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ON

THE DEVELOPMENT AND HOMOLOGIES

OF

THE MOLAR TEETH OF THE WART-HOGS

(*Phacochærus*),

WITH ILLUSTRATIONS OF A SYSTEM OF NOTATION FOR THE TEETH IN THE CLASS MAMMALIA.

BY

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XXIV. *On the Development and Homologies of the Molar Teeth of the Wart-Hogs* (Phacochœrus), *with Illustrations of a System of Notation for the Teeth in the Class* MAMMALIA. *By Professor* OWEN, *F.R.S. &c.*

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IN a paper by EVERARD HOME, Esq., read before the Royal Society, May 30, 1799, some observations were communicated upon the form, structure and succession of the teeth of the Wart-Hogs of Africa, now included in the genus of the Hog-family called *Phacochœrus,* but noticed in that paper as a single species under the name of *Sus Æthiopicus.* The observations are illustrated by two plates. The first (tab. xviii.) gives "a side view of the skull of the *Sus Æthiopicus* (half the natural size), to show the situation and appearance of the large grinder, and the remains of the alveoli belonging to the fangs of the preceding one*." The second (tab. xix.) gives a "side view of the skull of the young *Sus Æthiopicus,* to show the mode in which the grinders come forward as the large one increases in size†." This plate includes also a side view and a transverse section of the crown of the large full-grown grinding tooth.

The conclusions drawn from the facts given are, that the *Sus Æthiopicus* resembles the Elephant "in the whole number of grinding teeth belonging to each side of the jaw being confined in a case of bone, so as to form one large grinding surface, and the teeth being pushed forward from behind, instead of a second set being formed immediately under the fangs of the first, as in other animals; which are peculiarities not met with in any teeth hitherto described, except those of the Elephant‡." The grinding teeth of the *Sus Æthiopicus* are described to be "four in number on each side of the jaw"§; .... the fourth or last large tooth is considered to be a second set of teeth, which, as it advances forwards, pushes the other teeth before it; ...."the most anterior of these, as soon as its body is worn away, has its fangs removed by absorption and drops out: the same thing takes place with the second and third; and, in this way, room is made for the large one to supply the place of all the others‖." The mode in which they succeed one another is stated to be illustrated by the side view of the jaw given in tab. xix., in which the fangs of the different teeth are exposed.

I have shown in my 'Odontography' ¶, that the facts detailed in HOME's paper were insufficient to enable him to explain all the necessary circumstances respecting the curious mode of dentition of the Wart-Hogs; that other stages of dentition, unknown to that author, had demonstrated a second set of teeth formed under the fangs of some

* Philosophical Transactions, 1799, p. 256. † Ibid. p. 257. ‡ Ibid. p. 247.
§ Ibid. p. 250. ‖ Ibid. p. 250. ¶ Vol. i. p. 554.

of the first set, or above them in the upper jaw; and also that the subsequent shedding of the teeth in advance of the last large grinder was not in the order in which they are pushed out in the Elephant, the Wart-Hogs deviating very remarkably from that and all other quadrupeds in this respect.

In the course of subsequent researches and comparisons, I have determined the original specimens in the British Museum and that of the Royal College of Surgeons, which were drawn and engraved to illustrate HOME's paper, by which I have ascertained that the drawings were taken from two distinct species of *Phacochœrus*; and I have been able to detect certain inaccuracies in the reduced figures in the engravings, which give countenance, not afforded by the specimens themselves, to the ideas of the mode of succession of the teeth described in HOME's paper. I propose, therefore, to give a more precise description of the subjects of the beautiful engravings, tab. xviii. and xix. of the Philosophical Transactions for 1799, and to add the additional facts and illustrations of the peculiarities of the dentition characteristic of the two species of Wart-Hog, and which determine the true number, kinds and succession of the grinding-teeth in both species.

Tab. xvii. (Philosophical Transactions, 1799) gives a view of the skull of an old *Phacochœrus Æliani*, VAN DER HOEVEN, the common species of Nubia, Abyssinia, Senegal and Cordofan, and sometimes called the North African Wart-Hog. It is well characterized by having, when fully grown, six functional incisors in the under jaw and two incisors (*i.* 1.) in the upper jaw, together with forms and proportions of the other teeth, which will be subsequently adverted to. The characteristic incisors are sufficiently indicated in the figure; the large posterior grinders are alone retained in the molar series of both jaws.

Tab. xix. fig. 1 (Philosophical Transactions, 1799) gives a view of the cranium of a younger individual of the *Phac. Pallasii*, VAN DER HOEVEN, the Wart-Hog most common, though not peculiar to the Cape and the Guinea coast districts. The molar teeth which are exposed in this figure are, taking them from before backwards, the last premolar, the symbol of which is p 4; the first true molar, m 1; the second true molar, m 2; and the last true molar, m 3.

The teeth are drawn somewhat reduced in size, but not in a just proportion to the reduction of the size of the cranium and of the upper tusks; nor are the relative lengths of the crown and fangs correctly given. The crown of the first true molar, *e. g.*, is represented of the same length as that of the fourth premolar which precedes it, and nearly of the same length as that of the second true molar, whereas in the original specimen it is much shorter in consequence of having been longer in use. Had the differences which these teeth actually show in the extent of the abrasion of their respective crowns been appreciated and duly considered, it might have excited the suspicion that the second tooth, with an almost exhausted crown and much-absorbed fangs, would be shed before the first tooth, the summit of whose long, obtuse and cement-covered crown had only recently been subject to the wear of mastication.

The grinder, which is the subject of figs. 2 and 3, tab. xix., is the last molar from the right side, lower jaw, of the *Phac. Æliani*, of the natural size.

To determine whether any successional teeth were developed above or beneath the fangs of pre-existing teeth destined to be displaced by such development, in other words, whether a true deciduous series and a premolar series of teeth existed in the Wart-Hogs, required an examination of the jaws of an individual younger than the youngest specimen examined and figured by HOME.

The subject of Plate XXXIII. fig. 1 of the present communication is of the required immaturity, and, with the other specimens to be described, supplies those links in the series which were wanting for the explanation of the entire course of the truly remarkable dentition of the genus *Phacochœrus*.

Fig. 1 shows a side view of the teeth in the young *Phac. Æliani*; the grinding surface of the molar teeth in use is given, from the upper jaw in fig. 2, and from the under jaw in fig. 3. These teeth include all the milk-molars which are developed, together with the first permanent true molar. The milk-molars are 3—3 in number in the upper jaw, and 2—2 in the lower jaw. The first true molar, *m* 1, is also fully developed and in use in both jaws. The summit of the second true molar (*m* 2) is just appearing above the socket.

The length of the skull exhibiting this instructive phase of dentition is 10 inches.

The milk-molars answer to the teeth of the typical dentition symbolized by *d* 2, *d* 3, and *d* 4 in the upper jaw, and to *d* 3 and *d* 4 in the lower jaw.

The first is implanted by two fangs, the second by three, the third by four fangs; the shape of these teeth is sufficiently illustrated by the figures.

Their rate of increase in size from the first to the last is considerable, yet not equal to that manifested in the true molars. Upon examining the substance of the jaws above the deciduous molars of the upper jaw and beneath those of the lower jaw, two formative alveoli and the trace of a third were detected in the upper jaw, one above *d* 4, containing the crown of a premolar; the other above *d* 3, and the rudimental cell above *d* 2. The matrix, which the latter might have contained, had not begun to be calcified. A small formative socket was found beneath the last milk-molar of the lower jaw containing the crown of a premolar. The gubernacular canal from this socket opened between the fangs on the inner side of the milk-tooth. A second still smaller socket of an anterior premolar was beneath the interspace between the two milk-molars.

The true nature of the molar behind the milk-teeth in both jaws was plainly shown by its long fangs extending beyond the parallel of the formative sockets of the successors of the milk-teeth, and widely open at their ends: this tooth has no vertical successor and is the first true molar, *m* 1. Only the crown of the second true molar (*m* 2) is formed at the stage here described; and a few detached columns of the still larger and more complex third molar (*m* 3) were all that were calcified in its commencing formative alveolus.

In none of the other members of the Hog family is the first true molar (*m* 1) so much worn down at the corresponding early stage of development of the second true molar, and it is upon this precocious growth of the first true molar that the chief peculiarity of the order of shedding of the teeth of the *Phacochœri* depends.

In the *Phac. Æliani*, the penultimate and last milk-teeth (*d* 3, *d* 4) in the upper jaw are displaced and succeeded by corresponding premolars, which therefore answer to *p* 3 and *p* 4 of the typical series. The anterior small milk-grinder, *d* 2, is sometimes succeeded by a minute premolar, but occasionally this is abortive, or absorbed before it cuts the gum. In the lower jaw both milk-molars (*d* 3 and *d* 4) are succeeded by the corresponding premolars *p* 3, *p* 4, at least in the *Phac. Æliani*.

The stage of dentition of the *Phac. Æliani*, given in figs. 1, 2 and 3, corresponds with that in the common Hog, illustrated by the teeth in the lower jaw in Plate XX. fig. 1 of the Philosophical Transactions for 1801. In that figure the last grinder in place is the first true molar, *m* 1; the penultimate is the last milk-molar, *d* 4; the next is *d* 3, the next *d* 2; and a little in advance of this, between it and the rudimental canine, is the small anterior premolar, *p* 1. The germs of the other premolars, *p* 2, *p* 3 and *p* 4, are shown in their formative sockets beneath the deciduous teeth they are destined to replace.

If the symbols above given be marked upon the teeth in the figure cited, the homologies of those in the reduced dentition of the young Wart-Hog will be readily appreciated. The teeth developed in the lower jaw of that species are,—*d* 3, *d* 4, *p* 3, *p* 4 and *m* 1 : in both jaws *m* 2 has only its crown developed, and *m* 3 only the commencement of its crown. The teeth which are suppressed in the *Phac. Æliani* are, in the lower jaw, *d* 1, *d* 2, *p* 1 and *p* 2. In the upper jaw *d* 1 and *p* 1 are suppressed, and sometimes also *p* 2.

The next stage of dentition (Plate XXXIV. figs. 4 and 5) shows the shedding of the deciduous molars to be concomitant with the coming into place of the second true molar, *m* 2 ; it is well illustrated in the cranium of a young *Phac. Æliani* from Senegal in the Museum of Comparative Anatomy in the Garden of Plants: in which each of the three deciduous molars of the upper jaw have been succeeded by a premolar (*p* 2, *p* 3, *p* 4, fig. 4), and the same with regard to the two deciduous molars in the lower jaw (*p* 3, *p* 4, fig. 5). The anterior angle of the crown of the last huge molar has also begun to protrude from the formative alveolus, so that the permanent or second molar series now shows $\frac{6-6}{5-5}=22$, which is the greatest number of grinders presented at any given time in the genus *Phacochœrus*. The first true molar, *m* 1, is however worn to near the fangs, and its grinding surface, as compared with that in Plate XXXIII. fig. 2, begins to be simplified. The homologies of the teeth at this period are indicated by the symbols attached to them in the figures.

The stage of dentition of the young *Phac. Pallasii*, figured by HOME in tab. xix. of his memoir, is a little more advanced than that of the *Phac. Pallasii* above described; but although scarcely half the grinding surface of the last molar, *m* 3, has come into use, all the premolars in advance of the last, *p* 4, have been shed, Plate XXXIV. fig. 8.

In the specimen of *Phac. Æliani*, of which the grinding surface of the teeth is figured in Plate XXXIV. figs. 6 and 7 of the present memoir, although the major part of the last large grinder is in use, the penultimate premolar (*p* 3) is retained as well as the last (*p* 4). The molar series here shows 5—5 in the upper jaw and 4—4 in the lower jaw; their homologies are indicated by the symbols attached. By reason of the precocious development of *m* 1, we now find it quite worn down to the fangs; and in the lower jaw (fig. 7) it is wedged between *p* 4 and *m* 2 into a space which is two-thirds less than the antero-posterior extent of the crown of the same tooth shown in the younger specimen (Plate XXXIII. fig. 2). The reduction of size of *m* 1 is however quite intelligible by observing the much-constricted neck from which the long fangs are continued in that specimen (see *m* 1, fig. 1).

The figures of the grinding surface (figs. 6 and 7) suffice for the characteristic forms of the grinding-teeth now in use.

The specimen of *Phac. Æliani* (No. 773. Mus. Coll. Chir.) shows the last remnant of *m* 1 wedged into the diminished interspace between *p* 4 and *m* 2, and the corresponding interspace in the lower jaw, from which such remnant of the first true molar has been shed.

The skull of an older *Phac. Æliani* (No. 772) shows the displacement of the first true molar in both jaws and the reduction of the molar series to $\frac{4-4}{3-3}$; the teeth being *p* 3, *p* 4, *m* 2 and *m* 3 above (fig. 9), *p* 4, *m* 2 and *m* 3 below (fig. 10). There is no vacuity now in the series to show a true molar to have been shed, as it has been in so unusual an order.

The next stage of dentition which I have observed in this species is the loss of the anterior premolar *p* 3, and the great wearing down of *m* 2 (fig. 11), and in one instance in the lower jaw *m* 2 was shed before *p* 3.

The skull of a male *Phacochœrus* in the British Museum*, from the Cape de Verd, measuring 16 inches 6 lines in length, with the incisors of the *Phac. Æliani*, viz. $\frac{1-1}{3-3}$, and the same broad and shallow posterior channel upon the canines $\frac{1-1}{1-1}$, shows the same numerical molar formula as No. 772, but the teeth are different in the upper jaw, they are *p* 3, *p* 4, *m* 2 and *m* 3; in the lower jaw they are *p* 3, *p* 4 and *m* 3; both first and second true molars being shed in this jaw, whilst the last two premolars are retained.

In the skull of a female *Phacochœrus*, $13\frac{1}{2}$ inches in length, from South Africa, in the British Museum, but with the incisive formula of the *Phac. Æliani*, the molar

* The term *Phacochœrus Æthiopicus* is retained for the species represented by this skull in the British Museum.

series is $p\,\frac{1}{1}$, $m\,\frac{2-2}{2-2}$; the teeth in both jaws being p 4, m 2 and m 3 : here the penultimate premolar has been shed before the penultimate true molar, the socket of which however alone indicates it in the lower jaw.

In a still older specimen, p 3 and m 2 have been shed in both jaws, and the dental series is reduced to $\frac{2-2}{2-2}$; the teeth being p 4, m 3 on each side of both jaws (fig. 12).

Finally, p 4 is shed, and only the great posterior molar remains, as in the old *Phac. Æliani* figured in tab. xviii. of HOME's memoir.

It is interesting and suggestive thus to observe that an analogous duration or longevity, so to speak, characterizes the last tooth of both premolar and true molar series; an analogy so little to be expected from their different size and widely different original position in the jaws, by which characters, HOME, not sufficiently extending his observations and trusting to the analogy of the Elephant, was misled.

With respect to the *Phac. Pallasii*, my opportunities of tracing the course of dentition are not so extensive as with regard to the *Phac. Æliani*. I have observed none younger than the specimen figured by HOME (tab. xix.), and am not acquainted, therefore, with the characters of its deciduous dentition.

All the four teeth on each side of the upper jaw of that specimen, and there are the same number in the lower jaw, belong to the permanent series; tracing them from before backwards they are p 4, m 1, m 2 and m 3 in both jaws. The homologue of p 3 in the upper jaw of *Phac. Æliani*, if it be developed, is sooner shed in the *Phac. Pallasii* than in the *Phac. Æliani*. From the defects that have been pointed out in HOME's reduced figures of these teeth, more accurate views of them of the natural size may be acceptable, especially as they have not been elsewhere represented. I subjoin, therefore (Plate XXXIV. fig. 8), a side view and a view of the grinding surface of each. These figures, also, preclude the necessity of verbal description. I will only state that p 4, in the upper jaw, is implanted by three fangs, and is relatively smaller than its homologue in *Phac. Æliani*: p 4 in the lower jaw offers corresponding differences with its homologue in *Phac. Æliani*; m 2 has a narrower crown in relation to its antero-posterior extent than in *Phac. Æliani*; and a similar and more compressed form distinguishes the third molars in both jaws of the *Phac. Pallasii*. In the skull of a female Phacochœrus, called 'Haruja,' from Caffraria, in the British Museum, which differs from the typical *Phac. Æliani* of North Africa in having only two incisors in each ramus of the lower jaw, the following is the dental formula:—

$$i\,\frac{1-1}{2-2},\; c\,\frac{1-1}{1-1},\; p\,\frac{2-2}{1-1},\; m\,\frac{2-2}{2-2}:$$

the grinders of the upper jaw are p 3, p 4, m 2 and m 3 : those of the lower jaw are p 4, m 2 and m 3. The first true molar has been shed, and its place obliterated in both jaws.

There is a stuffed skin of this species which shows the same number of incisors, viz. $\frac{1-1}{2-2}$.

I have seen no stage of dentition of the *Phac. Pallasii* corresponding with figs. 6 and 7 of *Phac. Æliani*. The next example, after the stage figured by HOME, is shown in a skull from the Guinea Coast, in which the grinding series includes 3—3 in both jaws, like that in the upper jaw of the *Phac. Pallasii* and lower jaw of the *Phac. Æliani*, figured in 'Les Dents des Mammifères' of M. F. CUVIER, Tab. 87. These teeth, in each case, are *p* 4, *m* 2 and *m* 3 on each side of both jaws. In the specimen before me, *p* 4 is much worn, and is pressed into close contact with *m* 2. The anterior half of the grinding surface of this tooth is worn down to the common dentinal base, and both the anterior and posterior surfaces of the crown are excavated by the pressure of the two contiguous teeth, as in fig. 10. That a large grinder, like *m* 1, figs. 4, 5 and 6, should have been interposed between the first and second grinders in the specimen here described, could never have been suspected without a knowledge of those earlier stages of the dentition of the genus which have been described.

Baron CUVIER describes the molar teeth of the Phacochere as being three on each side of both jaws in the 4to edition of the 'Ossemens Fossiles' (1822)*, and the same numerical formula is retained in the posthumous 8vo edition of 1834†. With regard to the mode of succession of these teeth, the Baron adopts the conclusions of Sir EVERARD HOME; and in both editions of the 'Règne Animal,' after noticing the similarity of composition of these teeth with the grinders of the Elephant, he adds that they, in like manner, succeed one another from behind forwards‡.

His brother, M. FR. CUVIER, adopting the same view in the 'Dents de Mammifères,' describes the dentition of the Wart-Hogs as differing altogether from that of the rest of the Hog-tribe. "Nous voici arrivés," he writes, "à un système de dentition tout à fait différent de celui des sangliers" (p. 213): he adopts the specimens represented in the pl. 87 above cited, and describes the figures of that plate as exemplifying the normal adult dentition of the genus§. The anterior of the three grinders is described as the 'première mâchelière' (p. 214); and the second as 'la seconde mâchelière,' the latter being said to be composed of four tubercles, which by usage present four little elliptical or circular figures surrounded by enamel. And this, indeed, is the case at the extreme stage of attrition which he has figured; but, at an earlier period of usage, the crown of the tooth presents ten of those enamel-girted circular or elliptical islands of dentine, surrounding two, three, or four median ones (figs. 4, 5, 6, *m* 2). The last large molar presents twenty-five of these islands in the upper jaw in three linear series, nine being central, and twenty-six in the lower jaw, nine

* Tom. ii. p. 123. † Tom. iii. p. 235. ‡ Tom. i. p. 244.

§ In this he is followed by LESSON (Manuel de Mammalogie, p. 340), FISCHER (Synopsis Mammalium, p. 423) and other systematic mammalogists, who assign molars $\frac{3-3}{3-3}$ as one of the characters of the genus *Phacochœrus*.

also being central, and the islands smaller and more regularly disposed. This tooth extends to within one or two lines of the thin compact inferior bony wall of the deep ramus of the jaw, where the constituent columns terminate in the basal openings of as many pulp-cavities, with the exception of the first four, which are blended together, and from which no root has begun to be developed. It is therefore plain that this large and singularly complex grinder will continue to serve the purposes of mastication long after the shedding of the molar in advance, and the substance of which is already wasting away by the pressure of the larger tooth. We shall see, in the next specimen, that that molar is actually worn away and shed, whilst the smaller grinder in advance of it remains.

In the lower jaw of the specimen (No. 775 A.), the gum has grown over the sockets of the second true molar between the persistent remnant of the fourth premolar and the third true molar. In the upper jaw the last remnant of the second true molar remains on the right side, the crown having been worn to its base and the fangs absorbed.

Thus, in the *Phac. Pallasii*, as in the *Phac. Æliani*, the last of the premolar series, like the last of the true molar series, is distinguished by its longevity, although inferior in this respect to the large true grinder which continues to do the work of mastication to the end of the animal's existence.

The analogy of the Phacocheres to the Elephants in the superior size, complexity, and duration of the last grinders is close and interesting; but it does not extend to the horizontal mode of succession, in other words to the absence of premolars or vertical successors of deciduous teeth, as HOME led CUVIER to believe. In the development and succession of these premolars, and in the shape, proportions and position of the true deciduous teeth, the Wart-Hogs much more closely and essentially agree with the rest of the *Suidæ*. They differ, however, as we have seen, in the inferior number of both milk-molars and premolars which are developed, and in the speedier loss of all the true molars in advance of the last large one; but, in the order of shedding of those teeth, more especially in the very early displacement of the first true molar, and the total obliteration of its place in the series by the approximation of the last premolar to the second true molar, and in the subsequent displacement of this tooth with the approximation of the last premolar to the last true molar, the genus *Phacochœrus* is quite peculiar and different from all other Mammalia.

The author, who first called the attention of naturalists to the peculiarities of the dentition of the *Phacochœri*, has indicated another difference between the Wart-Hog and the common Hog, by affirming that the latter has a molar tooth developed behind the third true molar, at least in the lower jaw; which, if it were so, would have shown the common Hog to differ, also, from almost every other placental mammal with two sets of teeth*. In the description of Plate XX. of the Philoso-

* The *Megalotis Lalandii* is the only example, as far as I have observed, of the constant occurrence of *four* true molars on each side the lower jaw: the typical number *three* being retained above.

phical Transactions for 1801, HOME states that "fig. 3 represents the jaw in a still more advanced stage of its growth, with the tooth which was only forming in the second figure now come to its full size, and in its proper place in the row of teeth: there is also a new cell formed for a succeding tooth*." The original specimen from which the figure is taken is preserved in the Hunterian Collection, and it shows that the supposed formative cell is one of a series of the medullary cells of the cancellous structure of this part of the jaw; it is itself subdivided into smaller cells, and is not a simple cavity like the true cell of a forming tooth. It is also represented of twice its natural size in the figure cited, not having been reduced in proportion to the other parts of the jaw.

The latest author on the subject of the dentition of the *Phacochœri*, has ascribed to that part of their structure a character which would have added a still more remarkable anomaly to it, viz. that the last true molar represents both that tooth and the penultimate one in the Wild Boar and other herbivorous mammals†.

To this conclusion M. DE BLAINVILLE was necessarily led by his determination of the antecedent teeth. Thus in a *Phacochœrus* with the dentition answering to that represented in figs. 4 and 5 of the present memoir, he regards the teeth marked *p* 3, *p* 4 and *m* 1 as belonging to the deciduous series, 'dents de lait‡,' and the rest as belonging to the second dentition; *p* 2 being described as a small, speedily lost, false molar, *m* 2 as the first or antepenultimate true molar, and *m* 3 as the penultimate and last true molars, "already blended together, although not yet protruded from their formative alveolus§."

With regard to the five teeth in the lower jaw, the first, *p* 3, is described as the first tooth of the second dentition; the two following, *p* 4 and *m* 1, as milk teeth; the fourth, *m* 2, as the antepenultimate molar of the second dentition, and the last, *m* 3, as the penultimate and last molar coalesced. The dentition ascribed to the adult *Phacochœrus* is that phase which is illustrated in figs. 9 and 10, Plate XXXIV. of the present memoir, of which the numerical formula is $\frac{4-4}{3-3}=14$. M. DE BLAINVILLE, struck by the resemblance in the degree of attrition which the molar, *m* 2, presents to the antepenultimate molar, *m* 1, in the adult common Hog, deems them homologous, and deduces from that resemblance another argument for the homology of the last great molar of the Phacochere with the penultimate and last molars combined of the Hog ||.

* Philosophical Transactions, 1801, p. 331.

† Ostéographie des Ongulogrades, *Hippopotamus* and *Sus*, 4to, 1847. ‡ Ibid. p. 148. § Ibid. p. 148.

|| "Mais quelle est la signification de cette dent par rapport à ce qui existe chez la sanglier? C'est la une question qui, malgré son intérêt, n'a pas même encore été soulevée.

"J'ai cru un moment qu'on pourrait la considérer comme représentant les trois arrière-molaires qui se seraient soudées de manière à n'en former qu'une, les trois molaires qui la précèdent étant alors celles de remplacement. Cette façon de voir était surtout appuyée sur la composition de cette dent à la mandibule où l'on peut voir dans les cannelures latérales des séparations plus marquées, paraissant indiquer l'antépénultième, la pénultième et la dernière avec sou talon.

"Mais en réfléchissant sur le caractère sérial des espèces de ce genre, il m'a semblé que cette opinion devait

But had the preceding stage of dentition, which is represented in fig. 7, Plate XXXIV., presented itself to the observation of M. DE BLAINVILLE, that acute observer would doubtless have seen that *m* 1,—the true homologue of the much-worn antepenultimate molar of the common Hog,—presented the same abraded condition. And the actual difference is as follows, viz. that, owing to its earlier development in the *Phacochœrus*, the true antepenultimate molar, *m* 1, is sooner worn out and shed; whilst, from the very long period during which the last molar is adapted to perform the work of mastication, the penultimate molar, *m* 2, undergoes the same exhaustive usage and premature expulsion.

I have figured in parallel juxtaposition the molar series of a Phacochere and a Wild Boar, in plate 141 of my 'Odontography,' to illustrate the corresponding extent of abrasion in the first or antepenultimate true molar (*m* 1) at the period when the last true molar has come into place in the Wart-Hog, and when two of the premolar series are retained; and I have indicated my conclusions as to the signification or homology of each of the teeth by the symbols, the aptness and exactitude of which all my later researches have convinced me of. With regard to the deciduous teeth of the Phacochere and other diphyodont mammals, I may remark that there is but one mode of determining and of distinguishing them from the premolars and true molars of the second dentition, in cases where some of the latter are obviously present, as in the young Phacochere with a grinding series of $\frac{6-6}{5-5}$ (see figs. 4 and 5) or of $\frac{5-5}{4-4}$ (as in Plate XXXIII.): that mode is to excavate the substance of the jaws above the fangs of the upper teeth and beneath those of the lower ones, as in the skull represented in Plate XXXIII., and in the lower jaw figured in my 'Odontography,' pl. 141, fig. 1*. The deciduous tooth is demonstrated by the formative

être modifiée, et que dans cette dent il ne fallait voir que les deux dernières, et alors la terminale aurait son talon dans la proportion convenable.

"Ce qui milite encore en faveur de cette manière devoir, c'est que la dent sur laquelle porte davantage l'usure dans le sanglier, l'antépénultième ou cinquième, a son analogue chez le sanglier d'Ethiopie dans la dent qui précéde la dent complexe, et qui serait en effet l'antépénultième, celle-ci représentant la pénultième soudée à la dernière.—*Loc. cit.* p. 148.

* "Le système dentaire de cet animal a été fort incomplètement figuré sans description par EVERARD HOME (Lect. on Comp. Anatom. t. 11. pl. 38 et 39), M. G. CUVIER lui a consacré un court paragraphe (Ossem. Foss. t. 11. p. 132, sans figures), et M. OWEN s'est borné à représenter la couronne des molaires supérieures du côté droit (Odontographie, pl. 140, fig. 31), mais personne n'en a soupçonné la signification." M. DE BLAINVILLE had overlooked pl. 141, where that signification is given: but he adds in a supplementary note,—"Il relève, comme inexacte, l'assertion de M. RUPPELL, que dans tous les individus des deux sexes, jeunes et adultes, il y a quatre molaires en haut et trois en bas; et en effet il en décrit une de plus, en reconnaissant que dans la première dentition il n'y en a que trois à la machoire et deux à la mandibule. Du reste M. R. OWEN accepte la distinction spécifique du *S. Æliani* et du *S. Pallasii*; le premier pourvu et le second dépourvu de dents incisives, mais sans autres différences vraiment spécifiques." If, however, the difference cited be of specific value, as M. DE BLAINVILLE seems here to admit, others were not needed for accepting the conclusion. I may, however, add that the upper canines of the *Phac. Pallasii* have the groove on their upper surface narrower than in the *Phac. Æliani*, and that the premolars are relatively smaller.

socket containing the germ of its successor in a vertical line with it; this is more especially the case with the last or hindmost deciduous tooth, because the hindmost premolar, its successor, is late in coming into place, and the contiguous true molar, which is always formed much sooner, is characterized by its deeply implanted fangs, and by the absence of any formative socket in vertical relation to them. Without the dissection of the jaws figured in Plate XXXIII., I could have had no true or scientific knowledge of the nature of the teeth there symbolized. As I availed myself of symbols to denote the signification or homology of the teeth of the *Phacochœrus* in my 'Odontography' (pages 549 to 557, pl. 140, 141), I shall sum up or indicate in the same way the results of the additional observations recorded in the foregoing pages.

Phases of the molar series of the genus Phacochœrus.

Phase

I. Plate XXXIII. $\frac{5-5}{4-4}$ viz. $\begin{cases} d\,2,\ d\,3,\ d\,4,\ m\,1,\ m\,2. \\ d\,3,\ d\,4,\ m\,1,\ m\,2. \end{cases}$

II. Plate XXXIV. figs. 4 and 5, $\frac{6-6}{5-5}$ viz. $\begin{cases} p\,2,\ p\,3,\ p\,4,\ m\,1,\ m\,2,\ m\,3. \\ p\,3,\ p\,4,\ m\,1,\ m\,2,\ m\,3. \end{cases}$

III. Plate XXXIV. figs. 6 and 7, $\frac{5-5}{4-4}$ viz. $\begin{cases} p\,3,\ p\,4,\ m\,1,\ m\,2,\ m\,3. \\ p\,4,\ m\,1,\ m\,2,\ m\,3. \end{cases}$

IV. Plate XXXIV. fig. 13 (*Phac. Pallasii*), $\frac{4-4}{4-4}$ viz. $p\,4,\ m\,1,\ m\,2,\ m\,3.$

V. Plate XXXIV. figs. 9 and 10, $\frac{4-4}{3-3}$ viz. $\begin{cases} p\,3,\ p\,4,\ m\,2,\ m\,3 \\ p\,4,\ m\,2,\ m\,3 \end{cases}$ $\left(\text{or} \begin{cases} p\,3,\ p\,4,\ m\,2,\ m\,3. \\ p\,3,\ p\,4,\ m\,3. \end{cases}\right)$

VI. Plate XXXIV. fig. 11, $\frac{3-3}{3-3}$ viz. $p\,4,\ m\,2,\ m\,3.$

VII. Plate XXXIV. fig. 12, $\frac{2-2}{2-2}$ viz. $p\,4,\ m\,3.$

VIII. $\frac{1-1}{1-1}$ viz. $m\,3.$

The above symbols express, with regard to the first phase, I. *e. g.*, that there are five grinders on each side of the upper jaw, and four grinders on each side of the under jaw: that those above answer to the second, third, and fourth deciduous molars, and to the first and second permanent true molars; and that those below answer to the third and fourth deciduous molars, and to the first and second true molars,—of the typical dentition. With regard to the second phase, the symbols express that there are six grinders on each side of the upper, and five grinders on each side of the under jaw: those above answering to the second, third and fourth premolars, and to the first, second and third true molars; those below answering to the third and fourth premolars, and the first, second and third true molars—of the typical dentition.

As to the fourth phase with four grinders on each side of both jaws, these answer, in both, to the fourth premolar, and to the first, second and third true molars of the typical dentition of the placental Diphyodonts.

These explanations will serve to render the symbols of the remaining phases readily understood by those who may not have studied the principles of dental notation which I communicated to the 'British Association' in 1848, and have more fully exemplified in the article 'Teeth' of the 'Cyclopædia of Anatomy and Physiology;' their utility will be obvious when they are found to express, in a few lines, facts in Comparative Anatomy which would require almost as many pages if recounted by ordinary description.

This system of anatomical notation is the practical fruit of the discovery or determination of a type or common pattern of dentition to which the teeth of a certain proportion of the Animal Kingdom could be referred, and of a concomitant attainment of the power to trace a particular tooth under every modification and disguise of size and shape, throughout the different species of those animals. Every tooth, thus capable of being individualized and determined, merits and, for the purposes of description, requires to have a proper name, and can be signified by a symbol, which is still more convenient for those purposes.

The dental system manifests this regular and determinable character in a large proportion of the mammalian Class; but not in any animal of inferior organization. Like the definition of a species, the definition of a tooth or other part of an organism becomes possible only when its characters are constant and definite, and is easy in proportion as those qualities are exalted. The definition of a mineral species is more difficult than that of a vegetable species, and the definition of a species of low cellular plant is more difficult than that of the highly organized dicotyledon. In proportion as wholes rise in the scale of nature or of life, their recognition and definition becomes easier, and the like obtains also of their parts. As animals ascend in the scale of complexity their organs and parts become more definite; and homologies are more extensively, easily and satisfactorily determinable.

We cannot point out in one species of Echinus the answerable spine of any given spine in another species, nor can we determine the homology of a tufted foot from one species of the many-jointed Annelides to another; but in insects each particular leg may be determined through all its modifications of form and function throughout the class. So, likewise, with the teeth: the same individual tooth cannot be traced from fish to fish, or from reptile to reptile; the teeth in the cold-blooded classes differ too much in their number in different individuals, and too little in their development and succession, to yield the requisite characters to the homologist who keeps his faculty of comparison under due control. In those Mammalia, likewise, as *e. g.* the Cachalots, Dolphins and Armadillos, in which the teeth are very variable in number and often very numerous, but without any definite order of shedding and replacement, no particular tooth can be identified and traced from one species to another.

The class *Mammalia* presents, in fact, two primary conditions of the dental system, according to which it might be divided into,—

1st. Those that generate one set of teeth, or the 'Monophyodonts *,' and

2nd. Those that generate two sets, or 'Diphyodonts †.'

The 'Monophyodonts' include the orders *Monotremata* and *Bruta* (or the *Edentata* of CUVIER) and the *Cetacea vera* of CUVIER.

The Diphyodonts include the *Marsupialia, Rodentia, Insectivora, Cheiroptera, Ruminantia, Pachydermata, Sirenia, Carnivora, Quadrumana* and *Bimana*.

I would not be misunderstood, however, as proposing this difference as a basis of classification: such dental characters are associated with too few corresponding differences of organization to lead to a natural binary division of the Mammalia. But, as regards the philosophy of the organs in question, considered in that class, the differences above enunciated form one of the highest generalizations, and the exigencies of clear and brief description require such general ideas to have their appropriate signs or names.

The Diphyodont Mammals, then, are characterized by having a first set of teeth, commonly called the 'milk-teeth' or 'deciduous teeth,' and a second set called the 'permanent teeth.' But the development of the latter, in relation to the milk-teeth, presents two modifications; some of the permanent teeth are found in the same vertical line with the milk-teeth, push them out and take their place; others are formed one after another behind the milk-teeth, in what may be called the same horizontal line, and come into place without pushing out any deciduous predecessors. Here, therefore, we have certain characters from development for particular teeth, and when to these characters are added others of equal constancy, derived from relative position, it will be readily understood how such characters, when clearly appreciable and firmly maintained through a series of comparisons, should enable the homologist to point out the very tooth in Man which becomes the great carnassial tooth in the jaw of the Tiger or the great complex grinder in that of the Wart-Hog. With respect to the accessory characters, one of the best is afforded by the relation of certain teeth to the constituent dentigerous bones of the complex jaws. Implantation in the premaxillary bone, or premaxillary part of the upper jaw, *e. g.*, characterizes the tooth called 'incisor,' whatever be its shape or size; and the true and constant character of such tooth being thus determined, the name 'incisor' becomes its arbitrary sign and loses all its primitive signification as descriptive of a particular shape or use. In like manner the tooth at the fore part of the maxilla, or the maxillary part of the upper jaw which coalesces with the premaxilla in Man, is called the 'canine.' The molar series, according to the characters of development and succession above described, is divided into 'milk-molars,' 'premolars' and 'true molars.' The two latter kinds constitute the adult or permanent set of molars. Now these, in the diphyodont mammals, do not exceed $\frac{7-7}{7-7}=28$, *i. e.* seven on each side of both jaws. In the marsupial Diphy-

* *Μόνος once; φύω I generate; ὀδοὺς, tooth.* † *Δὶς twice; φύω* and *ὀδούς.*

odonts three of the seven on each side of both jaws are 'premolars,' four are 'true molars.' In the placental Diphyodonts four of the seven on each side of both jaws are 'premolars,' and three are 'true molars.' The exceptions, by way of excess to this typical number, are few and are confined to the marsupial order, *e. g.* in the Myrmecobius: the deviations from the type by deficiency are numerous, especially in the placental series. But to whatever point the number may be reduced, the teeth that are retained may be identified with their homologues in the typical series. This power is fortunately given by the constancy in respect of their existence of the contiguous teeth of the premolar and molar series, those, *e. g.* marked *p* 4 and *m* 1 in Plate XXXIII.; and by the absent teeth being taken from a definite part of each of those series, viz. from the fore part of the premolars and from the back part of the true molar series.

The Bears and some Carnivora offer a partial exception in the occasional retention of *p* 1 when *p* 2 and *p* 3 may be absent, but *p* 4 is constantly present.

Thus it needs only to determine, in any given species of diphyodont mammal, the last premolar and the first true molar, as has been done in the young Phacochere, Plate XXXIII., in order to know the homologies of the rest. The true molars are counted from before backwards,—'first,' 'second,' 'third:' the premolars from behind forwards,—'fourth,' 'third,' 'second,' 'first,' or as far as the series may extend. In Man, *e. g.* it stops at the third; the first and second, which exist in the Hog, being absent, but all the true molars are present. The teeth being thus determined their symbols can be applied to them, *m* 1, *m* 2, *m* 3, for the molars,—*p* 4, *p* 3, *p* 2, *p* 1, for the premolars. It needs only to apply the symbols to one side of each jaw, the teeth being symmetrically repeated on the opposite side: and in most cases they are alike in both jaws. The right canine is the homotype of the left canine, as the right arm is of the left arm, agreeably with the principle of 'bilateral symmetry:' the first true molar in the lower jaw is the homotype of the first true molar of the upper jaw, as the leg is the homotype of the arm, in accordance with the law of the composition of the vertebrate framework of a successive series of essentially similar segments. In whatever direction or to whatever degree two or more of these segments may deviate from the type, the same elements may be discerned in them beneath those modifications. If the neural arch be vastly expanded, as in the cranial vertebræ of mammals, we trace the broad and bifid neural spine from one to the other, and recognise, *e. g.* the frontal bones and parietal bones as homotypal elements. If the diverging appendages be the seat of adaptive development, as in the occipital and pelvic vertebræ, we find the same plan of modification is followed, and we can trace the homotypal parts, *e. g.* *humerus* and *femur*, *radius* and *tibia*, *ulna* and *fibula*, *carpus* and *tarsus*, as also the homotypal ossicles in the carpus and tarsus, even when the common plan is so varied in such appendages, as to produce the different powers and functions which characterize the leg and the arm in Man.

So, likewise, when two costal arches are converted into jaws and made to support teeth, we find the same laws of development so strictly followed as to enable us to determine the homotypal teeth in those two jaws with the same certainty as the homologous teeth in the jaws of different species.

When the mouth is shut the teeth in the lower jaw are a little in advance of their homotypes in the upper jaw; thus in the Carnivora the great canine tooth of the lower jaw always passes in front of the canine above. Even in the human subject this characteristic relative position is shown by the molars and premolars, when the upper incisors are produced beyond the lower ones.

The existing species of Mammalia that retain the typical formula of dentition, viz.

$$i\,\frac{3-3}{3-3},\ c\,\frac{1-1}{1-1},\ p\,\frac{4-4}{4-4},\ m\,\frac{3-3}{3-3}=44,$$

are few: but that formula was much less frequently departed from in the species of placental Mammalia which were first introduced into this planet. This is a very significant fact, and became manifest in the course of working out such typical formula by tracing and comparing the development of the teeth in the recent species.

In the oldest known strictly carnivorous mammal, *e. g.* the *Hyænodon*, remains of which have been discovered in the newer eocene deposits of Hampshire, and in the miocene formations of France, the complete typical dentition is retained, and each of the three true molars presents the peculiar trenchant form of crown which characterizes the single tooth called by CUVIER 'la dent carnassière' in the Lion: here, therefore, we use the term 'molar' in the same technical or arbitrary sense as the term 'incisor' when applied to the tusks of the Elephant or the prongs of the Hippopotamus. In the mixed-feeding *Amphicyon*, a larger extinct miocene Carnivore, allied to the Plantigrades, the three true molars have broad tuberculate crowns. Almost all the herbivorous genera of the eocene and miocene tertiary periods had the typical number and kinds of teeth, as, *e. g.*, *Anoplotherium*, *Palæotherium*, *Dichodon*, *Chæropotamus*, *Dichobune*, *Anthracotherium*, *Hyopotamus*, *Hyracotherium*, *Oplotherium*, *Merycopotamus*, *Hippohyus*, &c. When a modern genus or family has been represented as far back as the miocene period by extinct species, it is usual to find some nearer approach made by such species to the typical dentition than is made by the existing species. Thus, in existing Ruminants, the first premolar is suppressed; but in the ancient *Dorcatherium* it was retained. In the modern *Hippopotami* the incisors are reduced to $\frac{2-2}{2-2}$, and the first premolar is speedily lost; in the oldest known representatives of the genus—the *Hexaprotodon* of the Himalayan tertiary beds—the incisors were in the typical number $\frac{3-3}{3-3}$, as the name imposed upon it by its discoverers, CAUTLEY and FALCONER, indicates, and the first premolar was long retained; the whole dentition, in short, presented the typical formula.

The existing species of the gigantic Proboscidian family, viz. the Asiatic and African Elephants, are totally devoid of incisors in the lower jaw, and all their grinding-teeth succeed each other horizontally; so that it is only by a more than proportional increase of size that the antepenultimate grinder is recognizable as the first of the true molar series, and the antecedent smaller grinders as the homologues of the milk-molars of other Diphyodonts, which milk-molars have no vertical successors in the Elephants. In certain Mastodons, however, which are the earliest known forms of the Proboscidian family, the last milk-molar was displaced by a vertical successor or premolar. Two incisors, moreover, were developed in the lower jaw of the young Mastodons, one of which was retained in the male of the *Mastodon giganteus* of North America, and both in that of the *Mastodon longirostris* of Europe.

The human dentition deviates from the typical formula by the suppressed development of several teeth; as might be anticipated from the characteristic shortness of the jaws, which is such as only to allow space for the comparatively few teeth retained, in close juxtaposition, without any break in the series.

The numerical formula is

$$i\frac{2-2}{2-2},\ c\frac{1-1}{1-1},\ p\frac{2-2}{2-2},\ m\frac{3-3}{3-3}=32;$$

the principal phases in the development of this dentition may be symbolized as follows:—

I. 3 years old, $i\frac{2-2}{2-2},\ c\frac{1-1}{1-1},\ m\frac{2-2}{2-2}=20;$

all of the deciduous series, the molars answering to $d\,3$ and $d\,4$ of the typical dentition.

II. 7 years old, $i\frac{2-2}{2-2},\ c\frac{1-1}{1-1},\ m\frac{3-3}{3-3}=24;$

the molars being $d\,3$, $d\,4$, $m\,1$.

III. 10 to 12 years old, $i\frac{2-2}{2-2},\ c\frac{1-1}{1-1},\ m\frac{3-3}{3-3}=24;$

the molars being $p\,3$, $p\,4$, $m\,1$, and the milk incisors and canines replaced by the permanent ones.

IV. 12 to 16 years old, $i\frac{2-2}{2-2},\ c\frac{1-1}{1-1},\ m\frac{4-4}{4-4}=28$, viz. $p\,3, p\,4, m\,1, m\,2$.

V. 18 to 30 years old, $i\frac{2-2}{2-2},\ c\frac{1-1}{1-1},\ m\frac{5-5}{5-5}=32$, viz. $p\,3, p\,4, m\,1, m\,2, m\,3$.

The teeth which are wanting in Man to complete the typical formula are $i\,3$, $p\,1$ and $p\,2$. The teeth in Man which answer to the carnassials of the Lion and other Feræ are $p\,4$ in the upper jaw, or the second bicuspis of human anatomy, and $m\,1$ in the lower jaw, or the first multicuspid molar. The tooth which is homologous to the great complex molar of the Wart-Hog is $m\,3$ in both jaws.

The symbols here proposed to denote the kinds of teeth are, it is hoped, so plain and simple as to present no obstacle to the ready comprehension of the facts which have been recorded by means of them. Had those facts been explained by means of the usual phrases or definitions of the teeth, *e. g.* "the second deciduous molar representing the fourth of the typical dentition," instead of $d4$, and so on, the descriptions must have run to much greater length, and have levied such a tax upon the attention and memory as to have proportionally enfeebled the judgment and impaired the power of seizing and appreciating the results of the comparisons.

Each year's experience strengthens my conviction that the rapid and successful progress of anatomy depends greatly on the determination of the nature or homology of the parts observed, and on the concomitant acquisition of the power of denoting them by symbols equivalent to their single substantive names.

In my work on the 'Archetype of the Vertebrate Skeleton,' I have denoted most of the bones by simple numerals, which, if generally adopted, might take the place of names: and all the propositions, *e. g.* relative to the centrum of the occipital vertebra, might be predicated as effectually and intelligibly of the figure 1 as of the word 'basioccipital.' The symbols of the teeth are fewer, are easily understood and remembered, render unnecessary the endless repetition of the verbal definition of the parts, harmonize conflicting synonyms, serve as a universal language, and express the author's meaning in the fewest and clearest terms.

The Entomologist has long found the advantage of such signs as ♂ and ♀, signifying male and female, and the like; and it is time that the Anatomist should avail himself of this powerful instrument of thought, instruction and discovery, from which the Chemist, the Astronomer and the Geometrician have obtained such important results.

Description of the Plates.

PLATE XXXIII.

Fig. 1. Side view of the skull of a very young *Phacochœrus Æliani*, natural size, with the outer walls of the alveoli removed to expose the deciduous molars, premolars and true molars, *in situ*.

Fig. 2. The grinding series, composed of milk-molars and true molars, from the upper jaw.

Fig. 3. The same from the lower jaw. (The symbols are explained in the text.)

PLATE XXXIV.

Fig. 4. Grinding surface and side view of the crowns of the molar series of the upper jaw of a young *Phacochœrus Æliani*.

Fig. 5. Grinding surface and side view of the crowns of the molar series of the lower jaw of the same skull.

Fig. 6. View of the grinding surface of the upper molar series of a full-grown but young *Phacochœrus Æliani*.

Fig. 7. A similar view of the molar series of the lower jaw of the same specimen.

Fig. 8. Side view and view of the grinding surface of the molar series of a similarly aged *Phacochœrus Pallasii*.

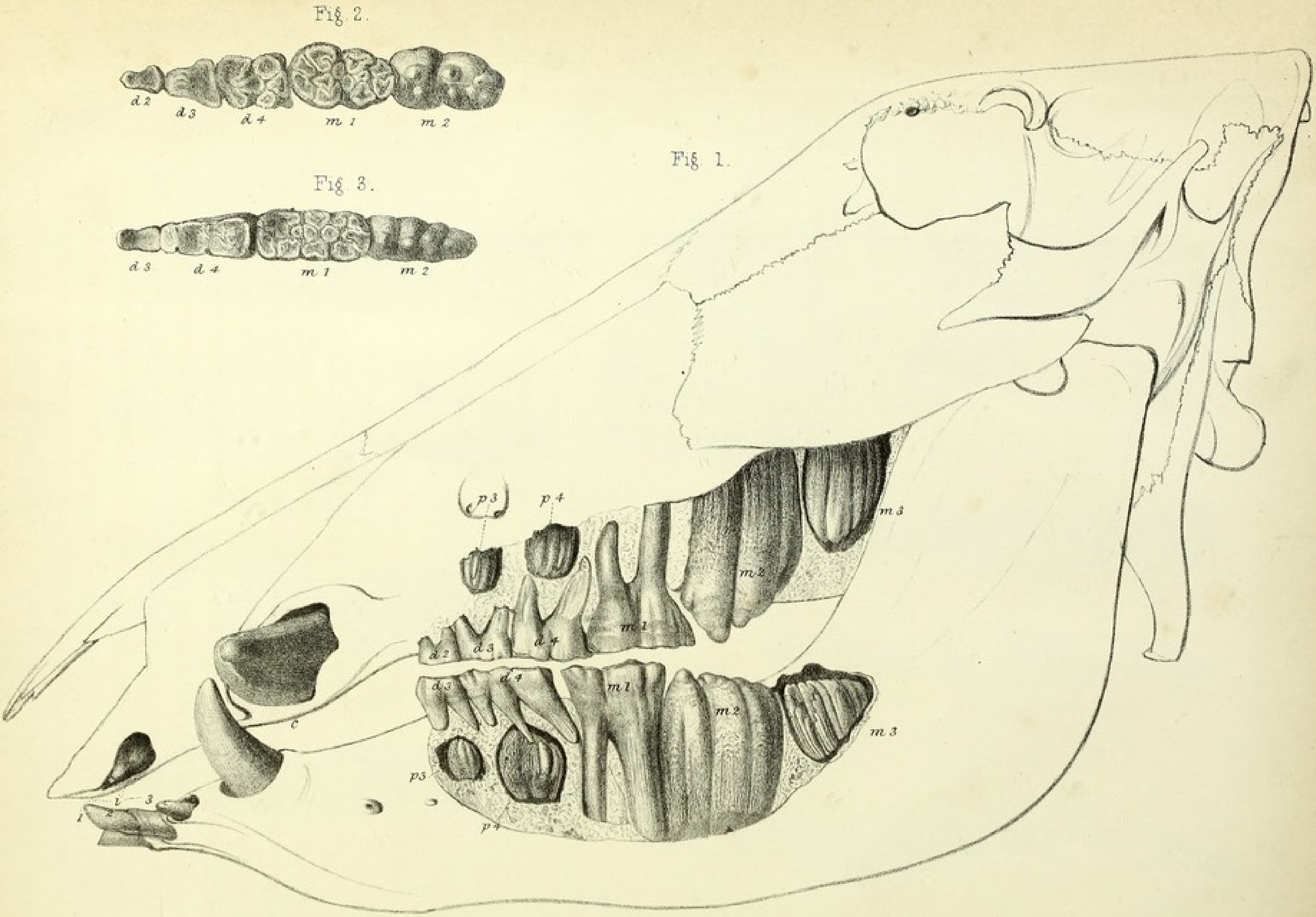
Fig. 9. View of the grinding surface of the upper molar series of an older *Phacochœrus Æliani*.

Fig. 10. Similar view of the lower molar series of the same animal.

Fig. 11. View of the grinding surface of the upper molar series of an older *Phacochœrus Pallasii*.

Fig. 12. Similar view of the upper molar series of a still older *Phacochœrus Æliani*.

(The symbols are explained in the text, especially at p. 491.



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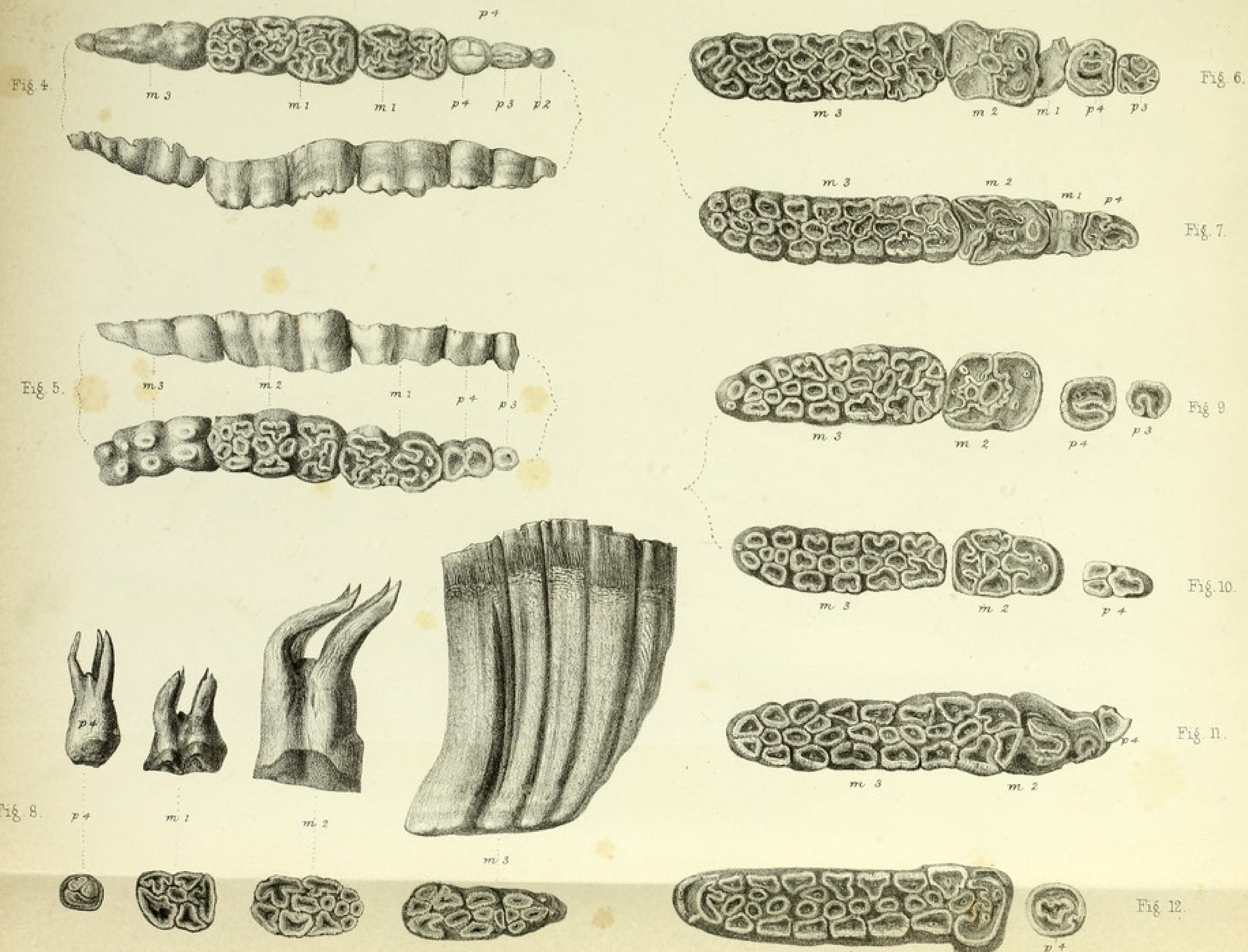

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Fig.s 1, 7, 9, 10 & 12, Phacochærus Æliani, Fig.s 8 & 11 Ph. Pallasii.

Phil. Trans. MDCCCL. Plate XXXIV. p. 497