. At the same border, about one line nearer the symphysis, the first or inner incisor is situated; it is about two lines in length, and half a line across the crown, which just peeps above the bone. There were no sockets of reserve beneath or behind these deciduous germs of incisors. The anterior end of the thin and small intermaxillary lamella of the same skull is expanded, and was covered by a thick, dried gum, but I could find no calcified rudiments of upper incisors; it is highly probable, however, that germs of these teeth or their matrices, may be manifested at an earlier period.

The permanent median incisors of the upper jaw have a peculiar and easily recognizable generic form in all the species possessing them; they are short, broad, much compressed, rhomboidal, or sub-triangular, the crown forming the base of the triangle and the

contain any reference to the teeth: Mr. Macleay, in the Entomological number of the same work, exaggerates in affirming of the genus *Rhinoceros*, "that the dentition varies extensively in almost every species." No. III, p. 6.

end of the fang the truncated apex: the crown, which is very short and thin in proportion to its breadth, usually commences by a sudden expansion, and terminates before it has suffered much abrasion, by an oblique trenchant edge, directed vertically downwards; they are less parallel in position, and are thicker in the Indian than in the Javanese one-horned Rhinoceros; they are a little smaller in the Sumatran two-horned species (Pl. 138, fig. 12, i 1). The external incisors are very small in all the above-cited species; and are lost before the animals attain maturity. They are each seven lines in length and two in breadth in the skull of a nearly full-grown Sumatran Rhinoceros (ib. i 2), and are situated close to the suture with the maxillary bone. In the nearly allied extinct *Rhinoceros Schleiermacheri* Dr. Kaup found them with an enamelled crown of four lines extent, which is longer than in the *Rh. Sumatranus*: the large mid-incisors of the *Rh. Schleiermacheri* are about two inches long, with a crown one inch and a quarter broad. In the *Rh. incisivus* (Pl. 138, fig. 1) these incisors have been found of nearly four inches in length, and with a short, oblique crown measuring upwards of two inches in breadth, but are relatively thinner.

The large external inferior incisors are procumbent, or project almost horizontally from the angles of the symphysial end of the lower jaw; in the Sumatran Rhinoceros the crown is an inch and a half in length, almost flat above and on the outer side, and convex below. The enamel is only laid upon the under and outer sides, terminating by a sharp edge along the inner part of the crown, and at its rounded termination. In the Javanese Rhinoceros they have a more definite trihedral form, and terminate anteriorly in a sharp-point: they are relatively thicker than in the Indian species in which Cuvier(1) has figured them as worn down to a thick truncated base. The small mid-incisors of the lower jaw are relatively larger and longer retained in the *Rhinoceros Schleiermacheri*(2), the outer incisors resemble those of the *Rh. Sumatranus*. In the *Rh. incisivus* (Pl. 138, fig. 1) these teeth acquire their greatest

(1) Loc. cit. Pl. II, fig. 4.

(2) Kaup, loc cit., tab. XI.

size, are more divergent, and directed more upwards; they have been found of the length of from eight to ten inches, of which the implanted base measured three-fifths of the entire length of the tooth, and the crown was one inch and a quarter in breadth; this is worn obliquely inwards at its upper enamelled part.

Not a trace of a canine tooth or its alveolus has been observed in the skull of a mature individual of any existing or extinct species of *Rhinoceros*, but such we must consider the small and simple tooth (Pl. 138, fig. 13, c) developed at the fore part of the superior maxillary bone in the foetal *Rhinoceros indicus*, two lines in advance of the alveolus of the first small deciduous molar (*p* 1) and one line behind the suture which unites the maxillary with the intermaxillary bone. The specimen in which I detected this tooth, the crown of which had pushed through the jaw, but not through the gum, appeared to be at the full-time, or newly born. The tooth and its socket must soon disappear, for in the specimen of the upper jaw of a young Indian *Rhinoceros* figured by Cuvier in the 'Ossemens Fossiles,' tom. cit. Pl. v, fig. 3, there is no trace of the alveolus of the rudimental canine in the tract of bone between the first deciduous molar and the intermaxillary suture; anterior to this the intermaxillary bone shows the sockets of the two comparatively large incisive teeth. This discovery of vestiges of canines in the genus *Rhinoceros* shows an additional character, although a transitory one, linking that genus with the nearly allied extinct *Palæotherium*.

The first of the permanent series of seven molar teeth is very small in both jaws, and is soon shed. The first upper premolar is notched on the inner side in the one-horned *Rhinoceros* (Pl. 138, fig. 3, *p* 1); the notch sinks deeper and expands in the African two-horned species; and in the Sumatran bicorn *Rhinoceros* it presents a detached lobe on the inner side: the second upper premolar is more suddenly enlarged in the one-horned than in the two-horned *Rhinoceros*. Before the crowns of these large and complex premolars and molars begin to be abraded, the eminences bounding the valleys terminate in sharp enamelled ridges, the principal extending along the outer border of the grinding

surface, and two others continued from this obliquely backwards to the inner border, one from the antero-external angle, the other from near the middle of the outer wall; the inner terminations of these two parallel oblique ridges form the summits of the two cones which constitute the inner half of the crown.(1) Small or secondary ridges project from the sides of the principal ridges into the intervening valleys, in extent and number varying according to the species, the most constant being the one, marked *f* in fig. 5, from the posterior oblique ridge. The first effect of mastication is to wear away the enamel from the summits of the ridges, and to expose a tract of dentine which widens as attrition proceeds, varying the pattern of the grinding surface as the valleys are thus progressively obliterated. These changes are illustrated by the figure of the molar series of the upper jaw of the *Rhinoceros indicus* (Pl. 138, fig. 3). The chief valley, marked *b* in fig. 5, is expanded and bilobed at its termination, and is deepest at each terminal division, and at the middle of its course; in the second true molar (*m* 2) its entire extent is shown; in the last molar (*m* 3) the posterior terminal division is insulated by the wearing away of the enamel from the shallower part of the valley between the two divisions: the same insulation has taken place in *m* 1, and the shallow entry of the valley is almost worn away; in *p* 4 it is obliterated, and the peninsular fold of enamel is converted into an island. The same change is effected in the short posterior fold *c*, it deepens as it penetrates the crown, and in *m* 4 its beginning has been worn down to the dentine, and its end converted into an island of enamel. The same three islands are shown in *p* 3 and *p* 2, with the addition of linear tracts formed by the wearing down of the crown to the basal ridge at the antero-internal lobe. The grinding surface is sometimes reduced to a plain tract of dentine before the molar is shed. There is no posterior fold *c* in the last molar.(2)

The modifications in the form of the valleys and secondary

(1) See the germ of the upper molar, Pl. 138, fig. 8.

(2) These, and similar details in other chapters of this work, may be deemed tediously, perhaps unnecessarily, minute: they are, however, indispensable to whoever would make successfully the noble application of anatomy to the restitution of lost species and the past history of the globe.

ridges of the upper molars are constant and characteristic of the species, and materially aid in the determination of fossil remains.

Even in existing species so nearly allied as the unicorn Rhinoceroses of India and Java, each might be determined by a single detached molar tooth. The principal valley is bent back at its termination in the Java species, but being shallower than the rest of the valley, it is obliterated and the valley simplified in form as in fig. 4. The posterior fold (*e*) is soon converted into an island; the chief fold is next insulated by the wearing down of the dentine to its beginning, and is the last to disappear.

The African *Rhinoceros bicornis* has a relatively larger molar, especially in its antero-posterior extent; the beginnings of the two folds (ib. fig. 5, *b* & *c*), being deeper than their terminations, no islands are formed in the progress of abrasion. In the Sumatran Rhinoceros the valley (*b*) is relatively wider at its commencement, and contracts to its termination, which is pointed, in little-worn molars; a simple secondary process projects from the posterior ridge into the valley, and partially detaches the narrow and at first triangular termination; when attrition has reached the shallow part of the valley at the end of the process, answering to *f* in fig. 5, the entire termination of the valley is insulated: a second and posterior island is formed when abrasion has removed the enamel from the wide and shallow beginning of the posterior valley *c*. Thus with regard to the first formed island *c*, which characterises the abraded molars of the Indian one-horned and Sumatran two-horned Rhinoceros, this results from the insulation of part of the blind termination of the principal valley in the one-horned species, and from the cutting off of the whole termination of the valley in the two-horned species. Cuvier, not having attended to this difference, failed to perceive that the fossil molar teeth which he figures, loc. cit. Pl. VI, fig. 5, and Pl. XIII, fig. 4, and which are copied in Pl. 138, figs. 6 & 7, belonged to two distinct species of Rhinoceros. (1) Figure 6 is the second true upper molar tooth

(1) He describes the tooth (Pl. 138, fig. 6) figured in his 'Ossem. Foss. Rhinoceros,' Pl. vi, fig. 5, as follows:—"Fig. 5, est la cinquième du côté gauche peu usée. On y voit aussi très-bien la fossette, résultant de l'union du crochet postérieur avec la colline antérieure et l'échancrure

of the *Rhinoceros tichorhinus*. It most nearly resembles the one-horned Indian Rhinoceros in the pattern of the grinding surface of the molars, the valley (*b*) has at first the same contracted beginning and expanded bilobed termination, and the island (*e*) is formed by the cutting off of the hinder lobe. Fig. 7 is a corresponding molar of the *Rhinoceros leptorhinus*, which in the structure of its upper molars, most nearly resembled the Sumatran Rhinoceros; the valley (*b*) has the same wide beginning and contracted end, which is wholly insulated at *c* by the obliteration of the enamel covering the shallow part of the valley between the end of the secondary process *f*, and the anterior lobe or ridge of the grinding surface: the upper molars of the *Rh. leptorhinus* are further distinguished from those of the *Rh. tichorhinus* by the longer ridge (*n*) along the base of the anterior side, and by the narrow prominent longitudinal ridge *o'* on the outer side of the crown. Both the above-named extinct species of Rhinoceros have left their remains in England as well as on the continent. The *Rh. incisivus*, which has not hitherto been found in British strata, is readily distinguished by the more simple form and almost uniform width of the valley *b*; and still better by the basal ridge which is continued from the anterior side along the whole of the inner to the posterior side of the crown of the molar, at some distance above the basal termination of the enamel; in these modifications it offers the nearest approach to the configuration of the upper molars in the *Palæotherium*. This basal ridge is also well developed in the molars of the *Hyrax*.

There are corresponding, but less marked differences in the molar teeth of the lower jaw of the different species of Rhinoceros; on which, however, I shall not here dwell. The first premolar is the smallest and simplest; the bilobed structure is at best feebly indicated by the undulations of the outer surface: and on the inner surface, by a simple depression or a notch: in the Sumatran Rhinoceros the notch is near the front margin of the tooth; it affords

postérieure commence à être cernée," p. 57. And the tooth (Pl. 138, fig. 7) figured in his Pl. XIII, fig. 4, as follows: "Fig. 4, Pl. XIII, est un sixième du côté gauche, peu usée, des Crozes, Département du Gard. Le trou antérieur y est déjà distinct par l'union du crochet de la colline postérieure avec la colline antérieure, mais l'échancrure postérieure n'y est point encore cernée."

a more marked difference by its position in relation to the symphyseal termination of the jaw; in the Rhinoceroses with persistent incisive teeth the symphysis is prolonged beyond the first premolar; but in the African species this tooth is situated close to the anterior end of the jaw. In the extinct tichorhine Rhinoceros in which the germs of the lower incisors endured longer and attained a greater relative size than they do in the living *Rh. bicornis*, the depressed spatulate symphysis is prolonged, as in the Indian and Sumatran Rhinoceroses, beyond the molar series, which begins opposite the posterior border of the symphysis, as shown in Pl. 138, fig. 10. In the leptorhine Rhinoceros (ib. fig. 11) the molar series extends closer to the anterior end of the symphysis, which both in form and relation to the molar teeth, more resembles that of the two-horned African Rhinoceroses. The first premolar (*p* 1) is soon shed, and all traces of its socket soon obliterated; this has led to the supposition that some of the fossil Rhinoceroses had only six molars on each side of the lower jaw; but specimens of young individuals have demonstrated the normal number in species where it has been most formally denied.⁽¹⁾ The second lower molar (*p* 2) has its lobes distinctly defined by the vertical furrow on the outer surface, but the variations of the form of its inner surface in different species are such as to make it, perhaps, the most characteristic tooth of the lower jaw; the anterior lobe is always the smallest and thinnest; and its internal indentation is shallow. The two lobes assume a more equal size and crescentic figure in the third (*p* 3) and fourth (*p* 4) premolars, which progressively increase in size: the three true molars resemble the fourth premolar, the last tooth not being distinguished by an accessory lobe.

216. *Microscopic Structure*.—Retzius⁽²⁾ describes the dentinal tubes as he saw them in longitudinal sections of the root of a molar tooth of a Rhinoceros, to proceed transversely from the pulp-cavity

(1) The specimen in Dr. Buckland's Museum, from Lawford near Rugby, Pl. 138, fig. 10, shows the first of the four premolars *in situ*, in the lower jaw of the *Rhinoceros tichorhinus*. M. Christol, who has figured a very perfect lower jaw of an older individual of the same species, in which the first premolar has been shed, describes it as 'munie de toutes ses molaires.' *Annales des Sciences*, 1835, p. 46, Pl. 2, fig. 1.

(2) Loc. cit., p. 32.

with an irregular and, in some parts, slightly curved course, but he could not consider them as being undulated: they were $\frac{1}{5400}$ th of an inch in diameter at their beginning, soon bifurcated, and gave off very numerous branches; the interspaces between the origins of the tubes, equalled the breadth of two tubes. The peripheral part of the dentine, close to the investing layer of cement contained a dense stratum of opake cells, in which many of the branches of the calcigerous tubes terminated; the extremities of the tubes meander through the interspaces of the cells, some terminating in the cells, other anastomosing with adjoining tubes in beautiful curves.

I have examined the microscopic structure of the molar of the Indian Rhinoceros, in vertical and horizontal sections of the crown. The pulp-cavity is continued in the form of fissures, into the middle of the eminences bounding the valleys of the uneven-grinding surface, and a few short vascular canals are continued into the dentine from the summits of the pulp-fissures, especially at their terminal angles. In horizontal sections dividing the vascular canals, their areas appear like large opake cells, with a clear border, and the adjoining dentinal tubes diverge, as it were, to give place for them: the ends of a few tubes, which were given off from those canals being seen in the clear border. Retzius makes mention of larger groups of opake cells in the middle of the dentine of the root of the molar, which seemed to have forced aside the main-tubes, which bent round these groups of cells, and sent off some branches which there terminated.

The major part of the coronal dentine of the Rhinoceros's molar, is fine-tubed and unvascular: I found the dentinal tubes, at their origin from the pulp-fissure, to have a diameter of $\frac{1}{9000}$ th of an inch, with interspaces averaging $\frac{1}{3600}$ th of an inch. They ascend (in the lower molar), inclining at first very slightly from the pulp-fissure, and gradually bending more outwards with the convexity of the curve upwards, until near their termination, when they gently curve in the opposite direction. Throughout their course they are undulated, the secondary waves being pretty regular and stronger than in the Human dentinal tubes. Transparent tracts,

wider than the interspaces of the tubes, extend here and there from the pulp-cavity, in the directions of the tubes and of the short vascular canals; the tubes next these tracts make a sudden bend obliquely across them with wider clear intervals. The tubes divide sparingly in the first half of their course; and, not decreasing much in diameter, appear closer packed as they approach the enamel. In the outer third of their course they make here and there abrupt secondary bends, and send off the minute lateral branches from both sides. Here and there the tubes present slight partial enlargements; they very gradually decrease in size, until close to the peripheral stratum of minute opaque cellules, (Pl. 139, $d'' d''$) where they chiefly end by a bifurcation, the forks diverging at an angle of 45° , and bending in opposite directions, sometimes anastomosing, sometimes irregularly dilating into, or communicating with, the opaque cellules. The traces of the compartments of the basal substance, or dentinal cells, are very faint; they are best seen in transverse sections, as in Pl. 139, $d^1 d^1$; especially that part of their contour next the enamel which curves across from four to five of the dentinal tubes; the compartments or cells increase in size as they approach the pulp-cavity, but soon become fainter and disappear from view.

The contour lines (ib. $l l$) are unusually conspicuous and numerous, with interspaces of $\frac{1}{600}$ th of an inch; they are not due to abrupt parallel bends of the tubes, nor to branches or opaque cells, but to a slight increase of opacity of the basal substance which seemed to be due to oblique cracks along the lines in question. The enamel fibres (ib. $e e$), in a transverse or horizontal section of the crown, proceeded from the surface of the dentine across the thickness of the layer, with a gentle degree of flexuosity; their diameter is $\frac{1}{4000}$ th of an inch. I could discern only a faint granular appearance in the fibre, certainly no transverse segmentation. The whole thickness of the layer of enamel is traversed by contour lines at varying intervals, running parallel to the border of the dentine. Here and there the fissures occur at the dentinal surface of the enamel, with irregular or stronger bends of the adjoining fibres. In a vertical section of the enamel the fibres were seen to run more obliquely

across the section, and those of one layer in an opposite direction to that of the subjacent layer of fibres.

Retzius notices the existence of radiate cells in both the radical and the coronal cement of the Rhinoceros's grinder: they were of various shapes, some round and $\frac{1}{2500}$ th of an inch in diameter, some angular, and others prolonged in the form of tubes; all receive numerous fine tubuli which are clustered around them.

217. *Succession*.—The deciduous dentition of the genus Rhinoceros, is:—

$$\text{incisors } \frac{2-2}{2-2}; \text{ molars } \frac{4-4}{4-4} : = 24.$$

In the Sumatran Rhinoceros the small mid-incisors of the lower jaw (Pl. 138, fig. 15, *d* 1) are first shed and replaced by a larger pair (*i* 1), which protrude beneath them; these are small in comparison with the lateral pair, and are also shed before the last true molar cuts the gum. The first true molar appears before any of the deciduous set are shed, but the first milk-molar soon yields place to the first premolar; the second milk-molar gives way to the second premolar, and about the same time the second true molar advances into place. Next the deciduous outer incisors (*ib.* *d* 2) their fang deeply excavated by the absorbent process excited by the pressure of their large successors (*i* 2), are pushed or broken out; the last deciduous molar is displaced, and the last premolar rises above the gum about the same time that the last true molar comes into place. Thus, notwithstanding the close similarity of form and structure between the premolars and molars, each division of the permanent masticatory series has its own order and progression of development, and thereby manifests its essential distinction. The last milk-molar is not more complex than the last premolar which takes its place.

218. *Palæotherium*.—The vast hiatus, which, in the series of existing Mammals, divides the Rhinoceros from the Tapir and this from the Elephant, was once filled up by interesting transitional species of anisodactyle Pachyderms which have long become extinct. I shall briefly notice the leading features of the dentition of some of those ancient forms of Mammalia, as indeed, this enduring part