Nitzsch in *Trachyphonus* and *Picus* and it also exists in *Iynx* and *Rhamphastos*.

A further likeness between the three families of birds concerned is in the surrounding of the oil-gland by the spinal tract. This occurs, as will be seen from Nitzsch's figures, in both *Picus* and *Rhamphastos*.

If Nitzsch's figures of *Capito* (*Micropogon*) *cayennensis* are correct, we may have in the pterylosis a means of differentiating the Old World from the New World Barbets. For in the latter the posterior part of the spinal tract is separated from the anterior and is composed of two distinct limbs which only join just at the oil-gland. I would further point out that the identity in the pterylosis of *Megalæma* and *Cyanops* is against their generic separation. On the other hand, the pterylosis of *Xantholæma rosea* is very different from that of *Megalæma*, which justifies its retention as a genus.

There is the usual interscapular fork, but there is no break, a rhomboidal apterion being enclosed, as is so far correctly shown in Nitzsch's figure; but although the two halves of the spinal tract do join, the junction is produced only by their lying close side by side and they immediately diverge to end at the sides of the oil-gland. The tract, in fact, has an hourglass-like shape, which is merely an exaggeration of that which, according to Nitzsch's figure, characterizes the Toucans.

In the lateral and femoral tracts *Xantholæma* agrees with *Megalæma*. I find, after examining *Selenidera maculirostris* and *Aulacorhamphus prasinus*, that all the Toucans do not agree with Nitzsch's figures of *Rhamphastos erythrorhynchus*. In the two just-mentioned birds there is no break in the spinal tracts, which are thus more like those of *Xantholæma*. The femoral tracts do not arise from the spinal tracts so high up as is figured by Nitzsch, and the lateral tract, apparently absent altogether from *Aulacorhamphus*, is very rudimentary in *Selenidera*, consisting of only three or four feathers.

3. Contributions to the Study of Mammalian Dentition.—Part II.[1] On the Teeth of certain Insectivora. By M. F. Woodward, Demonstrator of Zoology, Royal College of Science, London.

[Received May 5, 1896.]

(Plates XXIII.–XXVI.)

In their general organization the Insectivora are undoubtedly very primitive, consequently one might reasonably expect to find their dentition in a similar lowly state. This at first sight appears to be the case, at least so far as the pattern of the molar teeth is concerned, for if we accept the tritubercular form as the primitive

[1] For Part I., see P. Z. S. 1893, p. 450.

one for those teeth, then we find this type apparently preserved in all its purity in certain living Insectivores (*Centetes*, *Ericulus*, and others), a condition almost unique amongst living mammals; in addition, some Insectivores exhibit molar teeth which are supposed to be but slightly in advance of this, having acquired a small heel above and below, thus presenting to us the trituberculo-sectorial type (well seen in the upper molars of *Tupaia*, *Sorex*, &c., and in the lower molars of the *Centetidæ* and *Chrysochloris*).

On the other hand, in many respects the dentition of this order cannot be regarded as primitive, for the ante-molar teeth are obviously specialized both with regard to their form and number. The molars, too, in many genera are clearly modified from a tritubercular standpoint, the upper molars being often quinquetubercular, while below the heel may attain equal importance with the trigon and develop numerous cusps; in others the paraconid is lost, thus producing a quadritubercular crown, an admittedly specialized type of lower molar.

As a whole the teeth of this order are characterized by the strong development of their cusps, a condition closely associated with their insectivorous diet; this, perhaps, accounts for their resemblance to the teeth of the early Jurassic mammals, it being highly probable that the latter were also insectivorous. If this was the case, then the presence of these supposed primitive tooth-patterns among living Insectivores may be due rather to the similar nature of the food of these two groups, so widely separated in time, than to an actual persistence of the unmodified tritubercular molar from Mesozoic times until to-day.

Until recently it was generally supposed that the Insectivora were quite normal in their tooth change, Owen (**18**), Rousseau (**21**), Dobson (**3**), and others describing a full milk-dentition in some genera. But at the same time, it was known, from the researches of Spence Bate (**1**) on the Mole (*Talpa*), that the milk-dentition might be very transitory.

Recently Leche (**7** & **9**) has published the results of an investigation concerning the relationships of the milk and permanent sets of teeth in a number of genera, adopting the more modern methods of microtomy to aid him in his researches, which were extended to fœtal as well as numerous stages after birth, until the full adult dentition was acquired.

In his first and preliminary communication, Leche (**7**) came to the most interesting conclusion that in the anterior tooth-region of the adult *Erinaceus* a mixture of milk and successional teeth was to be met with. The adoption of these results unfortunately led me to put forward the view (**30**) that *Erinaceus*, in respect to the relation of its sets of teeth, was intermediate between the marsupial condition with its persistent milk set and the typical diphyodont placental stage. This now turns out to be quite erroneous, for Leche, in his later and complete work (**9**), shows conclusively that *Erinaceus* possesses vestiges of two complete dentitions, and that those anterior teeth, which are apparently only represented in one set, belong to the replacing series, being preceded by tooth-vestiges referable to the milk-dentition. This last conclusion I can now entirely confirm and strengthen, for the specimens which I have investigated exhibit these features much better than Leche's embryos did[1].

Both Leche and myself have investigated *Erinaceus*, *Ericulus*, *Sorex*, and *Talpa*, and he has further studied *Crossopus*, *Scalops*, and *Condylura*, whilst I have independently investigated *Centetes* and *Gymnura*. These are unfortunately representatives of only 5 out of the 9 families of living Insectivora (Flower and Lydekker, **4**), thus leaving at least 4 other families, some of which are extremely interesting, still to be investigated.

In addition to studying the relations of the two sets of teeth, I have attempted to trace the origin of the cusps of the molar teeth, noting especially the order of development of those structures in the light of the researches of Osborn, Röse, and Taeker.

Erinaceus europæus.

Of our common English Hedgehog I have examined two specimens intermediate in age between Leche's stages E and F, that is between his oldest fœtus and his new-born young. Further, I have examined a large series of dried skulls, including those in the collection at the British Museum.

The statements concerning the milk-teeth of this genus and allied forms in many, especially the older, text-books are most misleading, and even in more modern works we find the whole group described as diphyodont. This, though strictly true, was not based on any detailed examination of the various genera, but rather hastily concluded from the knowledge that one form was found to exhibit this condition, or else copied from some old and unreliable accounts, as, for instance, that of Rosseau (**21**), who stated that *Erinaceus* had a deciduous dentition composed as follows, viz.:— i. $\frac{2}{4}$, pm. $\frac{4}{1}$, which were shed at the age of 7 weeks. Dobson (**3**) also speaks of a full milk-dentition, but it is obvious that he simply described as milk-teeth all those teeth which were visible in the jaw of the young Hedgehog at birth, and that he had never seen any actual replacement. He states, in contra-distinction to Rosseau, that at 6 weeks all the permanent teeth were present.

The erroneous nature of these conclusions has been pointed out by Leche (**9**); and it may be ascertained by anyone, from the study of a few young skulls, that the only milk-teeth recognizable by the ordinary methods of dissection or examination of dried skulls are i. $\frac{2}{1}$, c. ($\frac{1}{-}$), pm. $\frac{2}{1}$. The remainder being only to be made out, and then with difficulty, by the examination of serial sections of fœtal jaws, a method not adopted by the earlier observers.

[1] It is just possible that our English Hedgehog differs in respect to the amount of development of these milk-tooth vestiges from its continental cousin, although they are considered as one species; on the other hand, my two specimens may represent individual variations.

The discovery by Leche (9) of the extremely variable nature of the upper deciduous canine (Plate XXIV. fig. 9, dc.) forms the key to his conclusions, for this enabled him to perceive that the milk set were in part undergoing reduction, and to formulate the belief that the knob-like labial growth of the dental lamina which he found in connection with $\underline{\text{i. 3}}$ was the last trace of the enamel-organ of the milk predecessor of that tooth: from this he concluded that the milk predecessors to the following teeth $\frac{\text{pm. 1}}{\text{i. 2, c., pm. 1}}$ had been entirely suppressed.

The conclusions may seem very bold, but their correctness is proved beyond a doubt by the two stages which I have been fortunate enough to obtain.

Taking as a starting-point the upper canine, I find that in my younger stage the enamel-organ of the permanent canine ($\underline{\text{pc.}}$) is in a very backward condition, whereas labially a small tooth is developing (fig. 1, $\underline{\text{dc.}}$; see also Leche, Taf. iv. figs. 41–50); from the condition of this latter structure it is possible that it might develop into a small functional milk-tooth (fig. 9, $\underline{\text{dc.}}$), and from its position and general relationship it is obviously the milk-canine. In the older stage we note (fig. 1 *a*, $\underline{\text{pc.}}$) that the enamel-organ of the permanent canine is more developed, and that attached to the labial side of the neck of this structure, *i. e.* the dental lamina, is a slight outgrowth, indenting which is a small irregular calcification ($\underline{\text{dc.}}$); this is in the position of the germ of the deciduous canine of the younger stage, and evidently represents that tooth in a more advanced condition, *i. e.* as regards calcification, but at the same time retrograded, for it is so small and irregular that it could not become a functional tooth and probably would not even cut the gum. Thus we see that the canine may vary from a functional tooth (Leche) to a minute irregular calcification of no physiological importance (*cf.* figs. 9 & 1 *a*, $\underline{\text{dc.}}$).

Considerable doubt has been expressed at one time or another concerning the exact homology of the first upper maxillary tooth of *Erinaceus*, its form in the permanent series being so unlike that of a typical canine, for the reason that it possesses indications of two fangs; moreover, it is apparently situated a considerable distance behind the premaxillo-maxillary suture. If, however, a young skull be examined (fig. 9), we find that the deciduous canine, when present as a conspicuous tooth, bears but a single fang and is situated close to the suture, as also is the developing permanent canine, the apparent change in position of the latter tooth being due to the forward extension of the maxilla, growing so as to embrace the premaxilla both labially and on its palatal border (fig. 9 *a*); thus the external premaxillo-maxillary suture in the adult is apparently situated far in front of the canine tooth. The true position of this tooth can be ascertained even in an adult skull if the palatal aspect of the latter be examined, then the canine is seen to be situated almost within the true suture and certainly not far behind it.

The Upper Incisors.

$\underline{\text{I. 1 \& i. 2}}$ are present as functional teeth both in the milk and replacing dentition, but the latter ($\underline{\text{pi. 1 \& pi. 2}}$) develop late, and in my sections are only indicated by well-marked lingual growths of the dental lamina. $\underline{\text{Pi. 2}}$ is the most variable in the different species, and in the younger stage examined no signs of it are yet visible. $\underline{\text{I. 3}}$ as a functional tooth is known only in the adult dentition. Leche refers this to the replacing series, because he finds a bud-shaped labial outgrowth of the dental lamina related to the enamel-organ of this tooth. In both my specimens I find a calcified structure connected with this labial growth (fig. 2, $\underline{\text{di. 3}}$); this in the younger stage is a distinctly cup-shaped dentinal body, while in the older specimen (fig. 2 *a*) the condition is more like that figured by Leche (Taf. vii. fig. 52, Jd. 3), save there is a small calcification indenting his Jd. 3 from behind. A comparison of this labial calcification (di. 3) with the reduced $\underline{\text{dc.}}$ (fig. 1 *a*) shows that these two structures evidently belong to the same order, *i. e.* are reduced teeth of the milk series, the incisior being more vestigial.

This confirms Leche's view that the adult $\underline{\text{i. 3}}$ belongs to the replacing series, and is the true $\underline{\text{pi. 3}}$.

The Lower Incisors.

The first enlargement of the dental lamina in the lower jaw is situated in front of the enamel-organ of the first functional incisor; it is a very conspicuous structure in the younger stage, being slightly bell-shaped and possessed of a small labial outgrowth (Plate XXIII. fig. 3); this evidently corresponds with what Leche believes to be a remnant of the true $\overline{\text{i. 1}}$ (see Taf. ii. figs. 13 & 14), which is here possibly represented both in the milk and permanent series.

The second incisor, *i. e.* the anterior functional one, is a very large and highly differentiated tooth in both specimens, and exhibits a strong lingual growth of the dental lamina, which eventually forms the enamel-organ of the successor, this tooth $\overline{\text{i. 2}}$ being well developed in both dentitions.

The posterior functional incisor $\overline{\text{i. 3}}$ is very backward in its development and variable, for it is larger in the younger of the two specimens examined. A long, narrow, cord-like (in section) band of cells grows out from the neck of the enamel-organ of this tooth on its labial side (fig. 4, $\overline{\text{di. 3}}$), being sometimes swollen at its free end and slightly indented; this evidently represents the last trace of an earlier dentition, and from a comparison with $\underline{\text{di. 3}}$ in the older stage, one is justified in concluding that it represents the enamel-organ of $\overline{\text{di. 3}}$ undergoing suppression.

Between $\overline{\text{i. 3}}$ and $\overline{\text{c.}}$ the dental lamina is very strongly developed, and suggests the possible presence of the last trace of one of the missing Marsupial incisors.

The lower canine is represented by a bell-shaped enamel-organ attached to the buccal epithelium by a well-marked neck of dental lamina; growing out from this labially is in both stages a small bud-like mass of cells (fig. 5, $\overline{\text{dc.}}$), in one case swollen at its free end, close to which is a small irregular calcification similar in appearance to the often vestigial $\underline{\text{dc.}}$, but smaller in size: this is obviously the vanishing milk-tooth $\overline{\text{dc.}}$, the canine of the adult belonging to the replacing series.

The Premolars.

In the upper jaw there are three premolars, which Leche believes to be the 2nd, 3rd, and 4th respectively. It is true there is a slight gap between the canine and the anterior of these premolars, but there is a more conspicuous one between the two posterior teeth, and in this latter gap the dental lamina has a slight tendency to become specialized and enlarged (Plate XXIII. fig. 6 *b*); but it is perhaps hardly large enough to be regarded as a tooth anlage, and, further, we know that when suppression affects the premolar series in the Placentalia, the 1st tooth of that series generally suffers suppression earliest.

In the lower jaw there are only two premolars, but between them is a long stretch of dental lamina, which exhibits a most distinct development from its adamantine face; this growth is slightly indented by a specialized mass of mesoblast (fig. 7 *b*), the whole structure presenting a great similarity to a developing tooth: this, I believe, represents the last trace of a suppressed tooth, corresponding with the middle premolar above.

The two posterior upper, and the posterior lower, premolars are present as functional teeth in both dentitions; but the middle upper one is very variable, and is often wanting in some adult skulls, while in *E. micropus* and *E. pictus* it is very minute.

The anterior premolar, above and below, in both my stages, exhibits a large enamel-organ, bell-shaped in the older specimen; attached to the dental lamina forming the necks of these structures, on the labial side, is in each case a mass of epitheloid cells (figs. 8 and 8 *a*, dpm. 2); the free ends of these buds are swollen and flattened: closely applied to these is, in each case, an irregular calcification, resembling the most reduced stage of $\underline{\text{dc.}}$; these are evidently reduced milk-premolars, the anterior functional premolars being then, as Leche supposed, replacing teeth.

With regard to the last premolar, its milk representative resembles a molar in form, thus differing markedly from its successor; a feature so characteristic of the 4th premolar of other Placentalia, that I think we may be quite safe in homologizing these two teeth with one another.

If we examine the mutual relations of the 4th premolar and its successor during their development, we find that the replacing tooth, $\underline{\text{ppm. 4}}$, originates almost entirely in front of its supposed milk predecessor from the dental lamina between $\underline{\text{dpm. 3}}$ and $\underline{\text{dpm. 4}}$, the enamel-organ of $\underline{\text{ppm. 4}}$ being more conspicuous in the sections in front and in the anterior region of $\underline{\text{dpm. 4}}$ than in its posterior region, thus resembling the condition which I described in the *Macropodidæ* (28. p. 467).

The antero-external cusp (protocone of Scott) of dpm. 4 develops first, the antero-internal or deuterocone second, and the tetarocone third, the tritocone being wanting.

The Molars.

Of the three molars of the adult, $\frac{\text{m. 1, m. 2}}{\text{m. 1, m. 2}}$ are alone developed in my specimens. The enamel-organs of these two teeth, both above and below, exhibit slight lingual continuations of the dental lamina; consequently these teeth do not develop in connection with the most deeply-seated portion of the dental lamina, but in relation to that situated nearer to the surface of the gum. The presence of this lingually-placed continuation of the dental lamina indicates that there is latent in the jaw the structure essential for the production of a second set of molars.

In addition to this lingual growth, we find also a slight but constant labial outgrowth from that portion of the dental lamina connecting the enamel-organ of the functional molar with the oral epithelium. If this labial growth be compared with the vestiges of the milk-dentition seen in connection with $\underline{\text{i. 3}}$ and $\overline{\text{i. 2}}$, it is found that it is impossible to distinguish these structures from one another, they being precisely similar in their relations to the dental lamina and to the adjacent teeth, differing only in the fact that the labial growth connected with the molars is the most reduced.

We find, then, in the molar region indications of three sets of teeth—a labial vestigial set, then a functional set, and lingual to this a structure capable of producing one or more replacing sets. Further consideration of these sets will be found in my general conclusions.

The Molar Cusps[1].

Erinaceus in the adult condition has three molar teeth in each jaw, the first of these being large, while $\frac{\text{m. 3}}{\text{m. 3}}$ are reduced.

The first two upper molars are quinquetubercular, being provided with two well-developed external cones, the paracone and metacone, two internal ones, the protocone and the hypocone, together with a small central metaconule, this last being the most variable constituent. In addition there is a slight but complete cingulum.

The lower molars (1 & 2) are also quinquetubercular, being modified trituberculo-sectorial teeth, in which the heel has

[1] In the descriptive portion of this paper Osborn's nomenclature of the molar cusps (13) is used, but I do not thereby imply that I believe in all cases the homology of the cones has been correctly interpreted; in fact, in the general summary I endeavour to show that the cusp usually termed the protocone in the Insectivorous molars is not homologous in all the genera.

attained equal importance with the trigon and developed two large cusps, an internal entoconid and an external hypoconid. This tooth is further specialized in the partial suppression of the paraconid, the antero-internal cone of the trigon, while the protoconid (antero-external) and the metaconid (postero-internal) are very large.

Taking the case of the upper molar first, in both my specimens $\underline{\mathrm{m.\,1}}$ was fairly advanced, showing indications of four cones, viz., the para-, meta-, proto-, and hypo-cones, here mentioned in order of size; the hypo-cone was obviously the last of the four to develop, as it is only just recognizable in the younger specimen; in the older stage these cones are larger, and the first trace of the metaconule is here apparent. Thus in $\underline{\mathrm{m.\,1}}$ we can say for certain that the metaconule appears last and the hypocone next to last, but the trigon was too advanced in my specimens to determine the developmental order of its cones. But where $\underline{\mathrm{m.\,1}}$ fails us $\underline{\mathrm{m.\,2}}$ comes to our rescue: in the younger stage two cones only were apparent, viz., the two external ones, the para- and metacones, and of these the former was much the largest and must obviously have developed first; immediately internal to this was a low shelf, in the position of the future *protocone*, but at present no cone was recognizable. In the older stage of this tooth the protocone has appeared in this position, and a faint indication of the heel is visible. We may thus state with certainty that the order of cusp ontogeny is as follows:—

$$\left.\begin{array}{l}\text{1. Paracone}\\ \text{2. Metacone}\\ \text{3. Protocone}\end{array}\right\}\text{Trigon.}$$

4. Hypocone.
5. Metaconule.

In the lower jaw, as in the upper, the first molar was too far advanced, all five cones being recognizable, but nevertheless differing greatly in their relative sizes; the following is their order according to size, viz., proto-, meta-, ento-, hypo-, and paraconid, the last being only just recognizable. An examination of $\overline{\mathrm{m.\,2}}$ throws more light on the subject, for here only three cones are developed as yet, viz., the proto-, meta-, and entoconid, a slight antero-internal extension of the tooth-germ indicating the position of the future paraconid, while a similar but larger postero-external platform marks the hypoconid. The protoconid is larger than the metaconid at this stage, and the metaconid than the entoconid, the probable order of development being:—

1. Protoconid.
2. Metaconid.
3. Entoconid.
4. Hypoconid.
5. Paraconid.

The ordinal position of the paraconid in the ontogeny may seem rather strange, but we must bear in mind the fact that this cusp is apparently of little importance in *Erinaceus*, as it is very small in adult and may be almost wanting on $\overline{\text{m. 2}}$.

A further consideration of these cusps will be found at the end of this paper.

The relations of the milk and permanent teeth of *Erinaceus* may be represented as under, the reduced teeth being indicated in italics, those which never cut the gum and are entirely functionless being enclosed in brackets, while the functional ones are represented by ordinary figures (Winge, **26**) :—

$$\text{I.}\begin{cases}1\ \ 2\ \ 3\\[4pt] \dfrac{1\ \ \ 2\ \ (\mathit{3})}{(\mathit{1})\ \ 2\ \ (\mathit{3})};\\[4pt] \ \ \ \ 2\ \ 3\end{cases}\ \text{C.}\begin{cases}1\\[4pt] \dfrac{\mathit{1}}{(\mathit{1})};\\[4pt] 1\end{cases}\ \text{P.}\begin{cases}0\ \ 2\ \ 3\ \ 4\ \ \ 1\ \ 2\ \ \ \ 4\\[4pt] \dfrac{0\ \ (\mathit{2})\ \ 3\ \ 4}{0\ \ (\mathit{2})\ \ (\mathit{3})\ \ 4},\text{or}\ \dfrac{(\mathit{1})\ \ 2\ \ (\mathit{3})\ \ 4}{(\mathit{1})\ \ \ \ \ \ (\mathit{3})\ \ 4};\\[4pt] 0\ \ 2\ \ \ \ 4\ \ \ 1\ \ \ \ \ \ 4\end{cases}\ \text{M.}\begin{cases}1\ \ 2\ \ 3\\[4pt] \overline{}\\[4pt] 1\ \ 2\ \ 3\end{cases}$$

Gymnura.

So far as I am aware, no young specimens of this genus have been examined in the flesh for their tooth change. Thomas (**23**) has, however, published a bare statement of two dentitions in this genus, based, I believe, on a young, dried skull in the British Museum collection; but there is a good deal of uncertainty attached to this method, for although the jaw has been cut to expose the underlying tooth-germs, no actual germs are visible, and one can only surmise their existence from the presence of cavities at the roots of the functional teeth (Plate XXIV. fig. 12), and by a comparison of these teeth with those of an adult specimen.

The dentition, according to Thomas, is :—

$$\text{I.}\begin{cases}1\ \ 2\ \ 3\\[4pt] \dfrac{1\ \ \ 2\ \ \ \mathit{3}}{1\ \ \ 2\ \ \ 3};\\[4pt] 1\ \ 2\ \ 3\end{cases}\ \text{C.}\begin{cases}1\\[4pt] \dfrac{1}{1};\\[4pt] 1\end{cases}\ \text{P.}\begin{cases}1\ \ 2\ \ 3\ \ 4\\[4pt] \dfrac{\mathit{2}\ \ \ 3\ \ \ 4}{0\ \ \ 3\ \ \ 4};\\[4pt] 1\ \ 2\ \ 3\ \ 4\end{cases}\ \text{M.}\begin{cases}1\ \ 2\ \ 3\\[4pt] \overline{}\\[4pt] 1\ \ 2\ \ 3\end{cases}$$

$\underline{\text{di. 3}}$ and $\underline{\text{dpm. 2}}$ being vestigial.

The specimen examined by me was a fœtus, with a head length of about 49 mm. and a total length of 205 mm.

The Incisors.

$\underline{\text{I. 1 \& i. 2}}$ are large and well calcified, each showing a marked lingual development of the dental lamina, indicative of a successional tooth. On the other hand, $\underline{\text{i. 3}}$ is more specialized, and only present in the permanent set of teeth. In my fœtus this tooth was very backward in its development, its enamel-organ being but slightly differentiated ($\underline{\text{pi. 3}}$), and exhibited on its labial side a large irregular calcification (fig. 10, $\underline{\text{di. 3}}$), provided with a reduced enamel-organ; this is evidently the milk predecessor of $\underline{\text{i. 3}}$, and probably would not cut the gum, although at times it may do so (Thomas, 23).

There is a complete replacement of the lower incisors, but the successors develop at very different times, $\overline{\text{pi. 1}}$ and $\overline{\text{pi. 3}}$ maturing long before $\overline{\text{pi. 2}}$. Consequently in my fœtus no sign of the future $\overline{\text{pi. 2}}$ was visible, although the enamel-organs of $\overline{\text{pi. 1}}$ and $\overline{\text{pi. 3}}$ were just recognizable. As a matter of fact $\overline{\text{pi. 2}}$ is, I believe, the last permanent ante-molar tooth to cut the gum, appearing soon after the eruption of $\overline{\text{ppm. 3}}$.

The Canines.

The milk-canines possess single roots, and are but slightly larger than the incisors (fig. 13); whereas the permanent canines are very large teeth, with pointed crowns, and each provided with two fangs.

The Premolars.

$\frac{\text{Pm. 1}}{\text{Pm. 1}}$ are said to be present in one dentition only. If this be the case these teeth would appear to belong to the milk-dentition, for there is present on the lingual sides of their enamel-organs well-marked continuations of the dental lamina, precisely similar in their relationship to that seen by the side of $\underline{\text{dc.}}$, which gives rise to the enamel-organ of $\underline{\text{pc.}}$, only the inner ends of the former are perhaps a trifle less swollen. It is just possible that these structures may give rise to the enamel-organs of successors at a late period, for the first premolar of the adult skull appears to be a slightly stouter tooth than that of the young animal.

The lingually situated dental lamina in both the upper and lower jaws gets smaller and more irregular behind pm. 1, but soon becomes definitely swollen, and forms the commencement of an enamel-organ (figs. 11 & 12, ppm. 2); this, from its position and backward condition, is evidently that of a successional tooth, viz., ppm. 2. This identification is rendered more certain by finding on the labial side of this structure a small calcified tooth (dpm. 2), devoid of enamel, but possessing a much reduced enamel-organ [1]. In the case of the upper tooth this reduced enamel-organ is attached to the gum close to, but independent of, the swollen, lingually-situated dental lamina above referred to ($\underline{\text{ppm. 2}}$). In the lower jaw, however, the enamel-organ of the vestigial tooth (fig. 12, $\overline{\text{dpm. 2}}$) is apparently attached to the corresponding lingual swelling of the dental lamina, thus exhibiting the normal relationships of a milk and a replacing tooth.

The deciduous 2nd premolar is then reduced and early lost, while its successor is somewhat precociously developed (*cf.* fig. 11,

[1] In a preliminary note, read before the British Association, 1895 (27), I stated that there were traces of five premolars in *Gymnura*: this is not the case; the error arose through a misinterpretation of a curious development of the pulp of this tooth, dpm. 2 (see Pl. XXIV. fig. 11, *p*), which was mistaken for a successor.

$\underline{\text{ppm.}2}$, and fig. 14, $\underline{\text{ppm.}3}$). The upper $\underline{\text{dpm.}2}$ is larger than $\overline{\text{dpm.}2}$, possibly at times it cuts the gum ; it is well seen in a specimen in the British Museum (fig. 13, dpm. 2), probably the one Thomas described ; no trace of $\overline{\text{dpm.}2}$ is seen in that specimen, and it is probable that this tooth is either shed *in utero* or absorbed.

$\frac{\text{Pm.}3}{\text{Pm.}3}$ are quite normal, the milk representative being large, and the lingual growths of the dental lamina, which give origin to the enamel-organs of their successors, being conspicuously swollen (fig. 14, $\underline{\text{ppm.}3}$). This tooth is somewhat similar in the two dentitions, but distinctly larger in the adult.

$\frac{\text{Dpm.}4}{\text{Dpm.}4}$.—These are the largest and most complex of the premolars, and both exhibit conspicuous lingual specializations of the dental lamina, the enamel-germs of their successors. These germs are developed in front of the deciduous teeth, and although the lingually-placed dental lamina is continued back by the side of dpm. 4, it is no longer swollen to form an enamel-germ.

The Molars.

In the stage examined two molars were present, above and below, but save in the case of $\underline{\text{m.}1}$ no labial or lingual developments of the dental lamina were to be seen. M. 1, however, exhibited both a lingual and a slight labial growth, similar to those seen in *Erinaceus*.

The Cusps.

The molar teeth of *Gymnura* resemble those of *Erinaceus* in pattern ; like that genus they exhibit five cusps, which are strongly developed, and in the upper jaw a well-marked cingulum, with a small anterior and posterior cusp, is present in addition ; in the lower jaw the paraconid is less developed than in *Erinaceus*.

My fœtal specimen was rather old for an exact determination of the cusp ontogeny, most of the cusps being well-formed. In $\underline{\text{m.}1}$ all five cusps were present, and had attained nearly their full development ; the following is their order in size : proto-, meta-, para-, and hypocones, the smallest being the metaconule. $\underline{\text{M.}2}$ was less developed, and here the para- and metacones were the most strongly developed, while the protocone was present in the form of a large antero-external shelf, but hardly as yet developed into a distinct cusp, though the hypocone and metaconule had done so.

Probable order of cusp-development :—

1. Paracone.
2. Metacone.
3. Protocone as a shelf.
4. Hypocone.
5. Metaconule.
6. Protocone as a cusp.

In the lower molar the protoconid evidently develops first, but it is closely followed by the metaconid, the entoconid, and the hypoconid, the reduced paraconid being last, the order being identical with that seen in *Erinaceus*.

The relation of the milk and permanent dentitions may be thus expressed :—

$$\mathrm{I.}\left\{\begin{array}{c}1\quad 2\quad 3\\[4pt] \dfrac{1\quad 2\quad (\mathit{3})}{1\quad 2\quad 3}\\[4pt] 1\quad 2\quad 3\end{array}\right.;\ \mathrm{C.}\left\{\begin{array}{c}1\\[4pt] \dfrac{1}{1}\\[4pt] 1\end{array}\right.;\ \mathrm{P.}\left\{\begin{array}{c}?\quad 2\quad 3\quad 4\\[4pt] \dfrac{1\quad \mathit{2}\quad 3\quad 3}{1\quad (\mathit{2})\quad 3\quad 4}\\[4pt] ?\quad 2\quad 3\quad 4\end{array}\right.;\ \mathrm{M.}\left\{\begin{array}{c}1\quad 2\quad 3\\[4pt] \overline{}\\[4pt] 1\quad 2\quad 3\end{array}\right.$$

Sorex.

The Shrews are generally regarded as possessing one dentition only, but both Owen (**18**) and Trauber (**25**) stated definitely that there was a minute calcified milk-dentition present, Owen ascribing to *Crocidura* $\frac{4}{4}$ milk-teeth, while Trauber states that in *S. vulgaris* there are $\frac{7}{3}$ and in *Crossopus fodiens* $\frac{6}{3}$ deciduous teeth. Leche (**9**) believes that these authors mistook the calcifying cusps of the replacing teeth for a set of minute milk-teeth—he himself coming to the conclusion, from the material at his disposal, that only one dentition is present in *Sorex* and *Crossopus*; this he regards as the successional set, the milk-dentition having been suppressed.

My own observations are based on the examination of one stage only, but it appears to be in a very interesting condition and shows distinctly traces of two dentitions.

The specimen measured 32 mm. long, the head length being 8 mm., while from the crown of the head to the posterior flexure of the body it was 13 mm., being just 1 mm. shorter than Leche's youngest stage.

The Incisors.

$\frac{\mathrm{I.}\,1}{\mathrm{I.}\,1}$.—These in the adult are two enormous procumbent teeth, and in my fœtal specimen are much in advance of the other teeth. The enamel-organs of these two teeth exhibit strong lingual growths of the dental lamina (Plate XXV. fig. 15, *d.l.*), so large and swollen, indeed, as to suggest the development of a successor; but such a condition could not possibly have been overlooked for it would involve the replacement of a large tooth at a comparatively late period, whereas the only suggested milk-teeth (Owen and Trauber) are said to be minute.

The 2nd upper incisor is backward in its development, but its enamel-organ exhibits a marked labial growth (fig. 16, $\underline{\mathrm{di.}\,2}$); this latter being swollen at its free end and slightly indented, evidently represented the enamel-organ of a predecessor to $\underline{\mathrm{i.}\,2}$ in a vestigial condition. A similar but non-indented labial growth is found related to $\underline{\mathrm{i.}\,3}$ (fig. 17), this condition being repeated in connection with the fourth tooth, the so-called $\underline{\text{i. 4}}$, but here the labial enamel-organ is more marked and bell-shaped (Plate XXV. fig. 18, dc.). The gap between the premaxilla and maxilla at this stage is so extensive that the germs of several teeth are contained within it, it being quite impossible to identify the future boundary line between maxillary and premaxillary teeth (fig. 19). But even if it be a fact, as Brandt states (1 *a*), that the four anterior upper teeth are situated within the confines of the premaxilla[1], I fail to see that it is proven that these teeth are the homologues of the four incisors seen in the Polyprotodont Marsupials, but would rather be inclined to regard Brandt's fourth incisor as a canine, abnormally situated; for among the Insectivora this tooth is very variable in its relations to the premaxillo-maxillary suture, due probably to the variations in relative extension of these two bones, the canine itself remaining constant in its position.

The 2nd and 3rd lower incisors were in a very backward condition; both, however, exhibit labial growths of the dental lamina, that connected with $\overline{\text{i. 2}}$ being the most marked (fig. 20). The 3rd lower incisor is, however, a vanishing structure and does not develop into a functional tooth (fig. 21).

In the upper jaw the tooth which I regard as the anterior premolar, usually called the canine (Brandt), was difficult of identification, it being hardly differentiated from the dental lamina (fig. 19, pm. 2?).

Of the two undoubted premolars the posterior is the largest and the most advanced in development, the enamel-germ of the anterior tooth being still in the club-shaped stage, but possessing a well-marked cup-shaped labial (fig. 22) enamel-organ belonging to its vestigial predecessor. A similar structure to this, but more highly differentiated and of still larger size, is attached to the posterior premolar (fig. 23, $\underline{\text{dpm. 4}}$), which, from its large size and close proximity to the molar teeth, is probably the true 4th premolar ($\underline{\text{ppm. 4}}$).

These three teeth I regard as premolars; in all probability they represent pm. 2, 3, & 4.

The enamel-organ of the single lower premolar, like $\underline{\text{ppm. 4}}$, was large and highly differentiated (fig. 24); it also exhibits the labial enamel-organ of its vestigial predecessor.

The Molar Teeth.

In the fœtus examined by me $\frac{\text{m. 1, m. 2}}{\text{m. 1, m. 2}}$ were distinguishable, but not very advanced in their development; $\frac{\text{m. 1}}{\text{m. 1}}$ exhibited slight lingual continuations of the dental lamina.

[1] A reference to Brandt's figures will show that it is only in *Crossopus* (fig. 2) that the 4 anterior teeth are quite within the limits of the premaxilla; in *Sorex* (fig. 1) the premaxillo-maxillary suture is so represented that the fourth tooth is situated in the gap between the two bones, a condition characteristic of the 4th tooth or canine of many Placentals.

Cusps.

The molar teeth of the adult belong to the trituberculo-sectorial type, the upper ones have square crowns bearing four cusps, *i.e.* 3 large equal ones belonging to the trigon and a small postero-internal cusp or hypocone. The lower molars are elongated, consisting of a trigon and a very large heel with two conspicuous cones (hypo- and entoconid); the cones in the lower trigon are not equally developed, the protoconid being much larger than the other two.

My specimen was too young to determine with any certainty the ontogeny of the cones, as only one of the main cones had made its appearance, the dental germ presenting the appearance of a high cone with a large posterior heel (metaconal region) and a slight internal extension. A plan of the dental germ at this stage shows that structure to be roughly triangular, the main and only cone being situated at the anterior extremity and slightly nearer the external border. From the position of this cone and from a comparison with the cusp ontogeny as seen in the molar of *Talpa*, with which it is identical in pattern, I think one may conclude that this single cusp is the paracone, the posterior extension representing the metacone, while the internal shelf indicates the position of the future proto- and hypocone.

In the lower jaw the main cusp is antero-external in position, and may be identified as the protoconid; a slight inward extension of the dental germ alone indicates the para- and metaconid, while a faint backward development foreshadows the future heel with its two cones.

The probable order of cusp-development is thus shown:—

1. Paracone.	1. Protoconid.
2. Metacone.	2. { Paraconid.
3. Protocone.	{ Metaconid.
4. Hypocone.	3. { Entoconid.
	{ Hypoconid.

A general examination of the Shrew's teeth shows that with the exception of $\frac{\text{i. 1}}{\text{i. 1}}$ and the almost undifferentiated 1st premolar, all the anterior teeth, viz. $\frac{\text{i. 2, i. 3, C. (i. 4), pm. 3, pm. 4}}{\text{i. 2 (i. 3) \quad\quad\quad pm. 4}}$, exhibit the labially situated enamel-germ of a predecessor, some of these being in a highly developed condition, possessing marked dentinal germs but no calcification. These structures, from a comparison with the teeth of other Insectivora, must be regarded as vestiges of that earlier developed set of teeth the milk-dentition: this homology is very striking when they are compared with the reduced milk-teeth seen in *Erinaceus*, and is rendered still more certain when we remember that there is indication of no other tooth replacement in the *Soricidæ*.

The relations of $\frac{\text{i. 1}}{\text{i. 1}}$ are very confusing, for the large development of the lingually-placed dental lamina would certainly suggest that they should be regarded as persistent milk-teeth; but against this view we have the fact that all the other anterior teeth (incisors, canine, and premolars) are now shown to be permanent teeth with vestigial milk predecessors, and also that in all other cases among the Placentalia where the teeth (especially the incisors) undergo great enlargement, as is the case with $\frac{\text{i. }1}{\text{i. }1}$ of the Shrew, it is invariably the permanent teeth which are enlarged, and not unfrequently the corresponding milk-teeth are reduced and even aborted (*Lepus* &c.). This condition is so universal that I am inclined to believe that in the Shrew, in the case of $\frac{\text{i. }1}{\text{i. }1}$ as with the rest of the incisors &c., the milk set has been reduced, but that here this reduction has been carried further until all trace of di. 1 has been lost, this being due to the large size and earlier development of pi. 1, these latter being developed far in advance of the posterior teeth. The lingual growth of the dental lamina is comparable to that which has been observed in connection with the successional teeth in so many forms (Seal (6), Dog (24), &c.), and which is there regarded as evidence of the existence of a 3rd or 4th set of teeth which might replace the permanent set, and to which the term postpermanent dentition has been applied. This structure may owe its greater development in the Shrew to the early appearance of the permanent set and to the complete loss of the milk series.

The relations of these teeth may be expressed as follows, bearing in mind that the milk-dentition is functionless and probably uncalcified:—

$$\text{I.}\begin{cases}1\quad 2\quad 3\\ \dfrac{\quad(2)\ (3)}{\qquad\ (3)}\\ 1\quad 2\ (3)\end{cases};\quad \text{C.}\begin{cases}1\,(\text{i.}\,4)\\ \dfrac{(1)\qquad}{}\\ 0\end{cases};\quad \text{P.}\begin{cases}0\quad 2\,(\text{c.})\quad 3\quad 4\\ \dfrac{\qquad\qquad(3)\ (4)}{\qquad\qquad\qquad (4)}\\ 0\quad 0\qquad 0\quad 4\end{cases};\quad \text{M.}\begin{cases}1\quad 2\quad 3\\ \dfrac{\qquad}{}\\ 1\quad 2\quad 3\end{cases}$$

Centetes.

My material for the study of this interesting form consisted of two fœtal specimens of different ages, measuring respectively in total length 36 mm., head length 12 mm., and 70 mm. with a head length of 20 mm., together with young and adult dried skulls in the teaching collection of the Royal College of Science and the more numerous specimens in the British Museum.

The relations of the milk and permanent teeth of the Tanrec are fairly well known, the most striking being the non-replacement of the 3rd upper incisor. This is especially interesting on account of what we have seen in *Gymnura* and *Erinaceus*, where that tooth is likewise only functional in one dentition; but here the resemblance seems to stop, for in *Gymnura* and *Erinaceus* the functional third incisor undoubtedly belongs to the replacing or permanent series, whereas in *Centetes* this tooth is developed nearly as soon as the undoubted milk-teeth and is shed about the same time as the members of that series.

On investigating the development of $\underline{\text{i. 3}}$ no indication whatever of a reduced successor is to be met with, the dental lamina being completely fused with the enamel-germ of this tooth, and consequently exhibits no lingual development. On the other hand, a slight outgrowth from the enamel-organ itself is visible on the labial side (Plate XXV. fig. 25, *x*), very similar to that figured by Kükenthal (**6**) in the Walrus (Taf. iii. fig. 7, *rvz.*), and which he there regards as the remains of an earlier dentition. One might therefore be justified in regarding this structure in *Centetes* as the last trace of $\underline{\text{di. 3}}$, and the functional tooth though early lost as $\underline{\text{pi. 3}}$. I am, however, very doubtful as to the advisability of basing a conclusion upon such slight evidence, more especially as I have never observed an undoubted reduced labial tooth in such a position, vestiges of an *earlier* dentition being always, so far as I am aware, related directly to the dental lamina, *i. e.* to the neck of the enamel-organ of the replacing tooth and not to the modified body of that structure.

Nevertheless, from the entire absence of any trace of a successor to this tooth and from the fact that the milk-dentition appears to be undergoing reduction in most Insectivores, and especially from the condition of the 3rd incisors in *Gymnura* and *Erinaceus*, I venture to suggest that this single $\underline{\text{i. 3}}$ of *Centetes* belongs to the permanent dentition, but that it is very early developed and shed with the milk-teeth.

It is interesting to note that in the closely allied genus *Hemicentetes* a 3rd upper incisor is present in the adult dentition; but although we know a little of the tooth change in this form (**3**. p. 75), yet we do not for certain know if this tooth is preceded by a functional milk-incisor.

The remaining incisors $\frac{\text{i. 1, i. 2}}{\text{i. 1, i. 2, i. 3}}$ together with the canines and the three premolars above and below are all present as functional teeth in both dentitions.

A very marked gap is noticeable between the canines and the first functional premolars both above and below: this tends to confirm the generally accepted view that the missing premolar is the 1st of that series. Unfortunately the dental lamina has been completely aborted from this gap in both stages examined, so that no indication of a missing tooth could be found.

The diastemata between these teeth are much more pronounced in the older stage and still more so in the adult; and from what I have seen in this and other long-nosed mammals (polyprotodont Marsupials), I am led to conclude that this elongation of the jaw is a secondary one, acquired since the reduction in the tooth series. This to my mind accounts for the absence of all vestiges of the suppressed teeth, for, when recently suppressed, tooth-vestiges are generally found even in short-nosed forms. The presence of four upper molars in this form appears to point to a very late elongation of the jaw, not to the retention of a primitive character.

The Molar Teeth.

In the younger of my two specimens $\overline{\text{m. 1}}$ alone was developed, while in the older stage two molars were present above and below; in the latter specimen a very strong lingual development of the dental lamina was noticeable in relation to $\frac{\text{m. 1}}{\text{m. 1}}$, that connected with $\underline{\text{m. 1}}$ being specially large (Plate XXV. fig. 26, *d. l.*), and a less marked but similarly related structure was observable in connection with $\overline{\text{m. 2}}$.

The Cusps.

The posterior premolars and all the molar teeth belonging to the upper jaw of this genus exhibit a high triangular crown surrounded by a low cingulum, this latter being most marked in the postero-internal region of the tooth (Plate XXVI. fig. 34); the trigon is characterized by the presence of 3 cusps, of which the antero-internal (5) is the dominant and is connected by an oblique ridge with the cusps usually regarded as the paracone and metacone respectively (2, 3)—this tooth apparently presenting an almost pure tritubercular type[1]. On examining $\underline{\text{m. 1}}$ in my oldest specimen, this tooth was found to be composed of a prominent main cone slightly inclined inwards, undoubtedly the protocone of the adult tooth; while growing out low down from the external surface of this main dental germ were two smaller cones—a slightly more pronounced anterior one occupying the position of the future paracone, and a less developed postero-external cone situated well behind the main cone, *i. e.* the exact position of the metacone. The order of cusp-development is given below:—

1. Protocone.
2. Paracone. } Nearly simultaneous.
3. Metacone.

In the deciduous 4th premolar likewise the protocone develops first, but here the metacone is in advance of the paracone.

The lower molars and posterior premolar are beautiful examples of the trituberculo-sectorial tooth, consisting of a high trigon and a low slightly developed heel; the three cusps of the trigon are pronounced—the protoconid (antero-external) being the largest, the metaconid is next in size and almost hidden by the former as it lies immediately internal to it, the paraconid being the smallest and most anterior cusp.

The development of these cones is well seen in $\overline{\text{m. 1 \& m. 2}}$ of my older specimen, and it is at once obvious that the protoconid is the original dentine germ, the other cusps being later outgrowths from

[1] The upper cheek-teeth of *Hemicentetes* should be examined by trituberculists, for in this genus a complete transition between the triconodont premolars and the trituberculate molars can be seen.

it; indications of the paraconid and metaconid are just visible as antero- and postero-internal shoulders to the main outwardly inclined cone (protoconid); of two former cones the metaconid appears to develop a trifle the earliest, as in $\overline{\text{m. 2}}$ the paraconid is not yet visible; in neither teeth had the hypoconid yet made its appearance. The order of development is thus shown to be:—

1. Protoconid.
2. Metaconid.
3. Paraconid.
4. Hypoconid.

This same order of development is presented by the cusps of $\overline{\text{dpm. 4}}$.

The probable relation of the dentitions is as follows:—

$$\text{I.}\left\{\begin{array}{ccc}1&2&3\\ \frac{1}{1}&\frac{2}{2}&\frac{0}{3}\\ 1&2&3\end{array}\right.;\quad \text{C.}\left\{\begin{array}{c}1\\ \frac{1}{1}\\ 1\end{array}\right.;\quad \text{P.}\left\{\begin{array}{cccc}0&2&3&4\\ \frac{0}{0}&\frac{2}{2}&\frac{3}{3}&\frac{4}{4}\\ 0&2&3&4\end{array}\right.;\quad \text{M.}\left\{\begin{array}{cccc}1&2&3&4\\ \hline \\ 1&2&3&4\end{array}\right.$$

ERICULUS SETOSUS.

The dentition of this genus is somewhat specialized, inasmuch as there is a distinct reduction in number of teeth, the 3rd incisor above and below being, in addition to the 1st premolar, completely wanting. In the case of the functional teeth possessed by *Ericulus*, the replacement is complete and may be represented as follows:—

$$\text{I.}\left\{\begin{array}{ccc}1&2&0\\ \frac{1}{1}&\frac{2}{2}&\frac{0}{0}\\ 1&2&0\end{array}\right.;\quad \text{C.}\left\{\begin{array}{c}1\\ \frac{1}{1}\\ 1\end{array}\right.;\quad \text{P.}\left\{\begin{array}{cccc}0&2&3&4\\ \frac{0}{0}&\frac{2}{2}&\frac{3}{3}&\frac{4}{4}\\ 0&2&3&4\end{array}\right.;\quad \text{M.}\left\{\begin{array}{ccc}1&2&3\\ \hline \\ 1&2&3\end{array}\right.$$

In a fœtal specimen examined, 78 mm. long with a head length of 23 mm., a slight differentiation of the dental lamina in the lower jaw was observed between $\overline{\text{i. 2}}$ and $\overline{\text{c.}}$, indicating the last trace of $\overline{\text{i. 3}}$; but above the reduction is more complete, for although there was a conspicuous gap present between $\underline{\text{i. 2}}$ and $\underline{\text{c.}}$, yet all trace of the dental lamina was lost.

The canines develop close to the 2nd premolar, and no indication of the missing 1st premolar was to be found.

Examination of the 4th premolar shows that ppm. 4 develops conspicuously in front of dpm. 4, the former being distinctly between dpm. 3 and dpm. 4, but on their lingual side.

Only a slight lingual development of the dental lamina was observed in connection with $\frac{\text{m. 1}}{\text{m. 1}}$.

The upper molars, like those of *Centetes*, are of trituberculate form, but possess in addition one slight antero-external cingulum cusp. The protocone is the largest cusp, while the para- and metacone form the outer border of the tooth and are separated by a slight notch only.

In the fœtus, in $\underline{\text{m. 1}}$ the protocone forms the main mass of the tooth, while the para- and meta-cones form two rounded external shelves not at present conical; in $\underline{\text{m. 2}}$ the protocone and a small antero-external paracone are alone visible. The order of formation being:—

1. Protocone.
2. Paracone.
3. Metacone.

The lower molars are trituberculo-sectorial, the heel being larger than in *Centetes* but still very low; here also the protoconid is the first to develop, but it is quickly followed by the paraconid and later by the metaconid; the hypoconid appears as a low backward continuation of the dentine germ, *i. e.* of the protocone, for it is a direct backward continuation of the base of that cone. The cusps develop in the following order:—

1. Protoconid.
2. Paraconid.
3. Metaconid.
4. Hypoconid.

In describing the upper molars of *Centetes* and *Ericulus*, I have regarded them, as is usually done, from a tritubercular standpoint; it is perhaps more correct to describe them as presenting a crown consisting of a large V-shaped internal cone sloping gently towards the external border of the tooth in the form of two ridges, which end in an external serrated margin consisting in *Centetes* of 4 small cusps (Plate XXVI. fig. 34, *a* & *b*, 1, 2, 3, 4), two of which (2 & 3) are regarded as the paracone and metacone. Internal the main cone (5) dips sharply down to an internal cingulum, which is slightly expanded posteriorly (7).

Talpa europæa.

It may seem unnecessary to reinvestigate the relationship of the milk and permanent teeth of the Mole, considering that all the details relating to these teeth appear to have been recorded by Spence Bate (**1**) as early as 1867, and that these have apparently been confirmed by Leche (**9**), who used the more modern method of serial sections; but unfortunately the former appears to have perpetrated one serious error, and the latter, owing to the fact that the specimens he examined where too young, has failed to rectify it. The point in question is the supposed presence of a needle-like deciduous first premolar in both jaws.

Reference to Bate's figures will show that he represents reduced but elongate needle-like predecessors to all the incisors, canines, and premolars, that preceding the 4th premolar alone being two-fanged and non-spicular in form.

On making an examination of the clarified jaws (Plate XXVI. fig. 29) of a young animal (hairless), one is immediately struck with the correctness of the greater part of these figures, but in respect to the first premolar they appear to be incorrect, for no trace is observable of Bate's dpm. 1. In order to be certain that I was not dealing with an abnormal specimen, I examined the clarified jaws of three specimens of about the same age as that studied by Bate, two others being cut one into horizontal and the remaining into frontal sections; three younger animals were also examined by the section method[1]. In all 10 half heads were investigated, and as these, obtained from various localities, all agreed amongst themselves in respect to the relations of the 1st premolar, I cannot but come to the conclusion that Bate's observations on this point are erroneous, and that the teeth which he describes as $\frac{\text{dpm. 1}}{\text{dpm. 1}}$ have no existence.

In the younger specimen all the deciduous teeth save the 1st premolar were well calcified, but the germs of the permanent teeth though distinct were but little differentiated. An examination of a horizontal section at this period (figs. 27 and 28) shows pm. 1 developing in a position precisely similar to that occupied by the reduced deciduous incisor, canines, and premolars; and, as is the case with the latter, the former exhibits a specialized portion of the dental lamina on its lingual surface, the only observable difference being that dpm. 1 is larger, uncalcified, and generally more backward than the other milk-teeth; also that the germ of ppm. 1 is slighter but might well be thought capable of developing at a later period. That this is not the case is seen from an examination of the older stage: here all the deciduous teeth are strongly developed and even dpm. 1 is now calcified (fig. 31); it is, however, very large and not at all of the nature of a vestigial needle-shaped tooth such as figured by Bate, but rather presents all the characteristics of the tooth regarded by him as ppm. 1. The permanent incisor, canines, and premolars (fig. 30) are now highly differentiated, with large enamel and dentine germs: a comparison of one of these with the indication of the germ of ppm. 1 (Plate XXVI. fig. 31, *d.l.*), shows that the latter is now less marked than in the earlier stage and is obviously aborting; consequently we may safely assert that it never attains any degree of specialization, but remains merely a slight swelling of the dental lamina.

The entire absence of any labial development from that portion of the dental lamina between the large enamel-organ of this tooth (dpm. 1) and the epithelium of the mouth, taken together with the position occupied by it, viz. one similar to that of the true milk-teeth, and the specialized thickening of the dental lamina on its lingual side, exactly resembling in appearance and position the true

[1] In all 3 stages were examined, including two specimens of stage 1, one of the 2nd, and five of the 3rd stage, all being older than Leche's stages.

(1)	55 mm. total length;	17 mm. head length.
(2)	58 „ „ „	18 „ „ „
(3)	95 „ „ „	30 „ „ „

successional teeth, shows conclusively to my mind that the first premolar is present as a calcified tooth in one dentition only, viz., in the milk-dentition; the milk-tooth $(\frac{\text{dpm. 1}}{\text{dpm. 1}})$ being very large and persisting in the adult along with the permanent teeth, a slight trace only of its successor being visible at a very early stage and only for a short period.

I must further conclude that the teeth figured by Bate as $\frac{\text{dpm. 1}}{\text{dpm. 1}}$ have no existence, his $\frac{\text{ppm. 1}}{\text{ppm. 1}}$ being in reality persistent milk-teeth.

I can only imagine that Bate was misled by the presence of the small needle-like teeth seen in connection with all the other antemolars into the belief that he had lost a similar one in connection with $\frac{\text{pm. 1}}{\text{pm 1}}$ during dissection.

Leche, while accepting Bate's account, which he was bound to do from the limited material at his disposal, states that pm. 1 was much more backward than the other milk-teeth, for while the latter had well differentiated enamel-organs, that belonging to pm. 1 was still club-shaped or only slightly advanced. Thus his specimens form with mine a perfect series, which together show that at no time is there more than one representative of pm. 1 differentiated as a tooth, *i. e.* dpm. 1, and only for a short period is there any indication of ppm. 1.

General Consideration of the Homology of Pm. 1.

Although there is undoubtedly but one calcified representative of pm. 1 present in the Mole, it is possible that some may be inclined to regard that tooth as belonging to the permanent rather than to the milk series; in that case the lingual growth of the dental lamina would have to be regarded as the representative of the post-permanent series, similar to that seen in connection with the permanent incisors and canines (fig. 28, *pc. dl.*). Such an interpretation has been adopted by Tims (24) for pm. 1 of the Dog and Pig[1], this author further stating his belief that in those cases (*Hyrax*, &c.) in which pm. 1 is duplicated, the two teeth represent the permanent and post-permanent series, and not the milk and permanent sets as one might suppose them to do. Against this possible interpretation of pm. 1 in the Mole may be urged in

[1] With regard to Tims's description of the 1st premolar of the Pig, in which he figures traces of three dentitions, I believe that there has been a mistake in the identification of the teeth, for which I am partially responsible, the sections and rough identification of the teeth being mine. On making a fresh and more careful examination of the sections, and comparing them with an older specimen, I find a very backward tooth-germ present between the canine and the supposed 1st premolar: this backward germ I take to be the true pm. 1, the tooth figured by Tims being dpm. 2; in that case the enormous development and swollen nature of the lingual growth of the dental lamina is accounted for, it being the germ of ppm. 2, while the labial growth must represent a trace of the pre-milk dentition.

addition the entire absence of any labial growth in connection with pm. 1, which one might naturally expect to find if the functional pm. 1 was ppm. 1, and if Bate's specimen was an exceptional one in which dpm. 1 had been retained.

One of the greatest difficulties met with in the study of tooth ontogeny is the want of a sure method for the determination to which set a given tooth belongs, for we may be dealing with a retarded member of an early set or an accelerated development of a later series, and, so far as I can judge, the identification can only be made through a study of the comparative morphology and phylogeny of the tooth, and not by its ontogeny alone. That the time of appearance of the enamel-organ does not help us is well seen in the Mole, where the germ of pm. 1 appears after the other milk-teeth and at the same time as $\underline{\text{pc.}}$; but this latter tooth appears long before the other permanent teeth, so that if we took the time of appearance of these tooth-germs as a criterion we should have to conclude that the deciduous incisors, canines, and three posterior premolars belonged to one set, the 1st premolar and permanent canine to a second set, and the other permanent teeth to a third series, a conclusion which, I think, condemns itself in the mind of all those who have studied this subject. Such a suggestion was put forward many years ago by Wortman (**31**), who regarded the four molars of the Placentalia as belonging to four distinct sets of teeth; this view does not appear to have met with any general recognition, it being more natural to suppose that the dental lamina though temporarily fused with the germs of the anterior molars yet retains its individuality and grows back with the elongation of the jaw to form fresh teeth belonging to the same series as the more anterior molars.

The only doubt arising in my mind as to whether I am right in referring the first premolar, in the Mole and in all animals where it is only known in one dentition, to the milk-series and so terming it dpm. 1, is due to the appearance seen in *Erinaceus*; for if in that genus the apparent tooth-vestige which I have mentioned (*ante*, p 562) as occurring between the two posterior upper premolars really represents a lost premolar, then the anterior premolar of *Erinaceus* is the true pm. 1; and as further I have shown that the deciduous predecessor of that tooth is a vestigial structure, the functional tooth must be referred to the replacing dentition. Consequently, if the above premises be true, we have here an example of the suppression of dpm. 1 and a persistence of ppm. 1, a conclusion antagonistic to that which I have arrived at concerning this tooth in the Mole, and I could only suppose that the homology of this tooth (pm. 1) varies in different and closely related animals.

I have thought it only fair to give this possible objection to my view here, but, as I have already mentioned, this supposed vestige of pm. 3 in *Erinaceus* is very slight and has not been observed by Leche in any of his stages; so it is highly probable that this structure has no morphological importance, and Leche's identification of the 1st functional premolar in this genus as pm. 2 may be quite correct, in which case the above objection would not hold, and the non-replaced pm. 1 may be regarded in all cases as a persistent milk-tooth.

The presence or absence of the 1st premolar appears to be intimately connected with the development of the canine, for in mammals, other than the Insectivora, it is commonly wanting or much reduced in all those forms possessed of a large canine tooth, while in those forms in which it is present in both dentitions the canine is either vestigial (*Hyrax*) or separated from the premolars by a wide diastema (*Tapirus indicus*). In the case with no succession to pm. 1, I should imagine that enlarged deciduous canine caused a slight decrease in size of dpm. 1, while the enormous permanent canine, which always develops early, caused a total suppression of ppm. 1; on the other hand, in those cases where pm. 1 is replaced, the non-development of the canines or their early removal forward allows the germ of ppm. 1 to mature and become functional. In forms such as the *Pecora*, in which both the canine and pm. 1 are wanting, this latter tooth was probably suppressed in some ancestor in whom the canine was well developed, and probably all trace of its germ has been lost, so that the subsequent loss of the canine has not caused pm. 1 to reappear; besides in these forms, as also in *Equus*, the posterior premolars have been so much enlarged that the anterior cheek-teeth became functionless and aborted.

Osborn (32) on palæontological evidence regards the single pm. 1 as a persistent milk-tooth.

The Molar Teeth of the Mole.

The lingual development of the dental lamina in relation to $\frac{\text{m. 1}}{\text{m. 1}}$ is most conspicuous, it being more strongly developed in the Mole and *Centetes* than in any other animals I have examined, so much so that it is highly suggestive of a rudiment of a successional tooth (Plate XXVI. fig. 32, *d.l.*); a similar but slighter growth is found in relation to m. 2.

The Cusps.

The molar teeth belong to the trituberculo-sectorial order; in the lower molars the heel is very large and bears two strong cusps; the heel in $\overline{\text{m. 1}}$ is larger than the trigon, but in $\overline{\text{m. 2}}$ and $\overline{\text{m. 3}}$ it is smaller; in all the protoconid is the largest and the paraconid the smallest of the main cusps; a small posterior cingulum-cusp is seen in $\overline{\text{m. 1}}$, while $\overline{\text{m. 2}}$ bears in addition a similar anterior cusp, in $\overline{\text{m. 3}}$ the anterior one alone is present. The upper molars (Plate XXVI. fig. 35) are mainly tritubercular, but a very small hypocone (8) is present; the protocone (7) is small, whereas the paracone and metacone (5 & 6), especially the latter, are very large and show a tendency to become crescentic or V-shaped, the summit of the cone being situated some distance from the outer border of the tooth; at the horns of the crescents, *i. e.* at the anterior and posterior extremities of the outer border, and in the middle of this edge where the two crescents meet, slight additional cones are raised up; these, however, appear very late (Plate XXVI. fig. 35, *a* & *b*, 1, 2, 3, 4).

Though no less than four stages were examined, yet it was not quite possible to determine which cusp was the first to appear, for even in the earliest stage of $\underline{\text{m. 3}}$ two slight prominences were already visible corresponding to the paracone and metacone. In the case of $\underline{\text{m. 1}}$ and $\underline{\text{m. 2}}$, three cusps were present in all stages, but of these the two external were alone conspicuous in the younger stages, the antero-external (paracone) being the largest, though in the adult it is smaller than the metacone; this, I think, shows that the paracone is the first to develop. The internal protocone (7) appears late as a low inward extension from the base of the paracone (fig. 32) and cannot possibly be regarded as the original axis of the tooth. The 4th cusp to appear is the small anterior external cusp, which is connected with the anterior slope of the paracone, the hypocone evidently appearing very late.

In the lower molars the protoconid forms the main axis of the dentine germ, and develops long before any of the other cusps, the next in order being the metaconid, followed by the hypoconid and entoconid, and lastly the paraconid. The heel itself minus its two cusps is developed very early before even the metaconid. The paraconid is especially late in its development; consequently the molar tooth before this cusp appears presents a very curious shape, the entire antero-external region of the dentine germ being absent.

Upper molars.	*Lower molars.*
1. Paracone.	1. Protoconid.
2. Metacone.	2. Metaconid.
3. Protocone.	3. Hypoconid.
4. Small antero-external.	4. Entoconid.
5. Hypocone.	5. Paraconid.

General Comparision of Results.

The 4th Premolar.

The homology of the 4th premolar of the Placentalia with the posterior premolar of the Marsupialia was first pointed out by Thomas, and there can be no doubt that this tooth in the two groups presents certain constant and striking features; thus dpm. 4 is nearly always molariform, whereas ppm. 4 is often almost unique in its pattern, being a highly specialized tooth, which in those cases where it resembles any other tooth has a striking similarity to dpm. 3 (*Hypsiprymnus*, *Canis*, &c.).

Some time ago I pointed out that in *Macropus* the so-called ppm. 4 developed from the dental lamina between dpm. 3 and dpm. 4 (**28**, pl. 36, fig. 19), and was evidently serially homologous with those teeth, but differed from them in being retarded in its development.

While investigating the development of dpm. 4 and ppm. 4 in the Insectivora, I have kept the above conclusion in mind, and allowing for the differences in the condition of the dentition in these two groups (Insectivora and Diprotodont Marsupials) I find a strong confirmation of this view, that ppm. 4 represents a tooth originally situated in front of dpm. 4, but retarded in its development, and subsequently displaced backwards or overgrown by dpm. 4.

This condition is more marked in the upper jaw, where in three of the genera investigated ppm. 4 develops distinctly in front of dpm. 4, in two slightly so, while only in one does it develop distinctly lingual to dpm. 4 (this is in *Sorex* probably a specialized form).

The molariform condition of dpm. 4 is well marked, but while in some Insectivora ppm. 4 is distinct in pattern, in others it is also molariform—the former condition being more marked in other groups of mammals, in some of which (Carnivora and Marsupials) ppm. 4 is so distinct in the characters of its crown from its predecessor that, taken in connection with the developmental features above recorded, I am forced to the conclusion that *dpm. 4 is a true molar accelerated in its development and growing forwards over the top of the retarded true 4th premolar*, or, in other words, dpm. 4 is the only true deciduous molar, while the tooth usually termed ppm. 4 is really the milk, but non-deciduous 4th premolar.

The above would account for the striking differences in character between the supposed deciduous and permanent 4th premolars of the "Kangaroo Rats," where dpm. 4 is molariform, and ppm. 4 that marvellous compressed cutting-tooth, identical in pattern with the anterior premolar dpm. 3. So also in the Carnivora with regard to the upper carnassial tooth. I think it is easier to conceive that the anterior molar should be accelerated in its development in order to supply the young animal with a crushing-tooth, than to believe with Cope (2) that the mere fact of a tooth-germ being shifted in its position relative to the angle of the mouth would cause such a total change in the character of two tooth-germs which were supposed to develop side by side as sisters from the same region of the dental lamina.

It is only fair to state that Leche (9. pp. 103 and 139) after considering the views put forward by me in a former paper (28), still concludes that the successor to dpm. 4 is the true representative of that tooth in the permanent series.

The Molars.

I have already described in my detailed account of the development of the molar teeth the presence of outgrowths from the dental lamina, to which structure the enamel-organs on these teeth are attached and from which they have arisen, both of the labial and lingual side of these teeth; these outgrowths, though more constant in connection with the 1st molars, yet were also found in the region of the 2nd molars in several genera.

The lingual continuation of the dental lamina was found in all six genera examined, whereas the labial growth was more irregular and only observed in three forms; this latter growth was most conspicuous in *Erinaceus*, where it was constant from the beginning of $\underline{\text{m. 1}}$ to the end of $\underline{\text{m. 2}}$.

A great deal of stress has been laid upon the presence of these structures, especially that of the lingual one, its presence having been said to prove that the molar teeth belonged to the milk-dentition. There is no doubt that if we simply compare such a section as fig. 26 (Plate XXVI.), representing the molar tooth of *Centetes*, with a developing milk-tooth which is known to have a successor, we should certainly conclude that the lingual growth of the dental lamina in the two cases was the same structure; and as it can in one case be shown to give rise to the enamel-organ of a replacing tooth, we might apparently be justified in concluding that in the case of the molar it represented a reduced enamel-germ of a permanent tooth, and that the molar tooth belonged in consequence to the milk-dentition. But it is now well known that we have in the Mammalia traces of three or four sets of teeth; and as it is highly probable that the Mammalia are derived from polyphyodont ancestors, it is possible that there might at any time appear traces of a polyphyodont dentition. It appears, then, to me that presence of a lingual continuation of the dental lamina does not necessarily imply that the labial tooth belongs to the milk-series; it might equally well belong to the permanent or to the post-permanent series, all traces of the earlier labial sets being lost, the lingual growth being not merely the enamel-germ of a successor, but the free end of the undifferentiated dental lamina, which may go on growing and producing fresh sets of teeth, as it does in the polyphyodont reptile, where it is the "anlage" of numerous enamel-organs.

Compare for a moment these two diagrams (p. 583): fig. 1 representing a section of the dental lamina of a reptile with a practically unlimited succession, while fig. 2 represents the milk-tooth of a mammal with a lingual development of the dental lamina, which is here known to give rise to a permanent tooth; we should not in this case be justified in concluding that "*m*" in fig. 2 was the homologue of 3 in fig. 1, merely because of the presence of this similar development of the dental lamina on its lingual side; we must either conclude that *m* is the homologue of 1 and the permanent tooth of 2, or perhaps 1 or both 1 and 2 have been completely suppressed, and therefore *m* is the homologue of 2 or 3 as the case may be. In fact we must start with the dental lamina from the gum, looking most carefully for labial rudiments, so as to be perfectly sure that none of the earlier sets of teeth have disappeared, before we can homologize the functional teeth, and we must naturally expect to find a lingual growth of the dental lamina constantly present, whether we are dealing with the 1st, 2nd, or 3rd sets, there being no reason to believe that there is an ultimate set which terminates the series. This is borne out by the discovery by numerous authors (**5, 7, 9, 20**) of a lingual growth of the dental lamina by the side of the germs of the permanent teeth.

Fig. 1. Fig. 2.

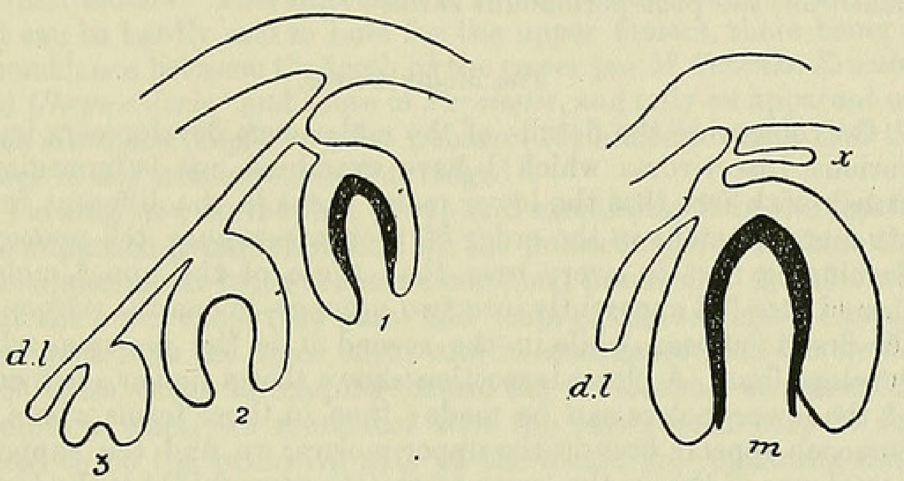

Fig. 1.—Diagram of the tooth-succession in a polyphyodont Reptile: 1, 2, 3, successive tooth-germs; *d.l*, dental lamina.

Fig. 2.—Diagram illustrating the relation of a molar tooth-germ (*m*) to the dental lamina (*d.l*).

Taking the above into consideration, the presence of *true and definite outgrowths* from the dental lamina nearer the gum than and thus labial to the molar germs is extremely interesting and suggests that possibly at least one set of teeth preceding the functional molars has been suppressed. These vestiges are, it is true, minute and variable, but when compared with the obvious vestiges of the anterior milk-teeth seen in *Erinaceus* it does seem rash to conclude that these labial growths in the molar region are the last indications of an earlier set of teeth.

If this is the case, then the molar teeth are not to be referred to the 1st, but rather to the 2nd dentition.

The question then arises, is the milk-dentition the 1st set of teeth? This has been answered in the negative by Leche, and I hope shortly to publish a further confirmation of this view.

Leche (**7** *a*) has discovered in the anterior region of the jaw of *Myrmecobius* a minute set of teeth which precede the functional set; and as the latter set are now usually regarded as the milk-dentition, this vestigial series is termed the pre-milk series, and may be compared with those small embryonic teeth seen in the Crocodile (**19** *a*) and Iguana (**8**)[1].

[1] Röse ("Das Zahnsystem der Wirbeltiere," Ergebnisse d. Anatomie u. Entwickelungsges., 1894) refers to traces of a pre-milk dentition in Man and suggests even an earlier set of teeth in the Vertebrata, a remnant of the placoid tooth-papilla, describing in all 5 sets, traces of at least four of which are found in the Mammalia.

I have adduced reasons elsewhere (29) to support the view that this pre-milk set, *i. e.* the first in order of time, has been completely lost in the molar region, and that these labial outgrowths of the dental lamina represent the now much reduced milk-dentition—the adult molars belonging to the 3rd or replacing set of teeth, the lingual continuation of dental lamina representing a potential 4th dentition, the post-permanent series.

The Molar Cusps.

On comparing the details of the molar cusp development in the various Insectivores which I have examined, one is immediately struck with fact that the lower molar cusps in the different forms are more constant in the order of their appearance, the *protoconid* developing first in every case, than those of the upper molars: these latter fall apparently into two groups—in one the *paracone* is the first to appear, while in the second it is the *protocone* which develops first. A closer inspection shows that a similar subdivision of the lower molars can be made; thus in those forms where the paracone appears first in the upper molars, we find the supposed homologue of this in the lower teeth (the paraconid)[1] is the last to develop, while those exhibiting the protocone as the first developed cusp above show the paraconid as second or third in order of development below.

These facts may be roughly tabulated thus:—

Group I. (4 genera).	Group II. (2 genera).
1. Paracone.	1. Protocone.
2. Metacone.	2. Paracone. } ? together.
3. Protocone.	3. Metacone. }
4. Hypocone.	
(5. Metaconule.)	
1. Protoconid.	1. Protoconid.
2. Metaconid.	2 or 3. Paraconid. } ? together.
3. Heel. { Ento. Hypo.	3 or 2. Metaconid. }
4. Paraconid.	4. Hypoconid.

A further examination of these groups reveals the fact that they are separated from one another by a second feature, which is possibly of greater importance than that of cusp ontogeny; I refer to the fact that the members of group I. possess either quadri- or quinque-tubercular upper molars, while in group II. these teeth are trituberculate.

It will be seen, then, that in the only living mammals believed to possess unmodified trituberculate teeth (molars and posterior premolars) which have been examined developmentally, the order of cusp ontogeny is in entire accord with the supposed order of

[1] The condition of this cone in *Sorex* is uncertain.

cusp phylogeny as advanced by the supporters of the Cope-Osborn tritubercular theory. This is a very striking and important fact, and one which will no doubt be considered by trituberculists as strongly supporting their theory, especially as it is generally stated that these trituberculate Insectivores most nearly, amongst living mammals, approach the Jurassic Trituberculata in the character of their molars. This statement is certainly true for the lower jaw, but can be hardly said to hold for the upper molars, there being no resemblance between the teeth of the upper jaw of *Centetes*, *Ericulus*, and *Chrysochloris* [1] and those of *Peralestes*, and only an apparent one with *Kurtodon* (*Stylodon*), for Osborn (**16**) himself states that this latter is not trituberculate but ridged [2].

Turning now to the first group and examining it in the light of the supposed primitive nature of the protocone, we find here that the upper molar teeth are more complex, possessing 4 or 5 cusps, that the outer cusps (the para- and meta-cones) are more strongly developed than the inner ones; and in accordance with this we find both these cusps developing before the protocone—an anomalous condition when we remember that the last-named cusp is supposed to be the primitive axis of the tooth, the remaining cusps being mere outgrowths from it. Perhaps, if these Insectivora were the only forms possessed of such a condition, we might agree with Osborn (**15**) that this is merely a case of accelerated development; but they are not alone in this respect, for in Man (**19**), in some Ungulates (**22**), and in certain polyprotodont Marsupials (**20**), the paracone invariably develops first, the protocone being either 2nd or 3rd in order of appearance. In fact, in every mammal so far examined, with the exception of the two Insectivores before mentioned, the paracone develops directly from the primitive dental germ and before either the protocone or metacone. The constancy of this condition is such that I do not think we can pass over it so lightly as Osborn does, as may be seen from the following quotation (**15**. p. 503): "In fact the external cusps not only appear before the internal cusp, which palæontology shows to be the more primitive, but they assume the crescentic form earlier. *In other words, their development is accelerated.*" (Italics mine.)

If the protocone represents the summit of the original protodont tooth of the ancestor of the Mammalia, it must be the direct continuation of the primitive dentinal germ, and as such should be found to develop in a line with the axis of that structure. That this is not the case is well seen in fig. 32 (Pl. XXVI.), where the paracone (5) is found to be identical with the primitive dentinal germ and the protocone (7) appears as a mere internal ledge growing out from

[1] *Chrysochloris* is trituberculo-sectorial, possessing a small heel, and not a pure trituberculate as usually stated. Lydekker (**10**) compares *Peralestes* and *Chrysochloris*, but I fail to see the resemblance.

[2] It is very difficult to ascertain Osborn's views regarding *Kurtodon*, for in his large memoir (**16**. p. 210) he states that there is no real homology between the *Kurtodon* and *Chrysochloris* dentition, whereas in his additional notes (**16** *a*) he appears to regard *Kurtodon* as one of the Trituberculata.

the base of this structure, the metacone and subsequently the hypocone being similarly derived from a backward extension of the base of the primitive dentinal germ. This primitive dentinal germ has, I believe, primarily a somewhat conical form in all cases, and one of the cusps of the adult tooth appears to be the direct continuation of this primitive cone, the remaining cusps being outgrowths usually from its base. It is *not* customary to find a blunt expanded table-like dentinal germ from which the cusps arise as secondary outgrowths—a condition which, it appears to me, must be necessarily assumed to support Osborn's view that the protocone is primary but retarded and the paracone its lateral derivative accelerated.

If it be the case that the paracone in the majority of Mammalia is the direct continuation of the primitive dentinal germ, and therefore of the single cone of the protodont mammalian ancestor, then we have the apparent anomaly of this primary cone giving rise, in the majority of forms, to the so-called paracone, *i. e.* the antero-external cone, while in a few it persists as the so-called protocone (antero-internal cone), a condition which suggests that the usually accepted identification of the cones of the *upper* molars is not in all cases the correct one.

It may be possible that in the above too much stress is laid on the ontogeny of the molar cusps; but, on the other hand, do we know sufficient of the phylogeny, as deduced from palæontological evidence, to prove that the primitive cone has in all cases been correctly identified in the upper molars? For though we have, thanks to the researches of Owen (**17**), Osborn (**16**), and Marsh (**11**), knowledge of a great number of Mesozoic mammals, yet the molar teeth found are nearly all lower ones, and but few upper molars (save multituberculate ones) are known until we reach Tertiary times [1], when the teeth have assumed forms whose cusps can be more easily homologized with those of living mammals than with the cusp or cusps of the Reptilian tooth or with that of the ancestral mammal. So that with regard to the evolution of the upper molars we are almost completely in the dark, for we know of no Triassic or Jurassic protodont upper molars, but three maxillæ (I believe) containing triconodont teeth, and but a few which, according to Osborn, contain trituberculate teeth.

I have tried to ascertain the exact number of *upper* jaws of Jurassic mammals possessing tritubercular molars or teeth approximating to that type, but have been unable to disperse the mystery which seems to envelop them. In England we certainly possess one specimen, which was described by Owen (**17**) as *Peralestes longirostris*, and is preserved in the British Museum; with this Owen associated a lower jaw which is now separated by Lydekker (**10**) from this form and assigned to *Amblotherium mustelula*. Owen also described four upper jaws, which he referred to *Stylodon pusillus*;

[1] Several isolated upper molars are known from the Upper Cretaceous rocks of N. America; some of these are said to be trituberculate (Osborn, "Mammals of tthe Upper Cretaceous Beds," Bull. Amer. Mus. Nat. Hist. 1893, p. 311), notably *Didelphops*, but this, though triangular possesses at least 6 cusps.

these have been separated from the lower jaws which Owen described under that name and placed in the genus *Kurtodon* (*Athrodon*) by Osborn (**16**), who first stated that they were not tuberculate, but now (**16** *a*) apparently regards them as examples of trituberculate molars.

In America, Marsh (**11**) has published the briefest note of the discovery of two upper jaws of *Dryolestes* and a single upper jaw of *Diplocynodon* (1 *c*, 8 cheek-teeth); these he has not figured, and his descriptions fail to show that they are tritubercular; in the case of *Dryolestes* he does not mention the cusps, while in *Diplocynodon* he mentions 5 cusps the arrangement of which does not suggest trituberculy.

In 1888 Osborn (**16** & **16** *a*) described the upper molars of *Kurtodon* (see *ante*), *Peralestes*, *Diplocynodon*, and also of the *Stylacodontia*, under which latter head he places *Dryolestes*, but on referring to this genus he states that the upper jaw is unknown!

In a later work (**14**) he only mentions the upper molars of *Spalacotherium* and of *all* the *Amblotheriidæ* as being trituberculate; evidently he refers *Peralestes* to *Spalacotherium*, as suggested by Lydekker (**10**), and *Kurtodon* to *Amblotherium* (Owen). These remarks will show what little material we have upon which to base the existence of the Jurassic tritubercular upper molar which is an essential feature in the tritubercular theory.

A perusal of Osborn's (**16**) description of the upper molars of *Peralestes* shows, however, that they are anything but typical trituberculate teeth, for instead of possessing one internal and two external cusps arranged in a triangle, the inner cusp forming the apex, we find *two internal* cusps[1], of which the anterior is the largest, and a serrated ridge extending along the external border bearing several small cusps; and as the anterior of these is slightly enlarged Osborn terms it the paracone, calling the two internal cones respectively the protocone (anterior) and the metacone (posterior). Now, according to the tritubercular theory, the metacone should be external and in a line with the paracone, not internal in a line with the protocone. Moreover, an examination of Osborn's figure and of the specimen shows that what he terms the paracone is here developed as an enlargement of the external cingulum and is not in any sense serially homologous with the metacone.

A comparison of Osborn's two published figures of these teeth shows considerable differences in them, and on examining the actual specimen one finds that the figure in his large monograph (**16**) is the most accurate, the more frequently copied figure (**13**) being rather exaggerated in favour of trituberculism; but with all he seems to have overlooked a small cusp on the antero-external shoulder of his protocone and between this main cone and this external paracone, which, to my mind, far better suggests the anterior homologue of the metacone (see Pl. XXVI. fig. 33) and consequently the paracone from a tritubercular standpoint, although I believe this tooth to be capable of a totally different interpretation.

If this tooth be compared with the molar teeth of the living Insectivora (figs. 34–36), it appears that the tuberculate external

[1] The specimen shows three internal cusps, see fig. 33.

cingulum seen in *Peralestes* is comparable with the similar structure so frequently present in this group, and well exemplified in the upper molars of *Talpa*. If so, it becomes further evident that the two larger cusps of *Peralestes* represent the paracone and metacone of these living forms, these cusps being commonly developed quite a long distance from the external border of the tooth (*Talpa*, fig. 35). Consequently the internal shelf, which we have seen in living Insectivores bearing the proto- and hypocone, is not developed in upper molars of *Peralestes*.

If this comparison is correct, we are justified in concluding that the upper molars of this fossil form were not tritubercular in the sense understood by the supporters of the Cope-Osborn theory, and, further, those of *Kurtodon* being undoubtedly ridged and not tuberculate, while those of *Dryolestes* and *Diplocynodon* are either undescribed or possess 5 cusps, we consequently have no palæontological evidence to support the assumption that a tritubercular stage was passed through by the mammalian *upper* molar in its evolutions from a protodont or possibly a triconodont tooth. Under these circumstances I see no reason to believe that the primitive cone must necessarily occupy an antero-internal position such as Osborn's protocone does.

Palæontological evidence being then wanting or so fragmentary, we are obliged to fall back on the less torn pages of ontogeny. On doing so, we find that the upper molar cusp, which develops first and as a direct continuation of the dental germ in the majority of the Mammalia, is the antero-external or paracone: this I think is strongly in favour of the view put forward by Röse (19), that the paracone is the most primitive cusp, though I think it would be rather confusing to apply Osborn's term "protocone" to it, seeing that this term has been already applied to another cusp in the same tooth.

Of the primitive nature of the paracone we have slight palæontological evidence if, as I have suggested, the largest cone of the *Peralestes* upper molar (Osborn's protocone) is the homologue of the paracone of living Insectivores. But if we further include the molariform premolars in our study, we find this view is supported both by ontogenists (22) and palæontologists, for Scott (21 *a*) has proved, and Osborn and Wortman (32) have accepted his conclusions, that the antero-external cone in these teeth is the primitive one from a palæontological standpoint, and Taeker has shown in the Ungulates, and I myself in the Insectivora, that this antero-external cone in the premolars develops first in the ontogeny of the premolar cusps.

With regard to the tritubercular upper molars of the *Centetidæ* &c. (fig. 34, *a* & *b*), I should conclude that the main cone of this type of tooth, usually termed the protocone, was really the paracone: the whole tooth representing only the antero-external triangle of such a form as *Talpa* (fig. 35, *a* & *b*), *i. e.* the crescentic paracone with its two external cingulum cusps, the two last named being commonly but incorrectly described as the para- and meta-cone in *Centetes*: that in the *Centetidæ* no marked indications of the protocone or metacone are as yet visible, while in *Chrysochloris* (fig. 36. 7) the first indication of the protocone has appeared, viz. the internal shelf.

This attempt to homologize the main cone of the upper molars of the *Centetidæ* and *Chrysochloris* with the paracone of other Insectivora is a modification of the view put forward by Mivart in 1868 (**12**). He regarded the tricuspid triangular crown of the molar teeth of *Centetes* as a concentration of the eight cusped teeth of *Talpa*. An examination of his figures and description will show that he believed the so-called paracone and metacone of *Centetes* and *Chrysochloris* to be external cingulum cusps, the main cone of these teeth being formed by a fusion of cones corresponding to the para- and metacones of *Talpa*, while the protocone and hypocone of the latter he regards as represented by the small internal lobe seen in *Chrysochloris*[1]. This view accords in its most important respects with mine, but I do not think that the ontogeny of the trituberculate insectivore molar justifies Mivart's fusion theory, but rather suggests that this tooth corresponds only with the paracone triangle of the Mole's tooth.

Such an interpretation would bring these forms into entire accord with the other Insectivores and the Mammalia in general, and we should then find that the cusp which directly continues the dental germ, and consequently is the first to develop, is in all cases homologous, though unfortunately the same name has not been applied to it in all cases.

Thus the primitive cone of the upper cheek-teeth of the ancestral mammal finds its homologue in the protocone of the premolar, in the paracone of most molars, but in the protocone of the molars of the trituberculate Insectivores and *Peralestes*. This has been proved ontogenetically for both the premolars and molars, phylogenetically also in the former, while in the latter the phylogeny of the primitive cusp is still doubtful.

The evolution of the primary cusp of the premolars and molars is now brought into harmony, and it is no longer necessary to suppose that the cusp arrangement of two teeth such as pm. 4 and m. 1, often identical in pattern, have evolved upon different lines.

To briefly recapitulate my conclusions :—

(1) The antero-external cone, or paracone above and protoconid below, is the primitive cone both in the molars and premolars.

(2) The protocone is borne on an internal shelf of secondary origin (internal cingulum).

(3) The metacone is a similar backward development of the paracone, arising very early long before the protocone.

(4) The hypocone stands related to the metacone as the protocone does to the paracone.

(5) The paracone as the primary cone in the upper molars finds its homologue in the protoconid below[2].

[1] Unfortunately the cones have been incorrectly lettered in his figure of the upper molar of *Chrysochloris*, as may be seen on reference to his description.

[2] A paper by Winge (**26**) in Danish evidently upholds the same view, viz., that the *paracone* is the homologue of the *protoconid*; unfortunately I am unable to read the paper, but his lettering in his plate and diagrams are very clear on this point.

(6) The evidence advanced in support of the tritubercular theory is insufficient to prove that the upper molars primarily evolved on the lines of that theory.

(7) Owing to want of material, trituberculists have been led to assume that the upper molars of the early Mammalia passed through similar stages to those which they have determined for the lower teeth, and consequently they have in most cases incorrectly identified the primary cone (save in *Peralestes* and the living *Centetidæ* and *Chrysochloris*).

(8) That as regards the primary cone, its ontogeny recapitulates its phylogeny.

I do not mean to deny for one moment the occurrence of the tritubercular type of upper molar tooth, nor even to underrate its phylogenetic importance; for no one who has studied cusp ontogeny can fail to notice the frequency of its appearance, and the fact that often (though not always) the three cones of the trigon are the first to appear during development. What I desire to point out is, that there is no evidence to show that this type of upper molar arose in the way suggested by trituberculists, and that they have in most cases overlooked the true primary cone.

If the triconodont tooth be a stage in the evolution of the mammalian molar, then I should believe that the anterior cone disappeared, the main cone becoming enlarged as the paracone and the posterior one as the metacone. At this stage the upper teeth overhang and bite outside the lower molars, and the future antero-internal cone (protocone) was developed as an internal shelf acting as a mortar for the cusps of the lower teeth, and at a much later period developed a cusp. The hypocone arose in a similar way with the elongation of the teeth.

The function and origin of the external cingulum with its numerous cusps (2–4) is difficult to understand, for in the living Mole it is quite outside and free from all contact with the lower molars; possibly it is of use to insect-feeding animals, giving them greater hold of their slippery prey.

In the *Centetidæ* and *Peralestes*, the upper molars could not have overhung the lower ones to the same extent, consequently no internal lobe bearing the protocone was developed and the external cingulum was very largely developed.

I have purposely left out all reference to the multituberculate and concrescence theories, having restricted my researches to endeavouring to ascertain whether the trituberculate theory respecting the upper molars rested upon any solid basis, and whether one of the molar cusps was more primitive in its mode of origin than the others.

Ontogenetically, I have failed to find any support for the concrescence theory, neither do I consider that any of the evidence put forward by Röse and Kükenthal is at all conclusive in its favour.

On comparing the several families which grouped together compose the order Insectivora, we find a considerable variation in their dentition, both as regards the number of their teeth and the specialization of the individual members of the dental series.

Thus in *Gymnura* and *Talpa* we find in the adult the full placental dentition of 44 teeth, while in two Shrews (*Diplomesodon* and *Anurosorex*) the dentition is reduced to 26 teeth, other families presenting numerous stages intermediate between these two. If *primitive,* the supposed presence of 4 upper incisiors in *Sorex* and the 4 upper molars of *Centetes* must be of great interest, but the former I believe is capable of being interpreted differently, and the latter to be a secondary character.

A closer examination of these dental variations shows that they can be grouped under four heads:—

(1) A tendency for a suppression of the 3rd incisor above and below, di. 3 disappearing first.

(2) A suppression in the premolar series, pm. 1 in the *Centetidæ*, pm. 2 in *Selenodon.*

(3) A suppression of the posterior molars, the number varying from $\frac{4}{3}$ to $\frac{2}{2}$, the normal number being $\frac{3}{3}$.

(4) A tendency for reduction in the functional importance of the milk dentition.

Although representatives of only 5 out of the 9 families of the Insectivora (Flower and Lydekker, 4) have been systematically examined, this last variation is so marked, that one is forced to the conclusion that the order as a whole is tending to lose its milk-teeth.

Among the forms examined, probably only *Ericulus* and *Echinops* possess the same number of functional milk and permanent antemolar teeth, but these forms have already a reduced dentition. Of those provided with 44 teeth, viz. *Gymnura* and *Talpa*, we find in the former $\frac{\text{di. 3, dpm. 2}}{\text{dpm. 2}}$ reduced and functionless, while in *Talpa*, omitting the 1st premolar, all the remaining milk-teeth are reduced and though cutting the gum can hardly function (if at all) for more than a week or two.

The remaining genera examined show this reduction in a varying degree, the maximum being attained in *Sorex*, where in all probability the entire milk series is reduced and functionless.

If then it be a fact, as is now generally believed, that the milk dentition preponderates in the early Mammalia and in the living Marsupials, then we must come to the conclusion that the living Insectivora are specialized forms tending towards a Monophyodont condition in which the preponderating dentition is the replacing or permanent set.

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EXPLANATION OF PLATES XXIII.–XXVI.

In all cases the teeth represented are from the left side, and when shown in section the anterior surface is represented, so that the left side of the Plate represents the lingual and the right the labial side of the jaw.

Plate XXIII.

Figs. 1–8 *a*. *Erinaceus*.

Fig. 1. Frontal section of the developing canine. *dc.*, upper deciduous canine; *pc.*, germ of permanent canine.

1 *a*. Ditto. Older stage. Deciduous canine calcified.

2. Frontal section of the developing 3rd upper incisor. *di.* 3, vestigial milk-incisor; *pi.* 3, germ of permanent tooth.

2 *a*. Ditto. Older stage. Vestige of *di.* 3 and neck of the enamel-organ of the functional tooth (*pi.* 3).

3. Frontal section of vestigial lower incisor, *i.* 1.

4. Germ of 3rd lower incisor (*pi.* 3). *di.* 3, probable last trace of deciduous tooth.

5. Developing lower canine (*pc.*) with its vestigial milk predecessor (*dc.*).

6. Three sections through the dental lamina between the 2nd and 3rd functional upper premolars. (These should incline from left to right.)

7. Ditto between the two lower premolars; *pm.* 3, germ of missing premolar.

8. Germ of 1st functional upper premolar (*ppm.* 2) with vestigial milk predecessor (*dpm.* 2).

8 *a*. Germ of *dpm.* 2 and *ppm.* 2.

Plate XXIV.

Figs. 9, 9 *a*. *Erinaceus*.

Fig. 9. Upper jaw of a young *Erinaceus*, side view. After Leche.

9 *a*. Ditto. Palatal aspect of adult.

Figs. 10–14. *Gymnura.*

Fig. 10. Developing 3rd upper incisor (*pi.* 3) with calcified vestigial milk predecessor (*di.* 3).
11. Germ of 2nd upper premolar (*ppm.* 2) with reduced milk predecessor (*dpm.* 2).
12. Germ of 2nd lower premolar (*ppm.* 2), milk predecessor (*dpm.* 2) still more reduced.
13. Upper jaw of *Gymnura* showing milk dentition and cavities occupied by germs of permanent teeth. *m.* 1, first molar; *dpm.* 2, 2nd deciduous premolar.
14. Germ of *dpm.* 3 and *ppm.* 3, the latter just appearing.

PLATE XXV.

Figs. 15–24. *Sorex.*

Fig. 15. Developing 1st lower incisor (*pi.* 1), lingual growth of dental lamina (*d.l.*).
16. Germ of *pi.* 2 with labial vestigial milk predecessor (*di.* 2).
17. Ditto, *pi.* 3; ditto, *di.* 3.
18. Ditto, permanent canine, *pc.* (i. 4); ditto, *dc.*
19. Plan of enamel germs of upper teeth in relation to the dental lamina and to the jaw-bones (*pmx.* and *mx.*).
20. Germ of *pi.* 2 with labial vestigial milk predecessor (*di.* 2).
21. Ditto of *pi.* 3 and *di.* 3 (vestigial).
22. Ditto of *ppm.* 3 and *dpm.* 3 (vestigial).
23. Ditto of *ppm.* 4 and *dpm.* 4 (vestigial).
24. Ditto of *ppm.* 4 and *dpm.* 4 (vestigial).

Figs. 25–26. *Centetes.*

Fig. 25. Germ of *i.* 3.
26. Germ of *m.* 1, showing specialization of lingually placed dental lamina (*d.l.*).

PLATE XXVI.

Figs. 27–32. *Talpa.*

Fig. 27. Horizontal section of the upper jaw, showing the tooth germs in relation to the dental lamina; the milk-teeth are well developed, while the germs of the permanent teeth are just visible as swellings of the dental lamina.
28. Enlarged drawing of a deep horizontal section passing through the germs of *dc.*, *dpm.* 1, *dpm.* 2, *dpm.* 3, and those of their successors in the permanent series. *pc.* very advanced; *ppm.* 1 transitory, never becoming more developed.
29. Clarified jaw of a very young Mole (hairless), showing the milk and permanent dentitions *in situ.*
30. Frontal section of a specimen about the same age as the last, showing *dpm.* 2 well calcified and the germ of *ppm.* 2.
31. Ditto, ditto, passing through the first premolar (*dpm.* 1), showing last trace of the lingual dental lamina (*d.l.*).
32. Ditto of a young stage, passing through the germ of *m.* 1, showing the primitive dentine germ giving rise to the paracone (5), and the first trace of the protocone (7), also a very prominent swollen lingual development of the dental lamina.

Fig. 33. (*a*) palatal, (*b*) external aspect of an upper molar (*m.*) tooth of *Peralestes.*
34. Ditto, ditto of *Centetes* (*m.* 1).
35. Ditto, ditto of *Talpa* (*m.* 2).
36. Ditto, ditto of *Chrysochloris* (*m.*).

The numerals attached to the last 4 figures represent an attempt to homologize the cusps.