3. On the Cranial and Dental Characters of the Canidæ. By T. H. Huxley, F.R.S.

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1. The unsatisfactory character of the attempts which have hitherto been made to determine the natural affinities of the numerous members of the group of Canine Carnivores must have impressed itself upon the mind of every one who has paid close attention to these animals. But I do not think that the discussion of the merits and demerits of the various systems of classification of the Canidæ which have been proposed would serve any useful purpose; and it is the less incumbent upon me to undertake the task at present, as I propose to deal with the question in a manner somewhat different, so far as I know, from any which has yet been pursued.

The general uniformity of the structure of the Canidæ is well known. There is a remarkable constancy in the characters of all the organs, down even to the minuter details of the patterns of the crowns of the teeth, accompanied by variations, within comparatively narrow limits, in the form and proportion of the parts. The number of the præsacral and sacral vertebræ always remains the same, and that of the caudal vertebræ varies only within narrow limits. In the skull, there is a considerable range in the proportions of the jaws to the brain-case, and in the extent to which the temporal ridges, always widely separate in young animals, approach and coalesce into a sagittal crest in the adult. The greater or less backward extension of the nasal bones, the union or separation of the nasal processes of the frontal bones with the ascending processes of the præmaxillaries, and the variations in the form of the supraorbital processes have been noted. The straightness or angulation of the line of the molar and præmolar teeth, and the proportions of the sectorial teeth to those which follow them, have been taken into account, as well as minor characters of the teeth themselves. Attention has been directed to the excess of teeth above the normal number in *Otocyon*, and to the diminution of the number in *Cyon* and *Icticyon*. The variation in size of the pollex and its disappearance in *Lycaon* are well known. The differences in the form of the pupil have been noted; and, of late, particular notice has been taken of the extensive modifications in the form of the cæcum. Weight has been attached to the presence or absence of a caudal gland.

The taxonomic value of these variations, however, has remained doubtful. That of the proportional lengths of the nasal bones, for example, is justly disputed by Wagner [1]. Satisfactory evidence of the form of the pupil is hard to obtain, and does not appear to have any definite correlation with diurnal or nocturnal habits. The presence or absence of a caudal gland has been investigated in only a few species; and as it occurs in Wolves, Dogs, Jackals [2], and Foxes, it is not likely to be of much importance. The proportions of the sectorial to the following teeth may be similar in Canidæ which are certainly not closely allied, and different in those which are. And the system of measurement hitherto usually adopted gives the absolute sizes of the teeth and their dimensions relatively to one another, but affords no clue to their proportions in relation to the size of the skull, or to the increase or diminution of individual teeth. The increase of the number of the teeth of *Otocyon* appears generally to be regarded merely as an anomaly.

There can be no doubt that the skulls and the teeth of the Canidæ vary from species to species more than any other part of their organization. One has only to put side by side with one another the skeleton of an *Otocyon* and that of a Wolf or that of a Fox, to see that the cranial and dental differences are very much greater than any which are observable elsewhere; and a glance at the skull and teeth of any other canine animal is sufficient to show that its characters give it a place somewhere between the former and the two latter. The problem therefore is how to give definite expression to the differences between *Otocyon*, Fox, and Wolf, and to determine by something better than vague eye-judgments the relation of the other forms to these.

2. When occupied with anthropological questions, a good many years ago [3], I was confronted by the same kind of difficulty in endeavouring to arrive at an exact conception of the morphological relations of the skulls of the different races of mankind; and I was led to adopt a method of estimating cranial characters which still commends itself to me as that which is best calculated to meet the end in view.

Every constituent of the skull, like all other parts of the body, varies from individual to individual, and from youth to age. But the central region of the base of the skull, formed by the basioccipital, basisphenoid, and præsphenoid bones, represents the foun-

[1] Schreber's Säugethiere, Suppl. Bd. ii. pp. 365, 384, notes.

[2] I have found a small caudal gland in a female *C. mesomelas*, which recently died in the Gardens.

[3] "On two widely contrasted Forms of the Human Cranium," Journal of Anatomy, 1867.

dation around and upon which the other parts are built, and reaches its adult condition early. Moreover it answers to one of the most important parts of the central nervous system, the base of the brain. It is therefore eminently fitted to furnish a relatively fixed unit of measurement and standard of position, to which the dimensions and the position of the other parts of the head and face, with the teeth, can be referred.

In order to obtain such a standard, a median line is drawn in the bisected skull, from the hinder edge of the basioccipital bone to the junction between the præsphenoid and the ethmoid in the base of the skull. I call this line the *basicranial axis*; and its value is taken as 100. The measurements of the other parts of the skull can then be expressed in terms of 100, and their development, irrespectively of the absolute size of the animal, becomes apparent. Sectional diagrams of different skulls, in which the basicranial axis has the same absolute length, show not only the different proportions of corresponding parts, but bring to light the relative depth, length, and inclination of the palate.

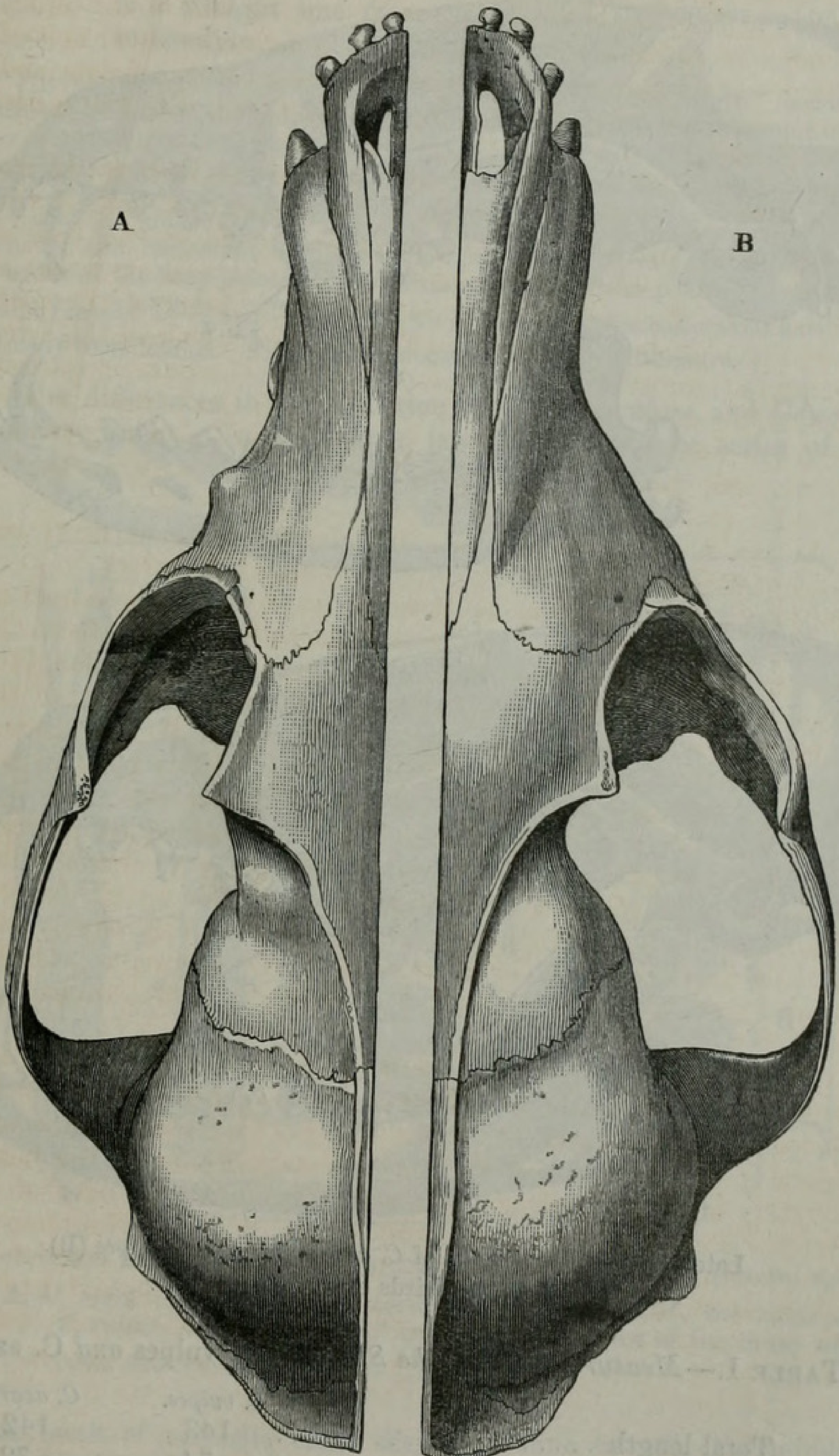
This method of procedure is a little troublesome at first; but practice makes it easy, and the results are very satisfactory.

When, as often happens, the skull under examination cannot be bisected, a sufficiently close approximation to the true length of the basicranial axis may be obtained by taking the distance along the median line of the base of the skull from the posterior edge of the basioccipital bone to a point opposite the middle of the distance between the optic and the ethmoidal foramina. This point always lies a little behind the posterior extremity of the vomer.

3. I will illustrate the method which I have described by comparing the skull of a common Fox with the skull of an animal which died in the Zoological Society's Gardens, and came to me labelled "*Canis azaræ*, South America." It corresponds very closely with the skulls also assigned to *Canis azaræ* by De Blainville ('Ostéographie,' *Canis*, pl. iv.) and by Burmeister ('Erläuterungen zur Fauna Brasiliens').

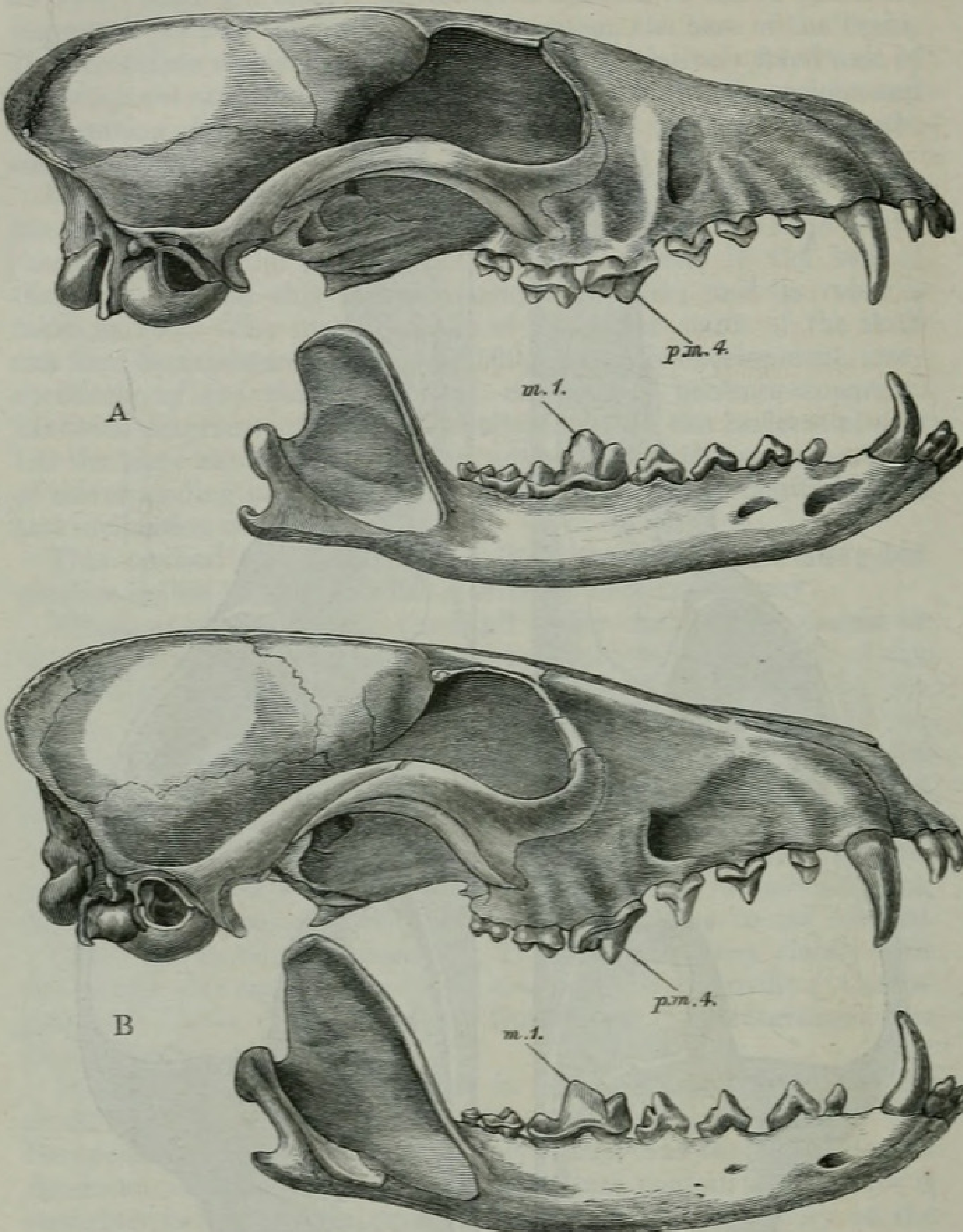
In their actual dimensions and in their general form these two skulls are very similar, except that the zygomatic arch of the European is stronger and more sharply arched than that of the South-American animal, and that the longitudinal contour of the face is straighter in the Fox, in consequence of a slight convexity of the interorbital and posterior nasal regions in *C. azaræ*. The ramus of the mandible of *C. azaræ* is somewhat deeper at the level of the last molar tooth, and its coronoid process is less high and less inclined backwards, while the ventral contour is more sinuous. Other minor differences will be obvious on comparison of the figures.

Fig. 1.



Dorsal view of the left half of the skull of *Canis azaræ* (A) and of the right half of the skull of *C. vulpes* (B), placed side by side. Natural size.

Fig. 2.



Lateral views of the skulls of *C. azaræ* (A) and *C. vulpes* (B).
Reduced to two thirds of the natural size.

TABLE I.—*Measurements of the Skulls of* C. vulpes *and* C. azaræ.

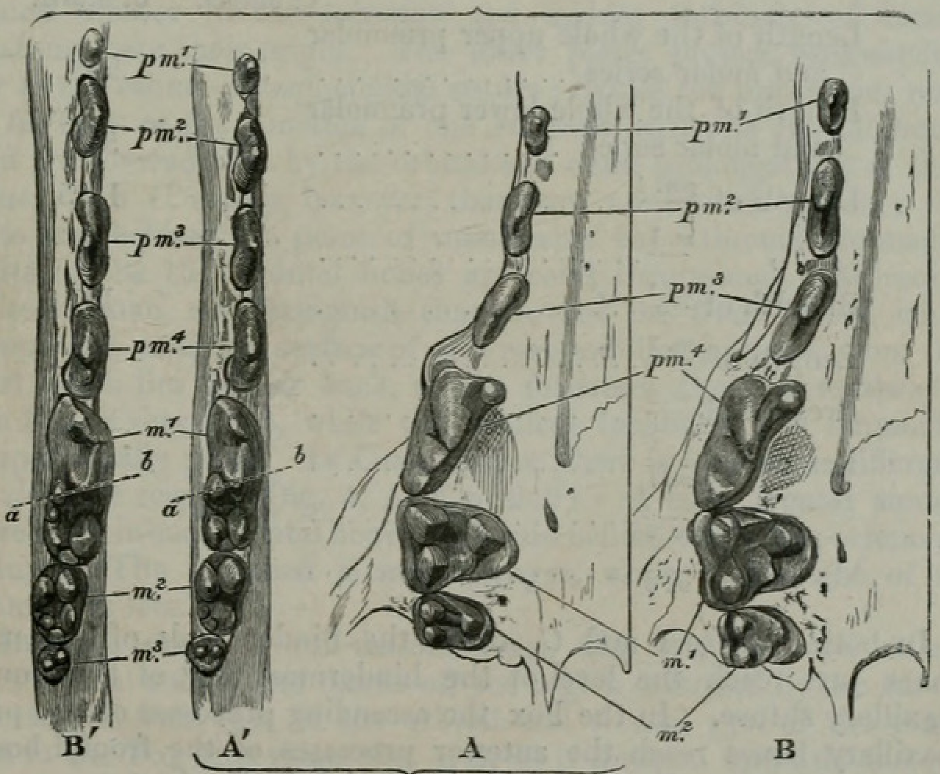
	C. vulpes.	*C. azaræ.*
Total length	143	142
Zygomatic width	74	72
Length of bony palate	73	72
Width ,, ,,	41	41
Length of basicranial axis	46	48

	C. vulpes.	*C. azaræ.*
Length of the ramus of the mandible in a straight line from symphysis to condyle	109	105

[In this and the following tables of measurements "total length" means the distance from the front edge of the præmaxillary bones to the extremity of the occipital spine. The "zygomatic width" is the greatest transverse distance between the outer faces of the zygomatic arches. The "length of the bony palate" is measured from the front edge of the symphysis of the præmaxillary bones to the hinder edge of the middle of the bony palate, not taking into account the inconstant median spine which is frequently developed. The "width of the bony palate" is the distance between the points at which the outer faces of $\frac{pm. 4}{}$ and $\frac{m. 1}{}$ meet. The "length of the basicranial axis" has already been defined. The measurements are given in millimetres.]

The differences in the dentition between *C. vulpes* and *C. azaræ* are very slight. In the upper jaw of the Fox the series of the

Fig. 3.



The crowns of the cheek teeth of *C. azaræ* (A) and *C. vulpes* (B). Natural size. A, A′, right upper and lower teeth of *C. azaræ*; B, B′, the same of *C. vulpes*; *a*, *b*, "cusp-line" traversing the apices of the inner and outer anterior cusps of $\frac{}{m. 1}$.

molar teeth of opposite sides slightly incline towards the middle line behind, while in *C. azaræ* they are almost parallel. Hence the angulation of the line of the cheek-teeth between the last præmolar and the first molar (fig. 3, A, B) is rather more marked in *C. vulpes*.

The præmolar teeth are smaller in *C. azaræ*; but as they are more worn it is difficult to make an exact comparison. The upper sectorial is not quite so long as that of the Fox. The transverse diameter is the same in front, but is less behind, in *C. azaræ*; and its inner cusp is less forward in position and less prominent. The lower sectorial is narrower and the anterior internal cusp somewhat larger in *C. azaræ*. In both, a line drawn from the anterior-external to the anterior-internal cusp (*a b*, fig. 3, p. 243) makes an acute angle with a transverse line, on account of the not very backward position of the latter. In the Fox there is a very small secondary cusp between the inner anterior and the inner posterior cusps, which is absent in *C. azaræ*.

The second lower incisor lies completely behind the first in *C. azaræ*; but this is probably only an individual exaggeration of a tendency to the displacement of the second incisor backwards, which is often observable in the Canidæ.

Table II.—*Measurements of the Cheek-teeth of* C. vulpes *and* C. azaræ.

	C. vulpes.	*C. azaræ.*
Length of the whole upper præmolar and molar series	54	50
Length of the whole lower præmolar and molar series	60	57
Length of $\frac{pm.\,4}{}$	13	12·5
" $\frac{m.\,1}{}$	9·3	9
Breadth of $\frac{m.\,1}{}$	11	11
Length of $\frac{m.\,2}{}$	5	5
Breadth of $\frac{m.\,2}{}$	7·3	7
Length of $\frac{}{m.\,1}$	15	14·3
" $\frac{}{m.\,2}$	7·3	7·5
" $\frac{}{m.\,3}$	3	3·5

In both *C. vulpes* and *C. azaræ* the hinder ends of the nasal bones just reach the level of the hindermost part of the fronto-maxillary suture. In the Fox the ascending processes of the præmaxillary bones reach the anterior processes of the frontal bones, while in *C. azaræ* there is a wide interval between the two.

In both, the temporal ridges unite into a crest for a short distance behind; but for the rest of their extent they are separate, inclosing a very narrow *sagittal area* (fig. 1, p. 241). At the anterior extremity of this the ridges diverge and pass outwards to the angles of the supraorbital process; and it is at this point that the principal external difference between the two skulls becomes apparent.

In the Fox (fig. 1, B, p. 241), the well-defined ridge runs nearly parallel with its fellow for some distance in front of the coronal suture, and then sweeps outwards, in a sharp curve, to the recurved supraorbital process, behind which a deep constriction marks the boundary between the interorbital and the temporal regions of the skull. In *Canis azaræ* the temporal ridge is not so well marked; and, beginning to diverge from its fellow a little in front of the coronal suture, it passes with a very slight curve to the angle of the supraorbital process, while the postorbital constriction is small (fig. 1, A). Moreover there is hardly any depression on the upper surface of the supraorbital process, the whole glabellar region being evenly arched from side to side. In the Fox, there is a well-marked depression on the outer part of the upper surface of the supraorbital process, and the glabella is flatter. These external differences answer to small but very definite distinctions which are seen in the longitudinal sections.

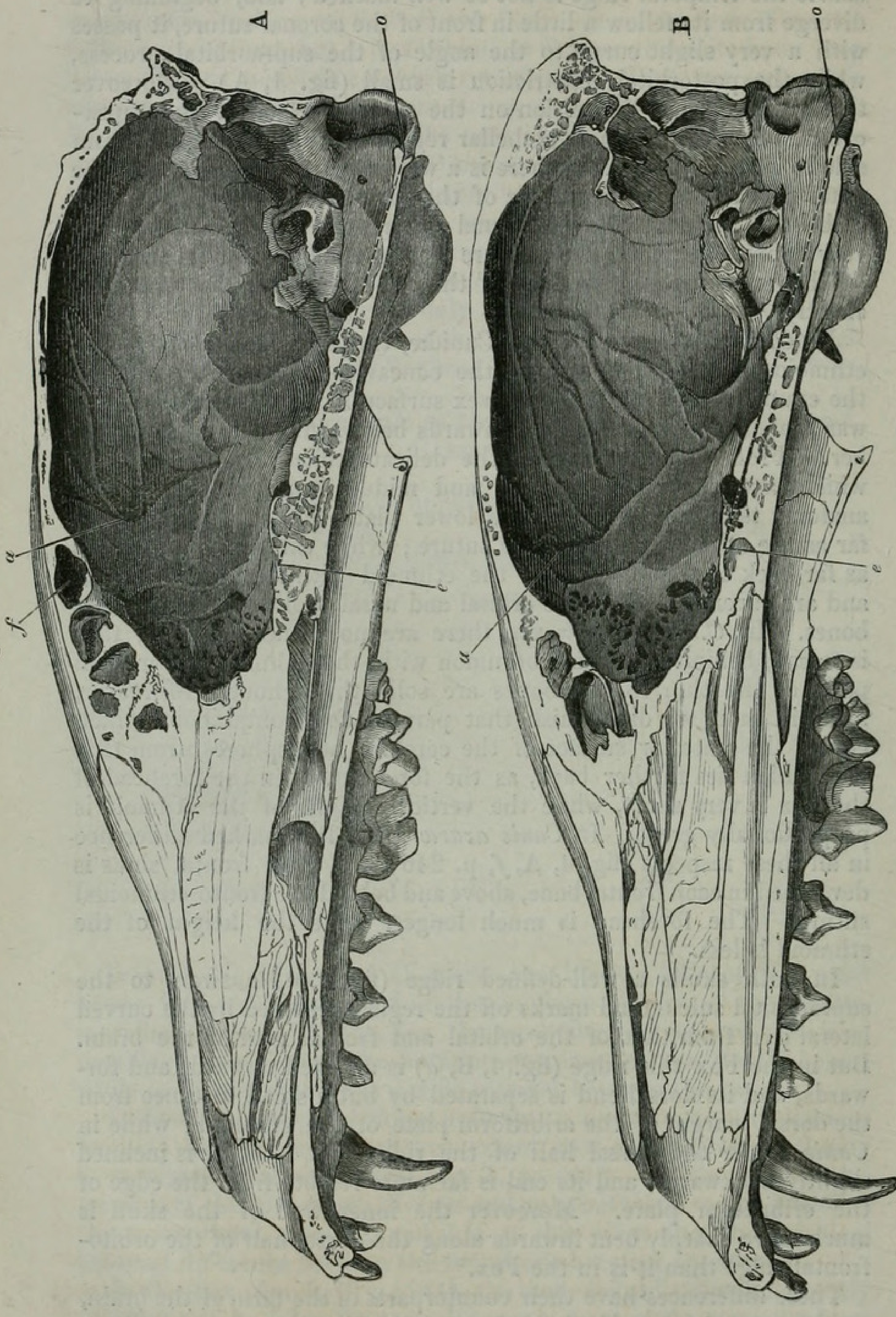
The superimposed sections of the two skulls correspond almost exactly.

In *C. vulpes*, as in all the Canidæ, the cribriform plate of the ethmoid bone is funnel-shaped, the concavity being turned towards the cranial cavity, while the convex surface looks outwards and upwards above, outwards and downwards below, into the nasal chamber. From its outer surface the delicate rolled laminæ of bone which answer to the superior and middle turbinals of human anatomy take their origin. The lower plates project backwards as far as the ethmo-præsphenoidal suture; while the upper ones reach as far back as the junction of the ethmoid with the frontal bones, and are covered over by the orbital and nasal prolongations of those bones. In *C. vulpes*, however, there are no frontal sinuses; that is to say, behind the point of union with the ethmoid the median parts of the thin frontal bones are solid throughout. Moreover, if, as in man, we distinguish that part of the frontal bone which covers the anterior surface of the cerebral hemispheres, from that part which lies further back, as the forehead, then the forehead of the Fox is very short, while the vertical height of the ethmoid is proportionally great. In *Canis azaræ* there is a marked difference in all these respects (fig. 4, A, *f*, p. 246). A large frontal sinus is developed in each frontal bone, above and behind the fronto-ethmoidal suture. The forehead is much longer, while the height of the ethmoid is less.

In both skulls a well-defined ridge (fig. 4, *a*) answers to the supraorbital sulcus, and marks off the region occupied by the curved lateral gyri from that of the orbital and frontal gyri of the brain. But in the Fox this ridge (fig. 4, B, *a*) is directed upwards and forwards, and its dorsal end is separated by but a small distance from the dorsal margin of the cribriform plate of the ethmoid; while in *Canis azaræ* the dorsal half of the ridge (fig. 4, A, *a*) is inclined slightly backwards, and its end is far more remote from the edge of the cribriform plate. Moreover the inner wall of the skull is much more sharply bent inwards along the dorsal half of the orbito-frontal ridge than it is in the Fox.

These differences have their counterparts in the form of the brain, and become very manifest when casts of the interior of the skull are compared (fig. 5, p. 247). In the Fox the contour of the brain, viewed from above, is that of a pear with the narrow end forwards. Late-

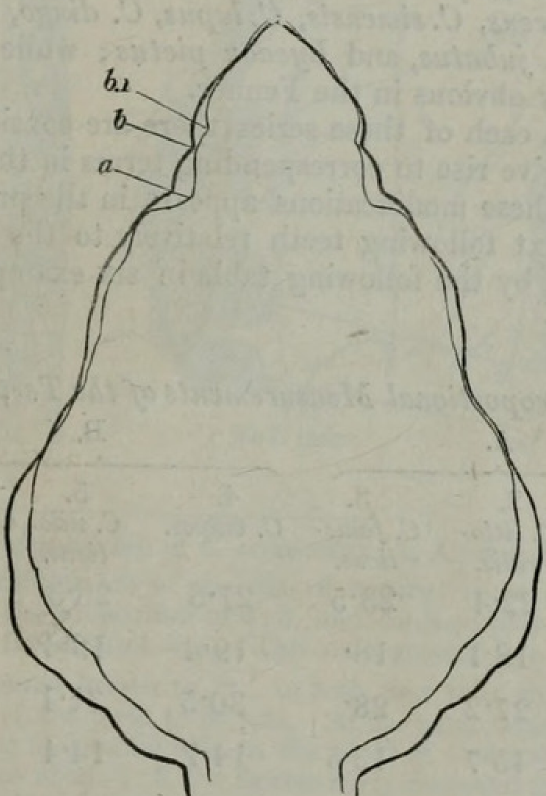
Fig. 4.



Longitudinal sections of the skulls of *C. azaræ* (A) and *C. vulpes* (B).
o e, basicranial axis; *f*, frontal sinus; *a*, orbito-frontal ridge.

rally the contour-line is undulated, presenting one slight incurvation in the region of the sylvian sulcus and another in that of the supraorbital sulcus (fig. 5, *a*), while a little angulation (fig. 5, *b*, b_1) marks the junction of the olfactory lobes with the cerebral hemispheres. In *Canis azaræ* the cerebral hemispheres immediately behind the supraorbital fissure widen out abruptly (fig. 5, *a*), and the lateral contour, instead of being slightly incurved at this point, presents a sharp rectangular inflection. The frontal lobe anterior to the supraorbital sulcus is much longer in *C. azaræ* (*a*–*b'*) than in *C. vulpes* (*a*–*b*); and the brain is considerably wider behind in the latter.

Fig. 5.



Superimposed outlines of the casts of the cranial cavities of *C. azaræ* and *C. vulpes*, viewed from above. The thin line belongs to the former, the thick line to the latter.

a, the supraorbital sulcus; *b*, the junction of the olfactory lobe with the cerebral hemisphere in *C. vulpes*; *b'*, in *C. azaræ*.

Thus, notwithstanding the extremely close resemblance of these two skulls, there is a very readily discernible difference between them in the presence of frontal sinuses and the peculiar character of the anterior part of the cranial cavity in *C. azaræ*, while both these features are absent in *C. vulpes*. These differences have nothing to do with size or age, inasmuch as the two skulls are almost identical in size and are both fully adult. Nevertheless I do not know that I should have been disposed to attach any great importance to such characters, if I had not found, on examining a large number of canine animals, that they may be disposed in two groups, in one of which the peculiarities of *Canis vulpes*, while in the other those of *C. azaræ* are always to be met with.

Similar to *C. vulpes* are *C. fulvus, C. argentatus, C. cinereo-argentatus, C. littoralis, C. niloticus, C. caama, C. zerda, C. lagopus*; and, on the other hand, *C. lupus*, all varieties of *C. domesticus*[1], *C. aureus, C. anthus, C. latrans, C. antarcticus, C. magellanicus*, and *C. cancrivorus* have the characters of *C. azaræ*.

We are thus enabled to distinguish two series of Canidæ, the one of which may be termed *Alopecoid* and the other *Thooid*.

The figures of the late Prof. Gervais, "Mémoire sur les formes cérébrales propres aux animaux carnivores" (Nouvelles Archives du Muséum, tome vi.), prove that the Thooid character of the brain obtains in *C. aureus, C. simensis, C. lupus, C. dingo, C. sumatrensis, C. primævus, C. jubatus*, and *Lycaon pictus*; while the Alopecoid features are very obvious in the Fennec.

4. But within each of these series there are considerable modifications, which give rise to corresponding terms in the two series.

The first of these modifications appears in the proportion of the sectorial and next following teeth relatively to the basicranial axis (=100), shown by the following table in six examples of the Alopecoid series:—

Table III.—*Proportional Measurements of the Teeth in Alopecoids.*

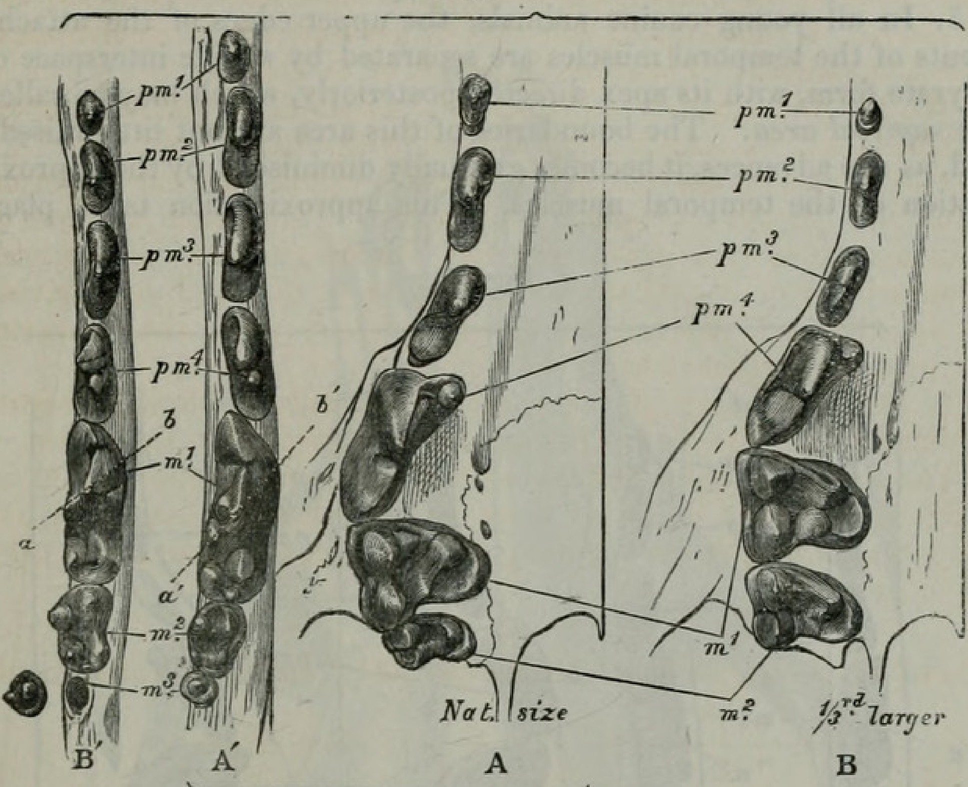
	A.			B.			
Length of	1. *C. zerda.*	2. *C. littoralis.*	3. *C. famelicus.*	4. *C. vulpes.*	5. *C. niloticus.*	6. *C. argentatus.*	1 : 6
$\underline{pm.4}$ ..	20·6	22·4	23·5	27·3	28·3	28·5	1 : 1·38
$\underline{m.1}$ ..	17·3	18·1	18·	19·4	19·4	20·5	1 : 1·18
$\overline{m.1}$ ..	24·	27·2	28·	30·5	31·1	34·4	1 : 1·43
$\overline{m.2}$ ..	14·	15·7	13·5	14·7	14·4	15·0	1 : 1·07

These measurements represent individual specimens; and it must be recollected that others might vary considerably on either side of the proportions here given. But they suffice to prove, firstly, that in the group A the sectorial teeth are relatively smaller than in the group B, so that it may be convenient to speak of the one as *microdont* and the other as *macrodont* Alopecoids; secondly, while $\underline{pm.4}$, $\underline{m.1}$, $\overline{m.1}$, and $\overline{m.2}$ all become larger between *C. zerda* and *C. argentatus*, the increase is far greater on the part of $\underline{pm.4}$ than on that of $\underline{m.1}$, and of $\underline{m.1}$ than on that of $\underline{m.2}$. Thirdly, while in *C. zerda* $\underline{m.1}$ is to $\underline{pm.4}$ as 1 : 1·19 and $\overline{m.2}$ to $\overline{m.1}$ as 1 : 1·71, in *C. argentatus* the former proportion is 1 : 1·39 and the latter as 1 : 2·26. In

[1] In a skull of a Blenheim Spaniel the frontal sinuses are totally absent, but the disposition of the orbito-frontal ridge is exactly as in other domestic Dogs. I do not know whether this peculiarity is general in the Blenheim breed or not.

other words, in the macrodont Alopecoids these teeth are not merely larger but they are more differentiated, the sectorial teeth becoming increased out of proportion to the rest.

Fig. 6.



The crowns of the cheek-teeth of *C. argentatus* (A, A') and *C. littoralis* (B, B'). Those of *C. argentatus* are of the size of nature; those of *C. littoralis* are enlarged in the proportion of 4 : 3, and consequently are larger by one third than the natural size. This enlargement has the advantage of giving the same length to $\underline{m.\ 1}$ in both, and thus enabling the relative dimensions of the teeth to be seen. At the same time, inasmuch as the length of the basicranial axis in the skull of *C. argentatus* is to that in *C. littoralis* as about 4 : 3, the figures fairly represent the actual morphological relations of the teeth.

a b, *a' b'*, cusp-lines of the lower sectorial teeth. The third lower molar in B' was absent, and is figured from another specimen; its crown is seen somewhat obliquely.

Similar relations are observable in the Thooid series, as the following table of proportional measurements clearly shows:—

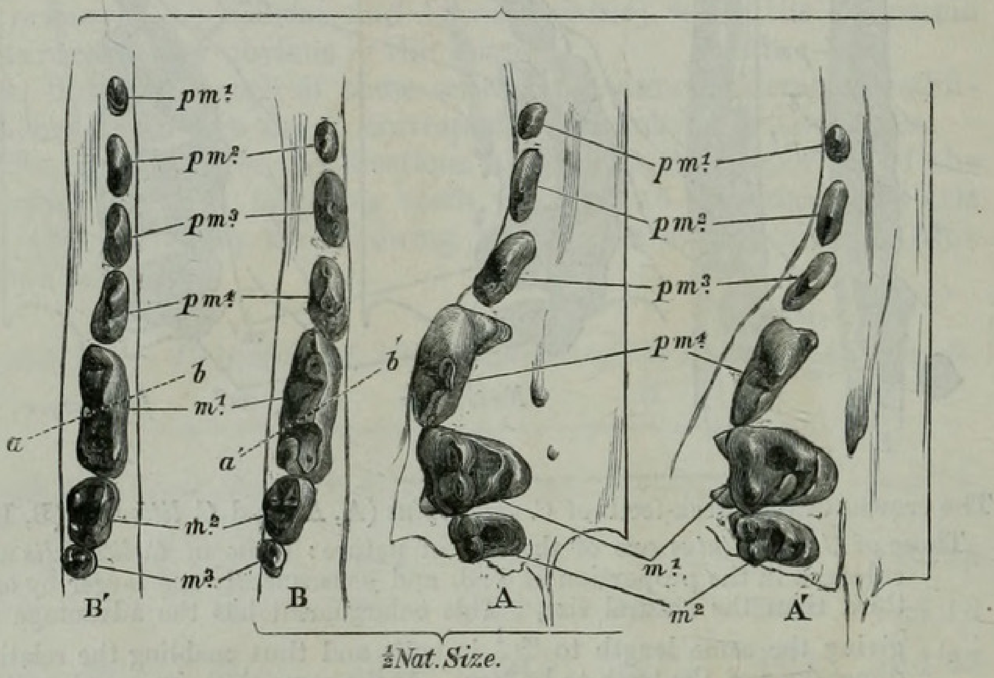
TABLE IV.—*Proportional Measurements of the Teeth in Thooids.*

	A		B			
	1.	2.	3.	4.	5.	
Length of	*C. azaræ* (a).	*C. magellanicus.*	*C. azaræ.*	*C. dingo.*	*C. lupus.*	1 : 5
$\underline{pm.\ 4}$ ..	22·4	24·4	26·3	30	32·5	1 : 1·45
$\underline{m.\ 1}$ ..	17·7	15·9	19·4	20	23·2	1 : 1·31
$\overline{m.\ 1}$ ..	27·7	26·5	30·0	33·2	36·9	1 : 1·33
$\overline{m.\ 2}$ ..	14·4	12·2	15·7	14·4	17·1	1 : 1·18

In this series $\frac{pm.\,4}{}$ and $\frac{}{m.\,1}$, as before, increase out of proportion to the rest, and $\frac{}{m.\,2}$ undergoes the least alteration; but the upper sectorial increases rather more than the lower, which is the reverse of the relation which obtains in the Alopecoid series.

5. In all young canine animals, the upper edges of the attachments of the temporal muscles are separated by a wide interspace of a lyrate form, with its apex directed posteriorly, which may be called the *sagittal area*. The boundaries of this area are but little raised; and, as age advances, it becomes gradually diminished by the approximation of the temporal muscles. This approximation takes place

Fig. 7.



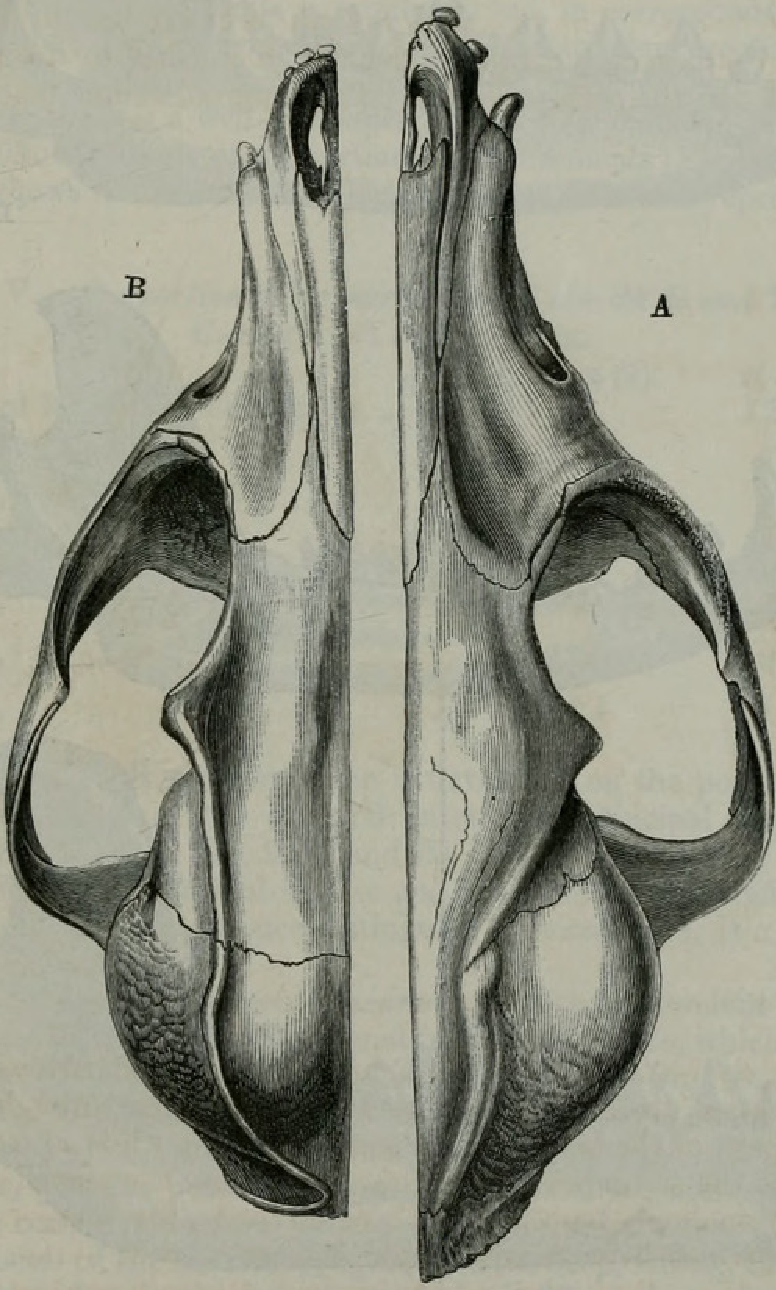
Upper (A) and lower (B) cheek-teeth of *C. lupus*, half the natural size; upper (A′) and lower (B′) teeth of *C. azaræ* (a), of the natural size. The first upper molars are thus brought to the same length, and the proportional increase of size of the sectorial teeth of the Wolf is apparent.

more rapidly behind than in front, and results in the narrowing, and in most cases coalescence, of the temporal ridges throughout the greater part of the length of the sagittal suture, while in front they diverge to the supraorbital processes and inclose the glabellar area.

In the smaller Alopecoids, such as *C. zerda*, the temporal ridges remain permanently separate, and inclose a wide lyrate sagittal area, the ridges themselves not being very strongly marked; but in *C. littoralis* and *C. cinereo-argentatus* (= *C. virginianus*) the ridges take the form of strongly-raised cord-like elevations, which impart a very characteristic aspect to the skull (fig. 8, p. 251). In this case there is no sagittal crest. But sometimes there is a well-defined though comparatively narrow sagittal area, from the centre of which a low sagittal crest rises. This is well seen in some Jackals, and especially in *C. antarcticus*.

6. In most of the Alopecoids, the contour of the inferior margin of the angular process continues the direction of that of the inferior margin of the ramus in front of it; and this slopes gradually upwards and backwards. In *C. littoralis* and *C. cinereo-argentatus*, however, the inferior contour of the ramus in the region of the

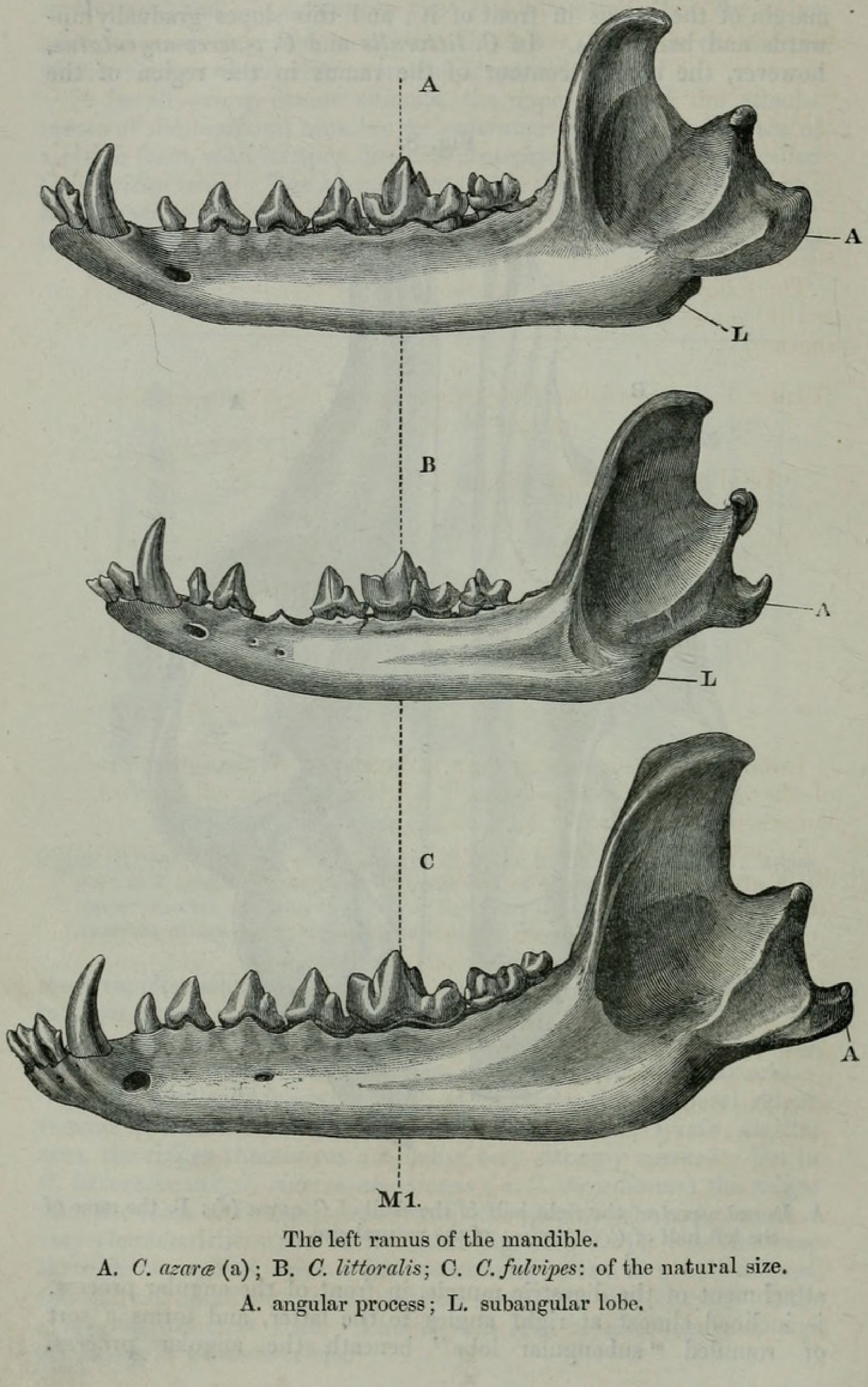
Fig. 8.



A. Dorsal aspect of the right half of the skull of *C. azaræ* (a); B. the same of the left half of *C. littoralis*: of the natural size.

attachment of the digastric muscle, in front of the angular process, is inclined almost at right angles to the latter, and forms a sort of rounded "subangular lobe" beneath the angular process.

Fig. 9.



The left ramus of the mandible.

A. *C. azaræ* (a); B. *C. littoralis*; C. *C. fulvipes*: of the natural size.

A. angular process; L. subangular lobe.

De Blainville long since figured and called attention to this feature of the mandible in *C. cinereo-argentatus*.

These peculiarities are closely reproduced in the Thooid series, by the skull of a South-American animal referred to *Canis azaræ*[1], which died in the Gardens of the Society, and to which I have alluded above as *C. azaræ* (a) (fig. 8 A, p. 251). The sagittal area is wide and lyrate; but the temporal ridges are not so strongly marked as in *C. littoralis*. There are no strong depressions on the supraorbital processes; and the glabella is evenly arched, in correspondence with the small but distinct frontal sinuses. The angular process of the mandible is extremely strong, and its margin is thick and tumid. Beneath it there is a well-developed subangular lobe (fig. 9 A, L).

The following table of proportional measurements (basicranial axis =100) shows how closely *C. azaræ* (a) and *C. littoralis* represent one another.

Table V.—*Proportional Measurements of the Skull and Teeth of* C. azaræ (*a*) *and* C. velox.

	C. azaræ (a).	*C. velox.*
Total length of bony palate........	125	122
,, breadth of ,, ...	78·9	71
,, length of $\frac{pm.\,4}{}$	22·4	22·4
,, ,, $\frac{m.\,1}{}$	17·7	18·1
,, ,, $\frac{m.\,2}{}$	11·1	13·3
,, ,, $\overline{m.\,1}$	27·7	27·2
,, ,, $\overline{m.\,2}$	14·4	15·7

In both, a small accessory cusp is developed on the posterior part of the outer face of the external anterior or principal cusp of the lower sectorial tooth (fig. 9, A and B).

Nevertheless the frontal sinuses and the form of the anterior part of the cerebral cavity at once distinguish *C. azaræ* (a), as a Thooid, from *C. littoralis*.

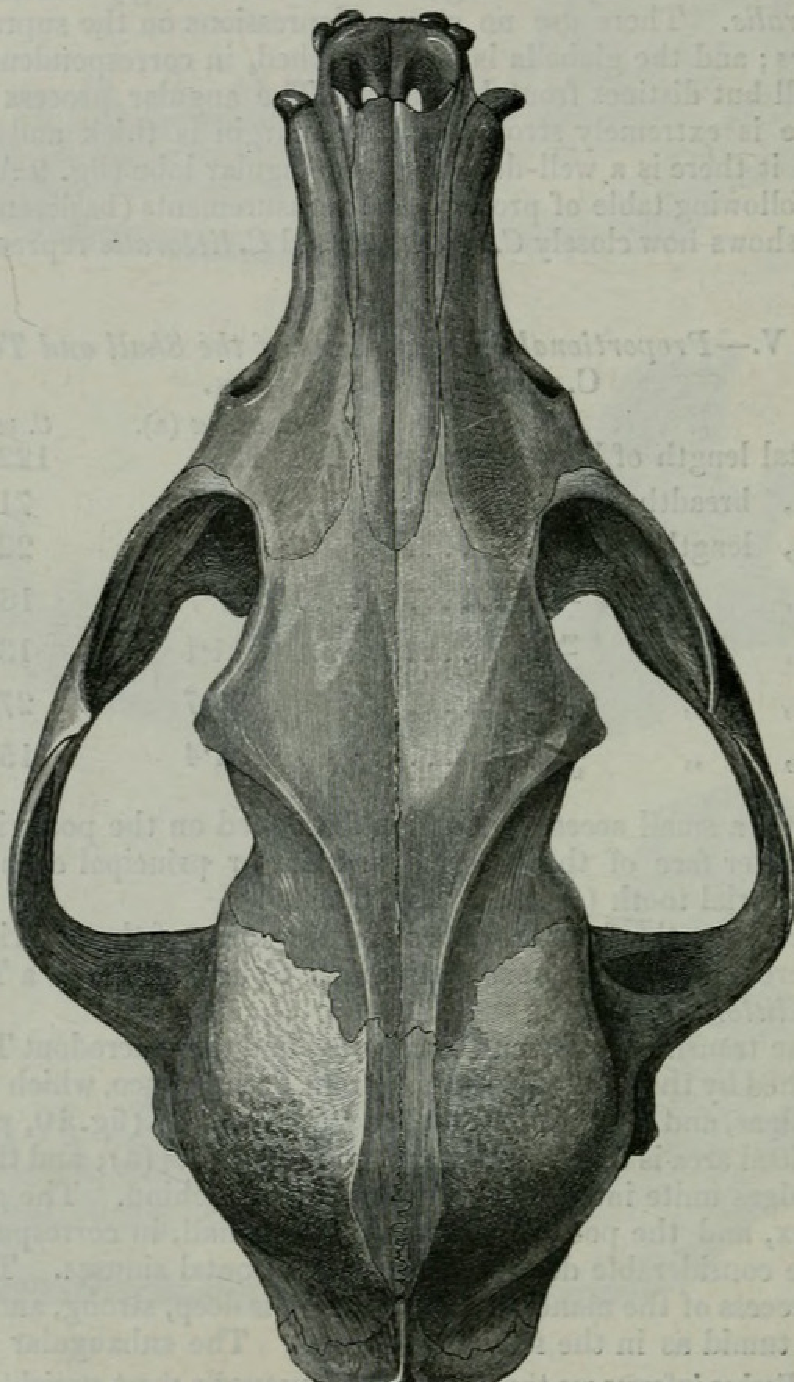
7. The transition between *C. azaræ* (a) and the macrodont Thooids is furnished by the skull of an animal from Pernambuco, which died in the Gardens, and came to me labelled "*C. fulvipes*" (fig. 10, p. 254). The sagittal area is much narrower than in *C. azaræ* (a); and the temporal ridges unite into a short median crest behind. The glabella is convex, and the postorbital constriction small, in correspondence with the considerable development of the frontal sinuses. The angular process of the mandible (fig. 9, C, A) is deep, strong, and thick, but not tumid as in the foregoing species. The subangular lobe is

[1] Mr. Forbes informs me that this animal possessed a short straight cæcum. *C. cancrivorus* has a similar cæcum. In *C. procyonoides*, *C. jubatus*, and *Icticyon venaticus* the cæcum is longer and larger, but almost straight. In all the other Canidæ (certainly in *C. lupus*, *C. laniger*, *C. domesticus*, *C. aureus*, *C. anthus*, *C. antarcticus*, *C. azaræ*, in *Cyon*, *Lycaon*, *Vulpes*, and *Otocyon*) it would appear that the cæcum is large and coiled. (See Garrod, P. Z. S. 1873 and 1878; Murie, P. Z. S. 1873; Flower, P. Z. S. 1880.)

far less developed; hence the inferior contour of this part of the jaw is not very much more prominent than it is in some of the Jackals.

I cannot distinguish the skull of this "*C. fulvipes*" from that

Fig. 10.



Dorsal view of the skull of *C. fulvipes.*

figured by De Blainville ('Ostéographie,' *Canis*, pl. viii.) under the name of *Canis cancrivorus*, from Cayenne—nor from the *C. cancrivorus* of Burmeister, which appears to be identical with the *C. bra-*

siliensis of Lund. Under these circumstances I presume that it should be named *C. cancrivorus.*

Another skull of a male animal which died in the Gardens has unfortunately lost its mandible. It is labelled "*C. cancrivorus,*" and differs from the foregoing only in having a much broader sagittal area, with slightly larger teeth and broader and longer palate in proportion to the basicranial axis (though not absolutely) than the foregoing.

A third skull, also labelled "*C. cancrivorus,*" ♀, is young, with the milk-teeth not yet shed. The permanent first molars above and below are just coming into place; and their actual dimensions are so nearly identical with those of the preceding skulls, that, though the mandible has not quite the characteristic degree of lobation, I am disposed to think that the differences which exist depend merely on age.

8. If the measurements of the skulls of *C. azaræ* (a), *C. cancrivorus,* and *C. azaræ* be now compared with one another and with those of *C. aureus, C. anthus,* and *C. lupus,* they will be found to form a gradual series of modifications.

TABLE VI.—*Proportional Measurements of the Skulls and Teeth of* Thooids.

	C. azaræ (a).	*C. cancrivorus.*	*C. azaræ.*	*C. aureus.*	*C. anthus.*	*C. lupus.*
Length of basicranial axis	100	100	100	100	100	100
Length of $\frac{pm.\,4}{}$	22·4	25·5	26·3	27	30	32·5
„ „ $\frac{m.\,1}{}$	17·7	20·8	19·4	21·4	20·4	23·2
„ „ $\frac{m.\,2}{}$	11·1	12·5	12·1	12	13·6	12·5
„ „ $\frac{}{m.\,1}$	27·7	29·1	30	30·9	34	36·9
„ „ $\frac{}{m.\,2}$	14·4	15·6	15·7	17·1	16·3	17·1
„ „ palate	125	125	150	124	137	146
Breadth of palate	78·9	79	85	94	95	99

The only considerable break in the regularity of the progression here arises from the large size of $\frac{m.\,1}{}$ in *C. cancrivorus* and the unusual length of the palate in *C. azaræ.* This regularity, however, is fortuitous. The measurements here given are those of individual skulls; and if several individuals of any given species are measured in the same way, the range of variation in some cases is remarkable. Thus, three specimens of the Indian Jackal yield the following results (basicranial axis = 100):—

TABLE VII.—*Proportional Measurements of Teeth and Palate of* Canis aureus.

	I.	II.	III.
Length of $\underline{pm.\ 4}$	27	31	33·8
„ „ $\underline{m.\ 1}$	22	24	21·6
„ „ $\underline{m.\ 2}$	12	12·2	13·2
„ „ $\overline{m.\ 1}$	30·5	34	35·8
„ „ $\overline{m.\ 2}$	17	16·9	16·6
„ „ $\overline{m.\ 3}$		7·5	7·5
Length of palate	125	141	143
Breadth of palate	94	90	90

The actual dimensions in millimetres are as follows:—

TABLE VIII.—*Cranial and Dental Measurements of* Canis aureus.

	I.	II.	III.
Length of basicranial axis. .	59	53	53
„ $\underline{pm.\ 4}$	16	16·5	18
„ $\underline{m.\ 1}$	13	13	11·5
„ $\underline{m.\ 2}$	7	6·5	7·1
„ $\overline{m.\ 1}$	18	18	19
„ $\overline{m.\ 2}$	10	9	9
„ $\overline{m.\ 3}$		4	4
„ palate	74	75	76
Breadth of „	56	48	48

The comparison of these two tables is interesting; for, according to the first, the variations of the dimensions of the teeth in proportion to those of the basicranial axis cover the whole range between *Canis azaræ* and the Wolves; on the other hand, the second shows that, while the basicranial axis, doubtless following the actual size of the animal, varies considerably, and while the teeth also vary, the two sets of variations do not correspond: hence, in the proportional table, the differences in the sizes of the teeth appear to be greater than they really are.

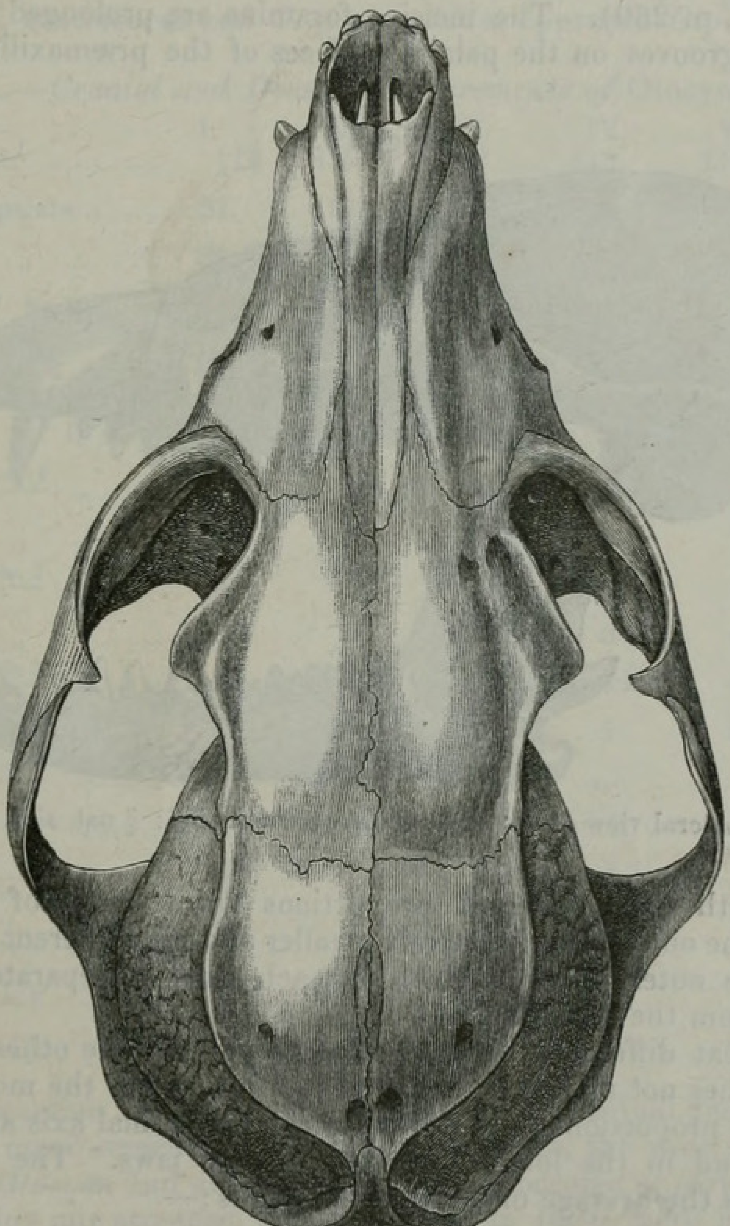
Similar results are attained when the measurements of any considerable number of specimens of other canine skulls are compared. In fact, while in both the Thooid and the Alopecoid series the species may be arranged in a scale characterized by the gradually increasing relative and actual dimensions of the sectorial teeth, each species occupies not a line but a broad zone upon that scale, which zone is overlapped by that of the species below and by that of the species above.

9. The lowest Alopecoids and the lowest Thooids agree in the relatively small size of their sectorial teeth; and many possess a large lyrate sagittal area and a strongly lobate mandible. The genus

Otocyon shares the last two peculiarities, and exhibits the first in a more marked degree than any other known canine animal, recent or extinct.

There are three skulls of this interesting form in the Museum of the Royal College of Surgeons, and three in the British Museum; and they all agree very closely with the figures and description given by De Blainville.

Fig. 11.

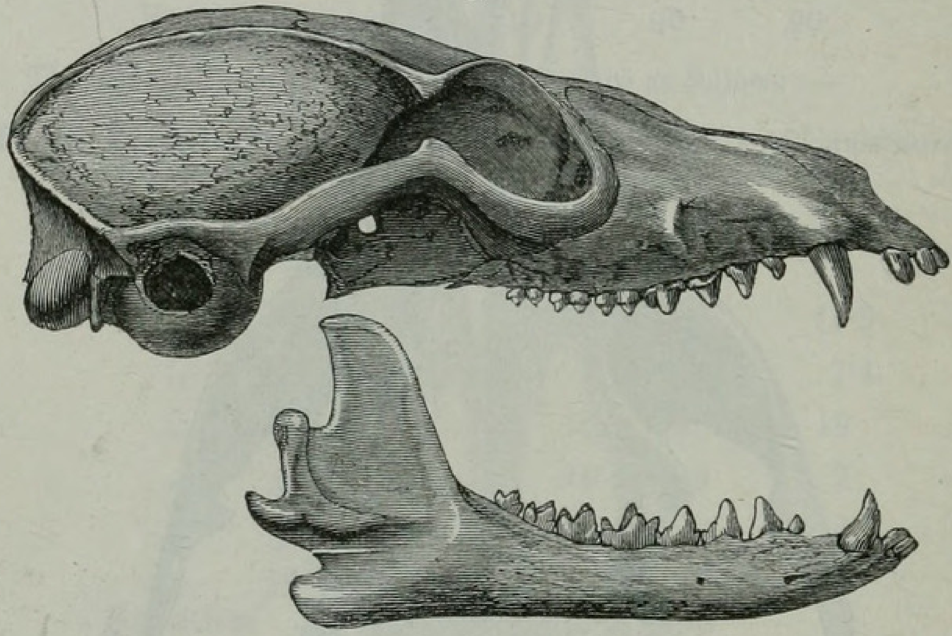


Dorsal view of the skull of *Otocyon lalandii*: nat. size.

In all, the posterior ends of the nasal bones extend beyond the fronto-maxillary suture; but they vary considerably in width. The frontal processes are well separated from the ascending processes of the præmaxillaries. The temporal ridges are much stronger and the sagittal area narrower in one skull, which appears to be the oldest. There are no frontal sinuses. In all, the subangular lobe of the mandible is very strong, thickened, and more or less incurved at its free margin. The angular process is strong, and projects inwardly as a horizontal shelf-like prominence, which is concave above, so that it somewhat resembles the bowl of a spoon (fig. 14, C, p. 263).

The posterior margin of the bony palate lies considerably behind the line of the hindmost molars. The line of the cheek-teeth is not angulated at the junction of the upper sectorial with the first molar, but nearly straight and almost parallel with that of the opposite side (fig. 13, B, p. 260). The incisive foramina are prolonged forwards into deep grooves on the palatal surfaces of the præmaxillæ. The

Fig. 12.



Lateral view of the skull of *Otocyon lalandii*: $\frac{3}{4}$ nat. size.

incisor teeth have different proportions from those of ordinary Canidæ, the outer being relatively smaller and less different from the rest. The outer upper incisor, on each side, is separated by an interval from the second.

The great difference between *Otocyon* and all the other Canidæ, however, lies not merely in the increased number of the molar teeth, but in the proportions of the teeth to the basicranial axis and to one another, and in the low development of the jaws. The following table gives the average of three of the skulls :—

Table IX.—*Proportional Measurements of the Skull and Teeth in* Otocyon.

Basicranial axis	100 (average absolute length 42 mm.).
Length of $\frac{pm.\ 4}{\ }$	12.7
„ $\frac{m.\ 1}{\ }$	13·4
„ $\frac{m.\ 2}{\ }$	11·8

Length of $\overline{m.\,1}$	16·1
,, $\overline{m.\,2}$	13·3
,, $\overline{m.\,3}$	9·8
,, palate	138
Breadth of palate	66

Thus the upper jaw is both short and narrow; and the slenderness of the rami of the mandible is not less remarkable, though in this respect *C. cancrivorus* and *C. procyonoides* approach *Otocyon.*

Table X.—*Cranial and Dental Measurements of* Otocyon lalandii.

	I.	II.	III.	IV.	V.	VI.
Total length	114	123	112	113	112	
Length of palate.........	57	61	53	54	58	59
Breadth ,, ...	28	26	27	27	29	27
Length of basicranial axis	......	......	40	41	43	41
Length of $\underline{pm.\,4}$	5·7	6·5	5·5	5·3	5·5	5
Breadth ,, in front	5	5·5	5·8	4·7	5	4
Length of $\underline{m.\,1}$	5	5·5	5	5·5	6	5
Breadth ,, ...	6·2	8	7	6	7	6·5
Length of $\underline{m.\,2}$	5	5·5	5	5	5	4·5
Breadth ,, ...	6·5	8	7	6·5	6·5	6·5
Length of $\underline{m.\,3}$	4·5	5	4	3·5	4·5	4
Breadth ,, ...	6	6	6	5	5·5	5·5
Length of $\underline{m.\,4}$	......	......	......	......	......	4
Breadth ,, ...	......	......	......	......	......	4
Length of $\overline{m.\,1}$	6	7	6·5	6·5	7	6
,, $\overline{m.\,2}$	6	6	6	5·5	6	5
,, $\overline{m.\,3}$	5	6	5	4·3	4·5	4
,, $\overline{m.\,4}$	3·5	4	3	3	3·3	*

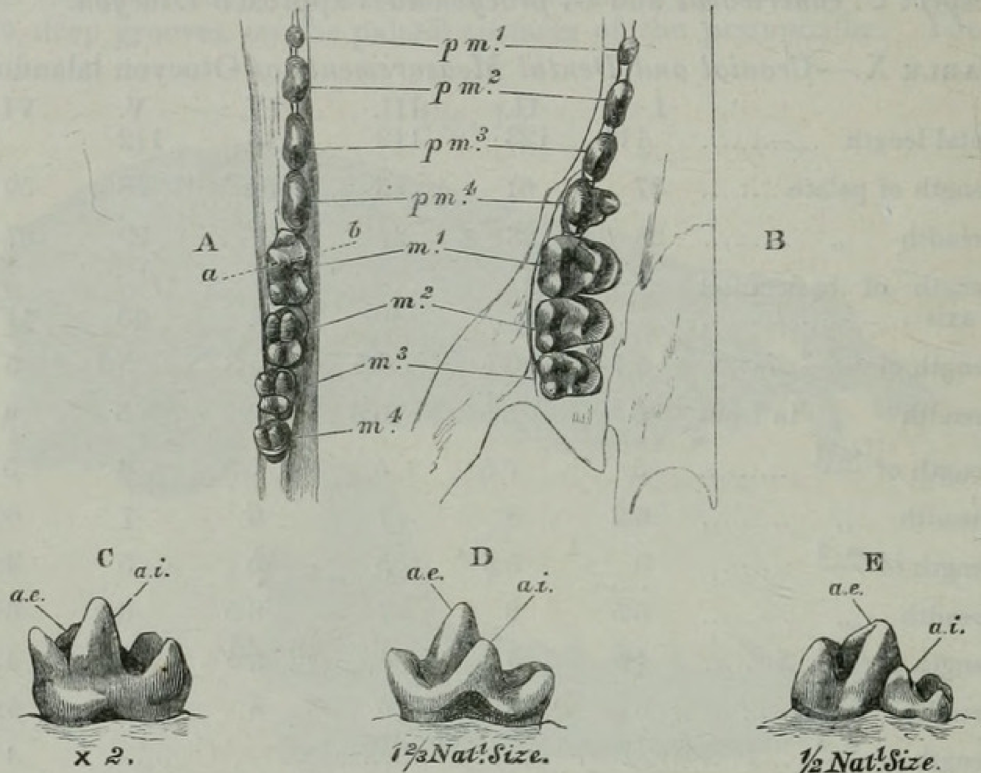
On inspection of the foregoing tables of the actual and the proportional measurements of the skulls and teeth, the wide differences between *Otocyon* and all the other Canidæ become apparent.

Confining our attention for the present to those teeth in *Otocyon* which answer to those met with in other Canidæ, it is obvious that the sectorial teeth are much smaller in proportion to the basicranial axis, that the difference between $\overline{m.\,1}$ and $\overline{m.\,2}$, $\overline{m.\,2}$ and $\overline{m.\,3}$, is much less, and that $\underline{pm.\,4}$ is never greatly longer and may be shorter than $\underline{m.\,1}$.

* Fallen out on both sides.

The patterns of the crowns of the upper cheek-teeth (fig. 13, B) are completely canine. The anterior inner cusp of the fourth upper præmolar is very thick and prominent, and gives the crown of the tooth the form of an almost equilateral triangle. There is a well-developed secondary cusp at the anterior end of the base of the principal cusp of this tooth, so that, viewed from the outside, it appears tricuspidate; and sometimes there is a minute cusp behind

Fig. 13.



A, lower, and B, upper cheek-teeth of *Otocyon lalandii*; the last molar in the upper jaw is absent; C, the lower sectorial tooth of *Otocyon* from the inner side, of twice the natural size; D, the corresponding tooth of *C. zerda*, and E, of *C. lupus*, reduced to the same absolute length and also viewed from the inner side; *a.e.* anterior external cusp; *a.i.* anterior internal cusp; *a b.* cusp-line. The tooth of the Fennec is obviously intermediate in character between that of *Otocyon* and that of the Wolf. The comparison of these figures with figs. 6 and 7 will give a very good conception of the extent and the nature of the modifications of the cheek-teeth in the Canidæ.

the principal inner cusp. In both points this tooth approaches the upper sectorial of *Nasua*. The crowns of the molars are broader than they are long; but the difference is less than in most Canidæ. Their four cusps, with the cingulum on the inner side, are very distinct; and the second upper molar is much larger in proportion to the first than in other Canidæ.

In the mandible, the third præmolar has a sharp cusp at the anterior end of its base; the first molar has the inner cusps higher than the outer ones; and the anterior paired cusps are set in a nearly transverse line, the inner hiding the outer when the tooth is viewed from within (fig. 13, C). In both these respects the crown of this tooth differs from that of other Canidæ and approaches the characters of the same tooth in the Viverridæ and, especially, in the Procyonidæ.

It is obvious that, in all these features, *Otocyon* represents a lower term in the series of the Alopecoids than *C. cinereo-argenteus* and *C. velox*; and although the interval between these and *Otocyon* is as wide as that between *C. velox* and *C. vulpes*, there would be no reason for separating *Otocyon* from the rest of the group were it not for the extraordinary excess in the number of molar teeth. Of these there are four on each side above in one specimen, three in the others, four on each side below in all. So far as any conclusion can be drawn from this limited number of examples, therefore, it would appear that the presence of the fourth upper molar is exceptional; and that the dentition is tending towards a higher type by its suppression. The crowns of the hindermost upper molars, in the one specimen in which they are shown, are of a triangular shape, the base of the triangle corresponding with the two distinct external cusps. On the inner side only one cusp remains. The crown of the small fourth lower molar exhibits two well-developed cusps, of which the outer is rather the smaller. These apparently represent the anterior cusps of the other molars, as the posterior pair of cusps are proportionally smaller than the anterior pair in the third molar.

10. The facts now adduced appear to me to permit of the arrangement of the Canidæ hitherto considered in the following manner:—

CANIDÆ.

I. *Molars* $\frac{2.2}{3.3}$.

A. Alopecoids.	B. Thooids.
a. Macrodonts.	
Ex. *C. argentatus.*	Ex. *C. lupus.*
C. vulpes.	*C. aureus.*
b. Microdonts.	
α. Mandible nonlobate.	
Ex. *C. caama.*	Ex. *C. azaræ.*
C. zerda.	*C. vetulus.*
β. Mandible lobate.	
Ex. *C. littoralis.*	Ex. *C. cancrivorus.*

II. *Molars* $\frac{4.4}{4.4}$.

C. Otocyonoids.

Otocyon.

It will, however, be readily understood from what has already been said, that it is not intended to suggest the possibility of sharply separating the macrodont from the microdont forms, or those with lobed mandibles from those with mandibles of the ordinary character. On the contrary, they pass into one another; while the lower Thooids, with small frontal sinuses, are so slightly separated from the lower Alopecoids, that it is hard to say whether we have any right to look for a Thooid representative of *Otocyon* or not. It is quite as reasonable to suppose that *Otocyon* is the nearest living representative of the primitive type of the Canidæ, whence all the rest have been derived, in the first place, by the differentiation of the Thooid from the Alopecoid series, and, in the second, by the occurrence of corresponding series of modifications leading up to the Fox on the one hand and to the Wolf on the other.

11. If this view of the facts is correct, the key to the morphological relations of the whole of the Canidæ must lie in the determination of the affinities of *Otocyon*. The facts hitherto considered primarily appear to me to suggest looking in two directions—in the first place towards the Procyonidæ, and in the second towards the Didelphia.

In studying the Canidæ it is impossible not to be struck by the wonderful persistency of the fundamental patterns of the sectorial teeth and of those which follow them. This singular uniformity can hardly be accounted for by adaptation to similar modes of life; for the pattern is as distinctly marked in *C. jubatus* and *C. procyonoides*, which live largely upon fruits and roots and never attack large animals, as in any of the more purely carnivorous Canidæ. It must therefore be regarded as a morphological fact of fundamental importance, and the best guide to the immediate affinities of this group of animals.

Now, in *Bassaris* we have a procyonine form, the teeth of which are extraordinarily similar to those of *C. zerda*, if we suppose the little posterior lower molar of the Fennec suppressed. The posterior margin of the bony palate is on a level with the hindermost molar teeth, and therefore does not extend further back than in the ordinary Canidæ. There are no frontal sinuses; and the ethmoid is high. In *Ælurus*, again, the patterns of the teeth are essentially canine, though inclining in some respects towards the Bears: the frontal sinuses are large, the ethmoid low, and the cranial cavity has a completely Thooid contour. In this genus, as Prof. Flower has pointed out, an alisphenoid canal is present. The small flattened bulla, with its long meatus, is unlike that of the Dogs; on the other hand, the carotid canal is long, and its posterior aperture opens into a depression common to it and the foramen lacerum posterius. The bony palate extends considerably further back than in any existing canine animal.

In *Nasua* the fourth premolar above is triangular; but a small second inner cusp is beginning to appear behind the large one. In *Procyon* this cusp has increased so much that the crown of the tooth is quadrangular. In this genus there is a small cingulum on the inner side of the first and second molars, which thus retain a resemblance to those of the Dog. In *Nasua*, however, it is no longer visible. In both these genera a line joining the inner and outer cusps of the lower sectorial teeth is almost transverse to the axis of the tooth, and the inner cusp is higher than the outer, as in *Otocyon*.

I find the proportional lengths of the teeth in *Nasua* and *Procyon* to be as follows:—

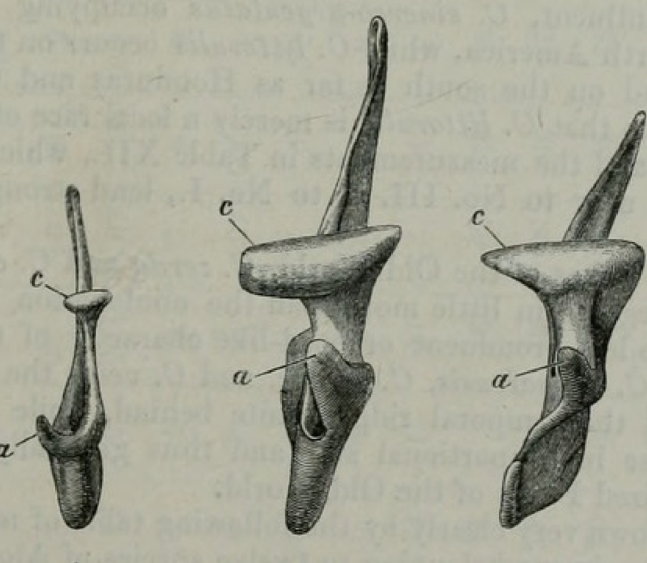
TABLE XI.—*Proportional Lengths of the Teeth in* Procyonidæ and Otocyon.

	Nasua.	*Procyon.*	*Otocyon.*
Length of $\frac{pm.\,4}{}$	16·6	16·6	12·7
" $\frac{m.\,1}{}$	17·7	17·7	13·4
" $\frac{m.\,2}{}$	16	12·7	11·8
" $\frac{}{m.\,1}$	18·8	20·5	16·1
" $\frac{}{m.\,2}$	20	19·4	13·3

The teeth of *Nasua* and *Procyon* are larger (and notably thicker) than those of *Otocyon*; moreover the hindermost molars, in their elongation and in other characters, tend towards the Ursine form. There is therefore no question of direct affinity between *Nasua* and *Procyon* and *Otocyon*; it is simply that, in dental characters, the lowest type of canine animal approaches the less-differentiated Procyonidæ.

In *Bassaris* and in *Procyon* the form of the ramus of the mandible is similar to that in the ordinary Canidæ; in *Nasua* it approaches

Fig. 14.



A B C

Right ramus of the mandible of *Perameles* (A), *Procyon* (B), and *Otocyon* (C), from behind: *a*, angular process; *c*, condyle.

that seen in *C. cancrivorus*; in *Ælurus* this peculiarity is still more exaggerated; and in *Cercoleptes* we have a mandible which resembles that of *Otocyon*, with a still more developed lobe. As to the base of the skull, it appears to me that, taking *Ælurus, Procyon*, and *Nasua* together, the arctoid characters are so modified, and the approximation to the canine type of skull becomes so close, that they almost present a transition from the one type of skull to the other.

I have elsewhere drawn attention to the fibrous epipubis of the Dogs as the homologue of the so-called "marsupial bone" of the

Didelphia and Ornithodelphia [1], and other indications of the approximation of the lower Carnivores to the *Didelphia* are not wanting.

If the mandibles of *Otocyon*, of *Procyon*, and of *Perameles* are viewed from behind (fig. 14, p. 263), it will be seen that the angular process is as distinctly inflected in the two former as in the latter, and that the difference in the angular process of *Thylacinus* is merely one of the degree of development of a homologous and similarly formed part [2].

I look upon the four molars of *Otocyon* as another character of the same order; as a survival, in fact, of a condition of the dentition exhibited by the common ancestors of the existing Canidæ and the existing carnivorous marsupials.

12. The geographical distribution of the Canidæ presents many points of interest when it is considered in relation to the morphological characters of the forms at present restricted to certain areas of the earth's surface.

Otocyon occurs only in South Africa, and apparently does not range beyond the southern extremity of that continent.

The microdont Alopecoids with lobate jaws (*C. cinereo-argentatus* and *C. littoralis*), which have been separated by Baird under the name of *Urocyon*, appear to me to be the nearest existing allies of *Otocyon*. But there is no representative of this group outside the North-American continent, *C. cinereo-argentatus* occupying the central States of North America, while *C. littoralis* occurs on the N.W. in California, and on the south as far as Honduras and Costa Rica. Baird suggests that *C. littoralis* is merely a local race of *C. cinereo-argentatus*; and the measurements in Table XII., which show that No. II. is as near to No. III. as to No. I., lend strong support to this view.

The small Foxes of the Old World, *C. zerda* and *C. caama*, differ from the foregoing in little more than the nonlobation of the mandible and the less prominent or cord-like character of the temporal ridges. In *C. bengalensis*, *C. corsac*, and *C. velox* the sagittal area narrows and the temporal ridges unite behind, while the sectorial teeth increase in proportional size, and thus gradually lead to the most specialized Foxes of the Old World.

This is shown very clearly by the following table of measurements of thirteen specimens belonging to twelve species of Alopecoids.

[1] Proceedings of the Royal Society, 1879. I have recently found the epipubis very well developed in a female Bengal Fox and in a female *C. mesomelas*. My friend Dr. Rolleston, F.R.S., has been good enough to compare *Thylacinus* with the domestic Dog; and he informs me that "the bone is disproportionately small in the marsupial in question; but it has precisely the same relation to the external oblique's bifid tendon, to the rectus and pyramidalis (which are only imperfectly differentiated from one another and from the inner or upper division of the tendon of the external oblique), and, finally, to the pectineus, which it has in the placental mammal."

[2] A comparison of the mandible of *Didelphys* with that of *Nasua* is even more instructive. In *Centetes* the angular process is slightly but characteristically inflected.

TABLE XII.—*Cranial and Dental Measurements of* Alopecoids.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.
Total length	97	104	...	84	108	...	112	112	126	...	136	143	146
Length of palate	45	51	57	42	50	53	60	60	64	63	67	73	74
Breadth "	27	29	34	25	33	30	32	34	40	38	40	41	44
Length of basicranial axis	36	38	45	36	42	39	38	...	44	...	49	46	50
" $\frac{pm.\,4}{}$	8·5	10	11	8	9	9·5	11	11	12·5	13	13	13	15
" $\frac{m.\,1}{}$	5·5	7·5	9	6	8	8	7	8	9	8·5	9	9·3	10·5
Breadth "	7·5	8·5	6	7·7	10	...	8	8·5	10·5	...	11	11	11·5
Length of $\frac{m.\,2}{}$	4·5	5·5	6	4	5·5	5	4	4	5	4	5	5	5·5
Breadth "	5·5	6·5	...	6	8	...	6	7	7·5	...	7	7·3	7·5
Length of $\frac{}{m.\,1}$	9·5	11·5	12·5	8·5	11	10	11·5	13·5	14	14	15	15	17
" $\frac{}{m.\,2}$	5	6	7·5	5	6	6·5	5·5	6·5	6·5	6	7	7·3	7
" $\frac{}{m.\,3}$	2.6	...	...	2·5	...	3	2	2·6	3	...	3·5	3	3

[Nos. I. and II. *C. littoralis*; No. III. *C. cinereo-argentatus* (=*virginianus*); No. IV. *C. zerda*; No. V. *C. caama*; No. VI. *C. bengalensis*; No. VII. *C. corsac*; No. VIII. *C. velox* (the measurements taken from Dr. Baird's figure of the skull of this species); No. IX. *C. niloticus*; No. X. *C. lagopus*; No. XI. *C. fulvus*; No. XII. *C. vulpes*; No. XIII. *C. argentatus*.]

Thus *C. caama*, *C. bengalensis*, *C. corsac*, and *C. velox* appear to be mere local varieties of a small Alopecoid form answering pretty nearly to the Jackals in the Thooid series, and occupying the southernmost part of the Alopecoid zone, from South Africa to Central America. The more differentiated Alopecoids, though largely coexistent with these, are preponderant in the north of the zone.

I can meet with no evidence of the existence of any true Alopecoid in South America, which appears to be the head quarters of the lower Thooids.

Among these, *C. vetulus* has the least modified dentition, and in this respect corresponds with *C. littoralis* among the Foxes. This species is figured and fully described by Burmeister. The skull has a low median sagittal crest; and the ramus of the mandible is slender and nonlobate. In the one imperfect cranium which I have seen (from which the measurements in Table XIII. are given) the length of the sectorial and first molar in the upper jaw is the same, and does not exceed 17 per cent. of the basicranial axis. The length of the lower sectorial is rather less than 23 per cent. The crown of the upper sectorial or fourth premolar is broadly triangular (breadth in front 5·5 millims. to length 7 millims.), on account of the great size of its internal cusp, and resembles that of *Otocyon*. The inner anterior cusp of the lower sectorial is lower than the outer; but a line drawn through both is almost transverse to the axis of the tooth, the heel of which is very stout.

In Brazil, in Demerara, and in Guiana the canine animals which have been named *Canis cancrivorus*, *C. fulvipes*, *C. brasiliensis*, *C. rudis*, and that to which I have referred above as *C. azaræ* (a) occur. The crania belonging to the first four which have come under my observation are, for the most part, rather larger than that of the last, have a less-marked subangular lobe and slightly larger sectorial teeth; but there is no sharp line of demarcation between the two sets, and I regard them all as local varieties of *C. cancrivorus*. Moreover, in those forms, such as *C. rudis*, in which the skull is largest, the approximation to *Canis azaræ* (the most widely distributed of the South-American Canidæ) is so close, that I cannot separate the two by any osteological or dental characters.

Canis magellanicus presents the same sort of relation to *C. cancrivorus* as *C. simensis*, in the Old World, bears to *C. aureus* and *C. anthus*. The size of the body, and notably of the jaws, has increased without any corresponding enlargement of the teeth (Table XIII.). In the large relative size of the upper molars, *Canis jubatus* adheres to the same type; while *C. antarcticus*, on the other hand, presents the closest approximation to some specimens of *C. latrans* (Table XIII.).

From the range of variation of *C. cancrivorus*, it can hardly be doubted that the examination of more extensive materials will prove the existence of an uninterrupted series of gradations from *C. vetulus* to *C. antarcticus* and *C. jubatus*. Burmeister [1] remarks that *Canis cancrivorus*, *C. fulvicaudus*, and *C. vetulus* are distinguished by the relative shortness of their jaws from *C. azaræ*, *C. griseus*, and *C.*

[1] Erläuterungen zur Fauna Brasiliens, p. 46.

Table XIII.—*Cranial and Dental Measurements of South-American* Thooids.

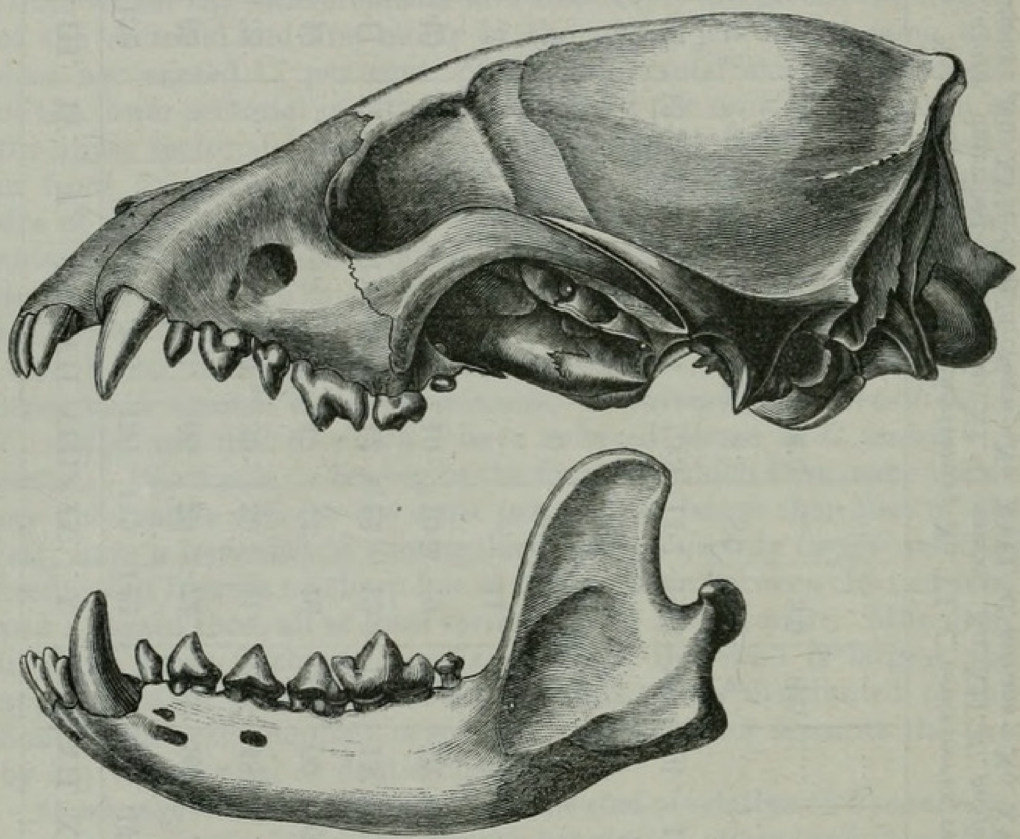
	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.	XIV.	XV.	XVI.	XVII.	XVIII.
Total length	...	116	132	...	...	124	125	130	119	142	...	187	177	215	160	166	180	174
Length of palate	48	57	65	...	...	62	61	66	59	72	64	92	...	108	84	84	92	89
Breadth ,, ...	29	36	38	...	...	40	39	39	39	41	38	48	...	60	55	53	50	55
Length of basicranial axis..	42	44	47	...	...	43	49	47	44	48	50	60	61	66	57	56	58	57
,, $\frac{pm.\ 4}{}$	7	10	11	11·2	12	11·5	12	12	12	12·5	14	15	15·5	18	18	17	18	19
,, $\frac{m.\ 1}{}$	7	8	10	8·5	9·5	9	10	10	10·5	9	10	10	9·5	15	12	11	11·5	12·5
Breadth ,, ...	8	10	...	...	...	11	11	...	...	11	...	12	...	15·5	14·5	14	14	14·5
Length of $\frac{m.\ 2}{}$	5	5	6	5·7	7	6	6	6	7	5	6	6·5	6·3	10	6·5	5·5	7	6·5
Breadth ,, ...	6·5	7·5	...	...	...	7·3	7·5	...	...	7	...	10	...	12	9	8	10	8
Length of $\overline{m.\ 1}$	9·5	12·5	14	13·2	14	...	14	13·5	14·2	14·3	15	16	16	21·5	19	19·5	19·5	
,, $\overline{m.\ 2}$	6·5	6·5	7·5	7·2	8	...	7·7	8	8·5	7·5	8	...	8·7	11	8·5	8·5	8·7	
,, $\overline{m.\ 3}$	3	3·7	4	4	4·5	...	4	4·5	...	3·5	4·5	...	3·2	5·5	4	4	4·5	
,, $\overline{m.\ 4}$	...	...	2	2·5	...	...	...	...	...	...	...	...	2·5					

[No. I. *C. vetulus*; No. II. *C. azaræ* (a); Nos. III., IV., and V. *C. cancrivorus*; No. VI. *C. cancrivorus*, referred to above; No. VII. *C. fulvipes*; Nos. VIII. and IX. *C. rudis*; No. X. *C. azaræ*, described above; No. XI. *C. azaræ*; No. XII. *C. magellanicus*; No. XIII. *C. magellanicus*; No. XIV. *C. jubatus*; No. XV. *C. antarcticus*; No. XVI. *C. antarcticus*; No. XVII. *C. latrans*; No. XVIII. *C. antarcticus*, skull without the mandible. The measurements of a specimen of *C. latrans* are given here to show the extreme closeness of the relation between the "Prairie-Wolf" and its southern analogue.]

magellanicus; but, so far as the measurements of his figures of the teeth permit me to form a judgment, *C. griseus* differs in no respect from some specimens of *C. cancrivorus*. With a shorter skull, Burmeister's specimen of *C. magellanicus* has larger sectorial teeth than either of the specimens I have seen.

In the lower jaws of two specimens of *C. cancrivorus*, and in one of *C. magellanicus*, in the British Museum, there is a well-formed though small fourth molar; and in a third specimen of *C. cancrivorus* there is a curious abnormal structure, consisting of a bunch of five minute crowns of teeth (whether united by their roots or not cannot be made out without injuring the specimen) in the place of the fourth lower molar on the right side.

Fig. 15.



Side view of the skull of *Icticyon venaticus*: $\frac{3}{4}$ nat. size.

Van der Hoeven [1] has described and figured a skull with a third upper molar on both sides, which he ascribes to *C. azaræ*, but which, according to Burmeister, belongs to *C. cancrivorus*.

In *C. cancrivorus*, therefore, the persistence of $\frac{}{m.\,4}$ seems to be a common occurrence, while $\frac{m.\,3}{}$ is found occasionally. Thus it would appear that we have under our eyes, in this species, another stage in the modification of the primitive dentition of the Canidæ, which, as

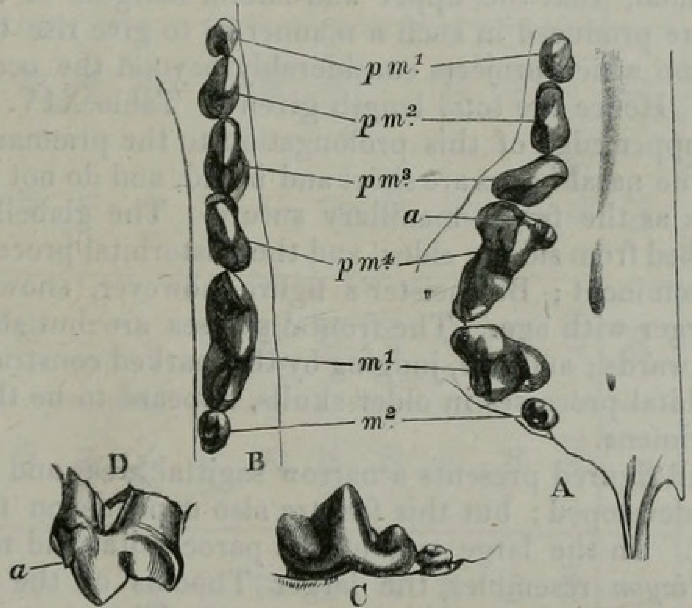
[1] "Over het geschlacht *Icticyon* van Lund," Verhandelingen der Koninklijke Akademie van Wetenschappen, Amsterdam, iii. 1856.

we have seen, has commenced even in *Otocyon*. And I think there can be no reasonable doubt that the occasional appearance of an extra molar in domestic dogs is not a monstrosity, but a reversion to the earlier and more complete dentition of the primitive stock of the Canidæ.

In *Icticyon* the dentition is modified in the opposite direction, by the suppression of $\frac{}{m.\,3}$ and the reduction of $\frac{m.\,2}{}$. Indeed this tooth was supposed to be absent altogether, until Professor Flower recently observed it in a specimen which has already been the subject of a communication to the Society.

I am greatly obliged to the President for enabling me give a figure of the skull (fig. 15) and teeth (fig. 16) of the specimen in question, which, though not quite fully adult, has the complete permanent dentition.

Fig. 16.



Upper (A) and lower (B) cheek-teeth of *Icticyon venaticus*; C, the right lower sectorial and second molar, from within; D, the right upper sectorial, from within; *a*, the accessory cusp; the inner anterior cusp is not sufficiently well defined.

In the following table of measurements I add those of an imperfect skull in the British Museum.

TABLE XIV.—*Cranial and Dental Measurements of* Icticyon venaticus.

	I.	II.
Total length	118	
Length of palate	56	59
Breadth ,, ...	40	41
Length of basicranial axis ..	52	
,, $\frac{pm.\,4}{}$	11·5	13

	I.	II.
Length of $\frac{m.1}{}$	7	8
Breadth ,, ...	7	8
Length of $\frac{m.2}{}$	3	
Breadth ,, ...	3	
Length of $\frac{}{m.1}$	13	14·5
,, $\frac{}{m.2}$	4	5

In the British-Museum specimen (No. II.) $\frac{m.2}{}$ is absent, and there is no trace of any alveolus for it.

In absolute length, the skull No. I. (fig. 15, p. 268) comes very near *C. cancrivorus* (Table XIII. No. VI.), but differs from this in the relative length of the basicranial axis and shortness of the palate. It is a peculiarity of *Icticyon* which I have not observed in any other canine animal, that the upper and lateral margins of the occipital foramen are produced in such a manner as to give rise to a tubular prolongation which projects considerably beyond the occipital spine (fig. 15). Hence the total length given in Table XIV. is measured from the upper edge of this prolongation to the præmaxillary symphysis. The nasal bones are short and broad, and do not extend quite so far back as the fronto-maxillary suture. The glabellar region is evenly arched from side to side; and the postorbital processes are but slightly prominent; Burmeister's figure, however, shows that these become larger with age. The frontal sinuses are but slightly developed backwards; and this, judging by the marked constriction behind the postorbital processes in older skulls, appears to be the case even in old specimens.

The skull figured presents a narrow sagittal area, and the sagittal crest is undeveloped; but this feature also depends on the youth of the animal. In the large size of the paroccipital and mastoid processes, *Icticyon* resembles the larger Thooids of the Old World rather than its North-American congeners. The characters of the base of the skull are completely canine. The palate is wider in front than in *C. cancrivorus*. Posteriorly it is somewhat more prolonged and narrowed towards the nasal passage than usual; but a good deal of the peculiarity of appearance of this part of the skull of *Icticyon* arises from the small size of the hindermost molars.

The tympanic bullæ are not evenly arched as is usual in the smaller Thooids; but the outer is separated from the inner moiety of the convex surface by a well-defined oblique ridge. The rami of the mandibles are ankylosed together throughout the long symphysis, which measures 27 millims. This ankylosis has also taken place in the second specimen; and I am not aware that it occurs in any other of the Canidæ. The angle of the mandible is thick, short, and not produced inwards. Its lower edge is straight, and passes so abruptly into the convexity which follows, that the jaw presents, as it were, the next remove from the lobate condition beyond that of *C. fulvipes* (fig. 9, C, p. 252).

Table XV.—*Cranial and Dental Measurements of North-American Thooids.*

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
Total length	180	......	172	180	190	192	190	205	216	265
Length of palate	92	84	84	91	93	92	95	98	108	129
Breadth „	50·5	49	52	54	55	54	54	63	67	79
Length of basicranial axis	58	......	52	59	59	57	61	69	73	85
„ $\underline{pm.\ 4}$	18	19	19	20	20·5	20	21	19·2	21	27
„ $\underline{m.\ 1}$	11·5	12	12	13·5	12	12	13	12	14·5	18
Breadth „	14	14	14·5	15·5	14·5	15·5	15·5	15·5	16·5	21·5
Length of $\underline{m.\ 2}$	7	6·8	6·5	8	7·5	7	7	6·5	8	9
Breadth „	10	9·5	10	10	10·5	11	11	10	11	13
Length of $\overline{m.\ 1}$	19·5	20	21	22·5	21	21	21·5	22·5	24	30
„ $\overline{m.\ 2}$	8·7	9	9	10	9·5	9	10	8·5	10	13
„ $\overline{m.\ 3}$	4·5	4	4	5	4	4	5·5	4·5	6	6

The upper incisors have the ordinary canine characters; and the large outer incisor is close to the second. The canines are very strong; and the first three præmolars are thick. Although the fourth præmolar has a length of only 11·5 millims., it is 7 millims. thick in front. The inner cusp, however, is very small. In both specimens a small but distinct cusp is developed from the anterior margin of the anterior blade-like cusp of this tooth. This is an unusual feature in the upper sectorial tooth of canine animals; and I am the more careful to draw attention to its existence, as, while Lund had mentioned the fact, Burmeister expressly denies it:—"Der Fleischzahn des Oberkiefers ist ganz Hundeartig, d. h. der innere Nebenhöcker sehr klein; und die äussere Höckerreihe ohne den dritten vordern Höcker, welcher den Viverrinen zusteht" (*l. c.* p. 9). It is to be presumed therefore that this minute cusp was absent in Burmeister's specimen[1].

The crown of the first upper molar is triangular and comparatively narrow, in consequence of the reduction of the cingulum and the disappearance of the posterior inner cusp. The crown of the minute second molar is nearly circular, with a median depression separating rudimentary outer and inner cusps (fig. 16, A). The lower sectorial presents peculiarities already noted by previous observers. Thus, the inner anterior cusp has altogether disappeared, the heel is very short, and the inner posterior cusp has also vanished. The second lower molar is very like the upper, its crown presenting a median depression bounded outside and inside by minute cusps, of which the inner is the lower (fig. 16, B, p. 269).

Thus the dentition of *Icticyon* is far more different from that of the ordinary Canidæ than that of any other known canine animal, whether recent or extinct, except *Otocyon*, standing in some respects at the opposite pole to the latter.

In all other points, *Icticyon* is not only, as Lund proved, unmistakably a member of the canine group, but it is so closely allied to the other North-American Thooids, that I can only regard it as a modification of the *Canis cancrivorus* type, analogous to that which, among the Old-World Jackals, has given rise to *Cyon*, but carried a step further.

In North America the Thooid division is represented only by such macrodont forms as *C. latrans* and *C. lupus* (*occidentalis*).

The foregoing Table (XV.) gives the measurements of seven crania of *Canis latrans* in the British Museum and in the Museum of the Royal College of Surgeons. The exact locality of No. I. is unknown; No. II. is from Hudson's Bay; No. III. from Grand Isle, Platte Rock; No. IV. from Medicine Creek, Nebraska; No. V. from Fort Colville; No. VI. from Fort Kearney; and No. VII. from Columbia River. They therefore cover almost the whole extent of North America in longitude, and, as might be expected, exhibit a

[1] Similar but better-developed anterior basal cusps occur in the upper sectorial of *Otocyon*, and occasionally in other Canidæ, as *C. anthus*, *C. zerda*, and *C. bengalensis*. Hence no great taxonomic importance can be assigned to this character.

considerable range of variation, though probably less than a larger series would show [1]. But, as they are, I must confess myself unable to find any important break in the series of gradations of cranial and dental structure between *Canis latrans* and *C. antarcticus*, on the one hand (see Table XIII.), and *C. latrans* and *C. occidentalis* (Table XV., VIII., IX., X.) on the other. Moreover, considering that only two sets of measurements of *C. magellanicus* are given, it is not unreasonable to expect that, with a larger series of this form, all the American Thooids, so far as their dental and cranial characters are concerned, would be susceptible of arrangement in a continuous series of almost imperceptible modifications. I may further remark that I can discern no difference of the slightest importance between skulls of *C. latrans* and those of some of our domestic Dogs [2].

Of the three skulls of *Canis occidentalis* (Table XV. Nos. VIII., IX., X.), No. X. is a very large typical Wolf-skull, nowise distinguishable from the most characteristic examples of the Old-World Wolves. Nos. VII. and VIII., on the other hand, have teeth not at all, or but little, larger than those of some specimens of *C. latrans*, from which they differ chiefly in the greater width of the palate and total length of the skull. Moreover, in these skulls the facial line, instead of being nearly straight or even slightly convex, as is usual in Wolves, Jackals, and domestic Dogs of the Greyhound type, is as concave as in the skulls of many Newfoundland Dogs and Mastiffs, to which they present striking resemblances.

If we now leave the New World for the Old, travelling westward, it is a very interesting fact that in Japan, in the Amur basin, and in North China we meet with a form of canine animal which has been made the type of a distinct genus, *Nyctereutes*, but which is essentially a low Thooid of the South-American type. This is the *Canis procyonoides* [3], of the external characters, the skeleton, and dentition of which a full account has been given by Schrenck ('Reisen und Forschungen im Amurlande,' Band i. 1858).

TABLE XVI.—*Cranial and Dental Measurements of* Canis procyonoides.

	I.	II.	III.	IV.
Total length	115	107	96	...
Length of palate	57	55	49	54
Breadth „	34	33·5	38	34

[1] Baird's observations ('Report,' under *Canis*) point to an extraordinary amount of local variation in *C. occidentalis* and *C. latrans*.

[2] The close resemblance of *C. latrans* to certain domestic Dogs of the Old World has already been noted by Jeitteles and Coues. See the former writer's excellent essay 'Die Stammväter unserer Hunde-Rassen,' 1877.

[3] The specific name appears to me to be as little applicable as the generic distinction of "*Nyctereutes*" is justifiable. Beyond a superficial external resemblance, there is nothing of the Raccoon about this animal.

	I.	II.	III.	IV.
Length of basicranial axis	39	...	39	41
„ $\underline{pm.\,4}$	9·7	10	10	11
„ $\underline{m.\,1}$	8	8	8·5	9
Breadth „	8·2	8·6	...	9
Length of $\underline{m.\,2}$	5	5	5	5
Breadth „	6	6	...	6
Length of $\overline{m.\,1}$	11	12	12	12
„ $\overline{m.\,2}$	6	6	6	6·5
„ $\overline{m.\,3}$	3	...	...	3

This is made manifest by the comparison of the measurements of the skulls I., II., III., IV. in the preceding Table (of which No. II. is from "North China," while the rest are Japanese) with those of *Canis azaræ* (a) given in Table XIII.

Nos. I. and II. are adult skulls having a narrow lyrate sagittal area, and curiously similar to *Otocyon* in the elongation of the jaws and the marked lobation of the mandible. The outer incisor above is separated from the others by a distinct interval; and the bony palate extends for 2–5 millims. behind the level of the hindermost molars. No. III. is young, the permanent teeth not having completely emerged.

The Japanese *C. hodophylax*, of which there is a fine specimen now living in the Gardens, appears to be simply a small form of Wolf; but in the absence of any accessible skulls of this form or of *C. nippon*, I refrain from giving any definite opinion about them. All the Asiatic Thooids, north of the Altai, appear to be mere varieties of *C. lupus*. But in the Altai range itself, in the upper basins of the Jenessei and the Lena, and as far eastward as the shores of the Sea of Ochotsk the *Canis alpinus* makes its appearance (Schrenck, *l. c.* pp. 48–50).

This species, *C. primævus*, *C. dukhunensis*, and *C. sumatrensis* have been separated as a distinct genus, *Cyon* (*Cuon*, Hodgson), on account of the constant absence of $\overline{m.\,3}$. They agree, not only in this respect[1], but in the breadth of the jaws and, very generally, in a marked convexity of the facial line. In this respect they depart from the ordinary Wolves and Jackals in the opposite direction to some Wolves and to the majority of the domestic Dogs, in which this contour tends to become strongly concave.

The following Table of the measurements of nine skulls shows the close affinity of the forms associated under *Cyon* :—

[1] Van der Hoeven (*l. c.*) mentions that he found $\overline{m.\,3}$ present in one specimen of *C. rutilans* out of six examined.

TABLE XVII.—*Cranial and Dental Measurements of* Cyon.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
Total length	163	...	167	164	184	177	...	174	183
Length of palate	77	82	77	82	85	85	98	85	90
Breadth "	55	57	59	60	61	61	68	65	65
Length of basicranial axis	...	...	60	60	68	67	69	65	61
" $\underline{pm.\ 4}$	19	19	19	20	20·5	20·5	20·5	22	21·2
" $\underline{m.\ 1}$	12·5	12	13	12	13	13	13	13·5	15
Breadth "	12·5	12	14	13	13·5	13·5	14·5	14	15
Length of $\underline{m.\ 2}$	6	4·5	5·3	...	5·5	5	5	5	7
Breadth "	8·5	5	8	...	7·5	8	8	7·3	10
Length of $\overline{m.\ 1}$	20	20	21	21	21	21·5	21·5	22·5	23
" $\overline{m.\ 2}$	7·5	7	8	8	7	7	9	8	9

[*C. sumatrensis*, No. I., is from Sumatra; No. II. from Malacca; *C. primævus*, Nos. III. and V., from Sikkim; *C. dukhunensis*, No. IV., from Central India; No. VI. from Cashmere; No. VII. from Cuttack; No. VIII. from Nepal; *C. alpinus*, No. IX., from the Altai.]

In none of these skulls was a trace either of the hindermost lower molar or of its alveolus to be seen. Jerdon states that *C. primævus* "is common in Ceylon, where it is called the Dhole by some, by which name it has been treated of by Hamilton Smith and other writers; and it is found all over the jungles of Assam, Burmah, and the Malayan peninsula," which is in contradiction to the commonly received opinion that there are no wild dogs in Assam and Burmah. According to S. Müller, the same species is found in Borneo.

The distribution of this group over an area which covers nearly 60 degrees of latitude and about as much of longitude in Eastern and Southern Asia is very remarkable, when taken in conjunction with the fact that the proper Jackals, although coexistent with *Cyon* in Hindostan, are absent over the rest of the *Cyon* area, except perhaps in Burmah; while, to the westward of Hindostan, *Cyon*, so far as is known, is absent in the vast area inhabited by the Jackals. For the species united under *Cyon* appear to me to be nothing but large and slightly modified forms of the Jackal type, which thus seems to have become somewhat specialized at the eastern extremity of its area of distribution.

I have already referred to the variability of *Canis aureus*; and the amount of variation exhibited by that species will become still more apparent by an inspection of the following Table of measurements of the skulls of thirteen specimens of *Canis aureus* from India. From this it appears that the skull of this species may vary in absolute length 28 per cent., in the length of the palate by nearly 30 per cent., in its width by more than 25 per cent., in the length of the basicranial axis by about 20 per cent., in the length of $\frac{pm.4}{}$ rather more than 25 per cent., in the length of $\frac{}{m.1}$ about 11 per cent.

If the measurements of *C. anthus, C. lateralis, C. simensis*, and *C. mesomelas*, given in the same table, are compared with those of *C. aureus*, it is obvious that the great majority fall into place somewhere in the series of *C. aureus*; and the only notable difference is in *C. simensis*, in which there is a remarkable elongation of the palate. But this is exactly that part of the skull which varies most in *C. aureus*; and the difference in length between the longest and shortest palate in this species, 19 millims., is exactly the same as that between the longest palate of *C. aureus* and that of *C. simensis*. I do not doubt that a larger number of specimens of *C. anthus* and of *C. simensis* would afford a complete series of intermediate forms between them and the Common Jackals.

Just as, at the eastern extremity of the Jackal area, the large *Cyon*-form with specially modified dentition is met with, so at its western extremity, in South Africa, the large *Lycaon*-form, with specially modified fore feet, occurs. In the breadth of the præmolar region of the upper jaw, and in a more or less marked convexity of the facial contour, *Lycaon* strongly reminds one of *Cyon*; but the dentition is complete, stronger, and more wolf-like, and the edges of the hinder præmolars are more deeply lobed.

Table XVIII.—*Cranial and Dental Measurements of Jackals.*

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.	XIV.	XV.	XVI.	XVII.	XVIII.	XIX.
Total length	136	154	140	145	159	150	165	147	157	150	175	168	168	150	165	...	203	155	155
Length of palate	66	76	72	70	75	71	78	70	77	74	85	84	83	76	81	87	104	82	79
Breadth "	45	51	48	47	51	50	54	50	52	54	57	54	53	53	53	54	53	45	48
Length of basicranial axis..	51	55	...	52	...	55	...	49	56	59	...	56	59	53	53	...	65	54	51
" $\overline{pm. 4}$	15	15	15·5	15·5	16	16	17	17	17	17	17	18	19	17	18	17	16·5	14·5	19
" $\overline{m.}$	12	...	13	11	11·5	12	13	12	12	13	14	13	12	12	12	13	13	11	12
Breadth "	12	...	13	12·5	13	12	14·5	13·5	12	14	15	13	14	14	15	15	13	12·5	14·5
Length of $\overline{m. 2}$	6	...	6	6	7	6	7	6	5	7	7	7	7	7	6·5	7·5	8·5	7	7·5
Breadth "	8	...	9	9	10·5	9	9	9·5	7	10	11	9	10	10	11	12	10	9	10
Length of $\underline{m. 1}$	19	19	19	18	18	19	20	19	19·5	18	21	19	20	19	19	20	19·5	17	20
" $\underline{m. 2}$	8	8	8	8	9	8·5	9	8	8	10	9·5	9	9	9	8·5	10	10·5	9	9
" $\underline{m. 3}$	4	4	4	3·5	4·3	4	4	4	5·5	...	4	4	4	...	...	5	4·2	5	5

[Nos. I. to XIII., *C. aureus*, from India; Nos. XIV. to XVI., *C. anthus*, from North Africa; No. XVII., *C. simensis*, from Abyssinia; No. XVIII., *C. lateralis*, from the Gaboon; No. XIX., *C. mesomelas*, from South Africa.]

Table XIX.—*Cranial and Dental Measurements of* Lycaon.

	I.	II.	III.	IV.	V.
Total length	185	194	203	...	250
Length of palate	88	91	100	98	100
Breadth ,,	76	73	69	71	74
Length of basicranial axis	63	69	68	71	69
,, $\frac{pm.\,4}{}$	20	20	20	20·5	21
,, $\frac{m.\,1}{}$	15	15	15	16·5	16
Breadth ,,	15·5	15·5	16	...	16·5
Length of $\frac{m.\,2}{}$	7	6	7	7·5	7·5
Breadth ,,	9	8	10·5	...	10
Length of $\frac{}{m.\,1}$	23·5	24	24·5	25	25
,, $\frac{}{m.\,2}$	9·5	10	9	9	11
,, $\frac{}{m.\,3}$	...	4	4·5	4·2	5

The Indian Wolf, *Lupus pallipes*, more nearly approaches the Jackals than any other Old-World Wolf I have seen. But only two skulls of this species have as yet come into my hands; and though they differ considerably, the chances are greatly against their representing the extremes of variation of the species. When the Canidæ of Turkestan are better known than at present, I have little doubt that the inconsiderable break between the Old-World Jackals and Wolves will be filled up.

It is obvious that the range of variation of the Eastern is as great as that of the Western Wolves (Table XX.); and I conceive that *C. pallipes*, *C. chanco*, and *C. laniger* must be regarded as mere local varieties of *C. lupus*, inasmuch as the table shows that the European Wolf (Nos. II., V., VII., VIII.) includes within its range of variation all the cranial differences presented by these so-called species.

13. The palæontological history of the Canidæ is, at present, very imperfect; but sufficient has been ascertained to enable us to obtain a general conception of the phylogeny of the group.

There is no question that Thooids and Alopecoids similar to those which exist at present inhabited Europe during the Quaternary epoch. Remains of the Dingo have been found in Australian deposits of apparently the same age; and the explorations of Lund in the Brazilian caves have demonstrated the existence of several forms of Canidæ of the existing South-American types—among the rest, of *Icticyon*, with which I conceive Lund's *Speothos* must be merged.

The *Palæocyon* of Lund, a large wolf-like animal with forty-two teeth, but with the second upper molar very small and with the

TABLE XX.—*Cranial and Dental Measurements of Wolves of the Old World.*

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Total length	215	223	234	236	240	240	250	237
Length of palate	109	102	110	111	109	119	111	116
Breadth „	72	71	72	70	73	77	82	79
Length of basicranial axis	71	62	74	...	71	77	78	75
„ $\underline{pm.\ 4}$	21·5	22	23·5	24	24	25	28	29
„ $\underline{m.\ 1}$	15	15·5	16	16	16·5	16	17	17
Breadth „	16·5	17	16·5	18	19·5	17	20	20
Length of $\underline{m.\ 2}$	8	8·5	8	8	9	8	9	9
Breadth „	10·5	13	10·5	12	13	11	13·5	13
Length of $\overline{m.\ 1}$	24·5	26·5	25·5	28·5	28	28·5	30	30
„ $\overline{m.\ 2}$	10	10·5	11·5	12	12	11	12	12·5
„ $\overline{m.\ 3}$	...	5·5	5·5	...	6	4	5	5·5

[No. I., *C. pallipes*, from India; No. II., *C. lupus*, from Belgium; No. III., *C. pallipes*, from India; No. IV., *C. chanco*, from Thibet; No. V., *C. lupus*, from Russia; No. VI., *C. laniger*, from Thibet; Nos. VII. and VIII., *C. lupus*, European, but the locality not certainly known.]

inner cusp of both the upper and the lower sectorials (which measure not less than 28 millims. in length) obsolete, has no representative in the existing fauna. This fact is the more interesting, as the dentition of *Palæocyon*, in some respects, presents a more thoroughly carnivorous aspect than that of the Old-World Wolves.

Information respecting the Pliocene Canidæ is scanty. One of the best-known forms is the *Canis borbonidus* (*C. megamastoides* of Pomel), briefly described and figured by Gervais in the 'Paléontologie Française' (ed. 2, p. 213, pl. xxvii. fig. 7). An almost entire skeleton was obtained from the Pliocene of Cerdé near Issoire. The skull is 150 millims. long; and Gervais justly observes that the ramus of the mandible resembles that of *C. cancrivorus*. From the figure I judge that the teeth were no less similar to those of this species. The humerus has an intercondyloid but no supracondyloid perforation ; and the digits are five in front and four behind.

Opinions differ as to whether the deposits of Œningen should be reckoned Lower Pliocene or Upper Miocene. The skull of the famous fossil Fox of Œningen, originally described by Mantell, and subsequently made the type of a new genus, *Galecynus*, by Professor Owen, is unfortunately not in a sufficiently good state of preservation for the determination of the question whether it belongs to the Alopecoid or to the Thooid series. In its cranial and dental measurements it agrees with surprising closeness with the common Fox ; and this correspondence extends even to the form and dimensions of the left upper sectorial tooth, which I have recently found could be readily exposed for about half its length in the specimen preserved in the Geological Society's Museum. There is, however, a rather stronger indication of a secondary cusp on the anterior part of the base of the blade of this tooth than is usual in the Foxes. At present I fail to see any sufficient gronnd for placing this animal in a distinct genus from the Foxes. Considering the known amount of variation in the pollex of different Canidæ, its slightly greater proportional length in the Œningen skeleton, though an interesting fact in itself, can hardly be regarded as of much systematic importance.

Much light has recently been thrown upon the palæontological history of the Canidæ by M. Filhol's [1] important researches upon the fossils of the phosphoritic deposits of Upper Eocene age in France, and especially upon the abundant remains of the genus *Cynodictis*. Of these "viverrine Dogs," as M. Filhol calls them, he distinguishes no fewer than seventeen varieties, which shade off, on the one hand, into true Viverridæ, and, on the other hand, into the Amphicyonidæ.

M. Filhol has so fully described and so well figured examples of a large suite of specimens of the different forms of *Cynodictis*, that it is possible for those who have not enjoyed the opportunity of examining his materials to form an independent judgment as to the conclusions which may be drawn from them ; and on one or two points I venture to dissent from his views.

[1] "Recherches sur les phosphorites de Quercy," Bibliothèque de l'École des Hautes Études, xv. & xvi. 1876, 1877.

Thus, in treating of *Canis filholi*, M. Filhol observes:—

"Je ne crois pas que ce soit là un *Canis* vrai, car le tubercule interne de la carnassière est beaucoup trop développé; il est fort élevé et se réunit par son bord antérieur au bord postérieur de la pointe antérieure; la portion moyenne de la face interne de la pointe principale n'est pas visible en dedans comme sur les Chiens vrais, elle est marquée à sa base par l'union des deux autres pointes"[1]. . . . . . . "Je serais assez porté à penser que le *Canis filholi* doit rentrer dans le groupe du *Cynodictis cayluxi*, auquel le rattache la forme de la carnassière du *Cynodictis intermedius*. Il indique certainement une tendance des *Cynodictis* à prendre les caractères des Canidés, mais l'ensemble de ses caractères est trop viverrien encore pour qu'on puisse le placer parmi les *Canis*. La même observation doit être faite pour le *Cynodictis crassidens*. Ces types sont excessivement interessants, car ils paraisaient peut-être indiquer par la dégradation successive des caractères de la carnassière l'origine ancienne de nos Chiens."

But the characters of the tooth to which M. Filhol refers cannot be regarded as sufficient to differentiate *Cynodictis* from the true *Canidæ*, when we have in *Otocyon* (fig. 13, C, p, 260) a lower sectorial which may be described in the same terms. In fact, apart from the number of the teeth, the dentition of *Otocyon* departs more widely from that of the more differentiated Canidæ than that of *Cynodictis* does, the teeth of the latter taking a place alongside of those of the lower Thooids and Alopecoids.

After describing the skull of *Cynodictis boriei*, M. Filhol remarks:—"Il n'y a rien dans le groupement des diverses parties dont j'ai successivement indiqué la position qui permette une comparaison avec les différents groupes de nos Carnivores. La base du crâne des Ursidés, des Canidés, des Viverridés, des Felidés, des Hyænidés, des Mustélidés, est tout-à-fait différente; celle des Marsupiaux l'est également" (*l. c.* t. xv. p. 74).

Without inspection of the specimens on which M. Filhol bases this opinion, it is hazardous to traverse it; but I confess his detailed description and excellent figures lead me to form a different conclusion, and to think that, in cranial characters, *Cynodictis* nearly approaches the South-American Thooids; and especially *Icticyon*, in the proportions of the face and skull.

In the actual measurements of the palate and of the teeth, *Cynodictis* comes extraordinarily near to certain living South-American forms. Thus, *C. leptorhynchus* is very like *C. vetulus*, while *Cynodictis gryei* almost as closely approaches *C. azaræ*—the chief difference, in the latter case, being the less transverse diameter of the sectorial and of the two molars of the upper jaw in *C. azaræ*.

[1] *Loc. cit.* tome xvi. p. 319.

Table XXI.—*Cranial and Dental Measurements of* Cynodictis *and* Canis.

	I.	II.	III.	IV.	V.
Length of palate	42	48	79	72	...
Breadth ,, ...	29	29	39	41	...
Length of $\frac{pm.\,4}{}$	8	7	13	12·5	14
Breadth ,, ...	5	5·5	9	6	10
Length of $\frac{m.\,1}{}$	6	7	...	9·3	11
Breadth ,, ...	7·5	8	...	11	15
Length of $\frac{m.\,2}{}$	4	5	6·5	6	8
Breadth ,, ...	6·5	6·5	9	7	9·5
Length of $\frac{}{m.\,1}$	7	9·5	...	14·5	13·5
,, $\frac{}{m.\,2}$	4	6·5	...	7·5	...
,, $\frac{}{m.\,3}$	3	3	...	4	...

[No. I. *Cynodictis leptorhynchus*; No. II. *Canis vetulus*; No. III. *Cynodictis gryei*; No. IV. *Canis azaræ*; No. V. *Cynodictis boriei*. The measurements are partly given by M. Filhol and partly taken from his figures.]

The skull of *Cynodictis boriei* is as large as that of an ordinary European Wolf, so that the microdont character is very striking, while the great thickness of the upper sectorial and the large size of the upper molar brings this form still nearer to *C. vetulus* than to *C. azaræ*.

Taking all the facts of the case into consideration, I am disposed not only to agree with the conclusion to which M. Filhol's remarks tend, that *Cynodictis* lies in the direct line of ancestry of the Canidæ, but to suppose that, in skull and teeth, it represents pretty closely the stock from which the branch of the Viverridæ has diverged, subsequently to give rise to the Felidæ and Hyænidæ.

On the other hand, as M. Filhol points out, certain forms of *Cynodictis* closely approach *Amphicyon*, a genus in which $\frac{m.\,3}{}$, usually aborted in all the existing Thooid and Alopecoid Canidæ, is present, though much smaller than $\frac{m.\,2}{}$ and evidently in course of suppression. In other respects, as in the shortness of $\frac{}{pm.\,4}$ relatively to $\frac{m.\,1}{}$, the large size of $\frac{m.\,2}{}$ relatively to $\frac{m.\,1}{}$, and of $\frac{}{m.\,2}$ relatively to $\frac{}{m.\,1}$, the dentition of *Amphicyon* repeats the general characters of that of *Cynodictis*.

None of the varieties of *Cynodictis* or of *Amphicyon* exhibits a distinctly lobate form of mandible; nor, so far as I am aware, has any specimen of the latter genus been discovered with more than three molars above and below. Hence, if I am right in supposing that in the dentition of *Otocyon* we have a representation of the number and the kinds of teeth which existed in the earliest ancestors of the Canidæ, and that the lobate mandible is similarly inherited from them, it becomes necessary to seek, for the primitive forms of the Carnivora which probably stood in the same relation to *Amphicyon* as *Otocyon* does to *Canis* and *Vulpes*, in still older formations. Nothing is at present known of the Mammals of the Cretaceous epoch; and from the older Eocene the only forms which bear upon the present question are *Arctocyon*, *Pterodon*, and *Hyænodon*. Of the first too little is known to warrant speculation. With respect to the two latter, M. Filhol's observations have conclusively proved that they have as little to do with the Didelphia in dentition as in other respects; and he has described an interesting form, *Cynhyænodon*, the upper dentition of which approaches that of *Pterodon*, while its mandibular teeth present resemblances to those of *Cynodictis*.

I do not suppose, however, that *Pterodon* (and still less *Hyænodon*) lies in the direct line of ancestry of the Canidæ. On the contrary, they appear to constitute a peculiar branch of the stock of the Carnivora, having closer relations to the Insectivora than are possessed by modern Carnivores.

In fact, in *Centetes*, the molar teeth of both jaws increase in size from before backwards, and the patterns of their crowns are such that those of all the Carnivora may be readily derived from them. The trihedral prism which constitutes the chief part of the first upper molar of *Centetes* obviously answers to the triangular elevation on the crown of the corresponding tooth of *Otocyon*, which terminates in the two outer and the two inner cusps; and the main difference between the two is that the cingulum is larger and extends much nearer to the summits of the cusps in *Otocyon* than in *Centetes*.

In the mandibular teeth, again, the first molar of *Centetes* presents exactly the same number of cusps, disposed in the same way as in that of *Otocyon*, the difference between the two lying merely in the different proportions of the parts. The exact correspondence in plan of these teeth is the more interesting, since, in *Centetes*, it is easy to trace the progressive changes by which the simple and primitive character of the Mammalian cheek-tooth exhibited by the most anterior præmolar passes into the complex structure of the crowns of the posterior teeth.

This is particularly obvious in the lower cheek-teeth, in which the crown of the most anterior præmolar is simply tricuspidate, with the anterior and the posterior cusps very small and the apex of the principal cusp simple. In the next præmolar the principal cusp appears cleft near its apex, in consequence of the development of a small secondary cusp on its inner side; the anterior cusp is higher and the posterior both higher and thicker. In the third præmolar, and in the molars, the anterior cusp is still higher; the secondary cusp is as large as that from which it is derived, so that it answers to the anterior internal cusp, while the former principal cusp takes the place of the anterior external cusp of the typical canine tooth. The posterior cusp, become very broad, and divided by a faint median depression, represents the posterior external and posterior internal cusps of the lower sectorial of the Dogs. A series of changes of just the same kind is observable in *Gymnura*; but the posterior cusps acquire a much greater size, and the molars take on a procyonoid character.

If the cheek-teeth of *Centetes*, *Gymnura*, *Otocyon*, and *Nasua* are placed side by side, it is easy to see that the first presents the least-modified condition of the pattern of the crowns of the molars common to the whole series. The reduction, or the less development, of the addition to the inner sides of the teeth, on the other hand, would give such crowns as those of *Pterodon* and *Hyænodon*.

The Insectivorous affinities of the dentition of the lower Carnivores harmonize very well with other peculiarities of the group.

The presence of a rudimentary clavicle and of a rudimentary hallux in the existing Canidæ leaves no reasonable doubt that they are descended from ancestors which possessed both in a complete state. And the suggestion is no less obvious that their digitigrade condition has resulted from the modification of a plantigrade form. Now we do not know whether any of the Eocene Canidæ possessed clavicles; but there is reason to believe that *Amphicyon* was plantigrade and pentadactyle.

M. Filhol has shown that *Cynhyænodon* had a brain more like that of an Insectivore than that of a Carnivore; and this fact is in accordance with a rule which now rests on a pretty broad basis of induction, that, in any given series of Mammals which is represented throughout the Tertiary series, the oldest forms had less highly developed brains than their modern representatives.

But, if the oldest Tertiary Carnivores were pentadactyle, plantigrade, claviculate, and had brains with relatively small cerebral hemispheres and large, completely exposed, cerebella, one may ask, by what characters were they distinguishable from the Insectivora? and why may not *Hyænodon* and *Pterodon* be an extreme development of that type of the Insectivora which is at present represented by *Centetes*?

On the other hand, if the primitive stock of the terrestrial Carnivora was represented by a plantigrade, pentadactyle, claviculate form with the dentition and jaw-angle of *Otocyon* and provided with epipubes, we should be furnished with that which is at present wanting, namely a link between the monodelphous and the didelphous Mammalia. According to our present system of classification, such a mammal would be grouped among the Insectivora, or as a transitional form between them and the *Didelphia*; and I have long entertained the conviction that the primary stock of all the groups of the monodelphous Mammalia will be found to occupy this position.

14. It may be desirable to state in a summary form the principal conclusions to which the facts stated in the preceding pages appear to me to point.

I. The existing Canidæ exhibit a gradual series of modifications, in the form and size of their skulls and the number and characters of their teeth, from *Otocyon*, as the least-differentiated member of the group, to the Wolves, Lycaons, Cyons, and Northern Foxes, as the most modified forms.

II. In the skull these modifications consist chiefly (*a*) in the increase of absolute size; (*b*) in the increase of the relative dimensions of the jaws, and particularly in the width of the palate; (*c*) in the persistence or disappearance of the sagittal area common to all young Canidæ, and the correlative development or absence of a sagittal crest; (*d*) in the diminution of the inflexion of the angular process of the mandible; (*e*) in the disappearance of the subangular lobe.

III. In the teeth, the most important modifications are the increase in the proportional size of the sectorials, accompanied by the relative diminution and, in some cases, suppression of the posterior molars. In *Otocyon*, $\frac{m.\,4}{\quad}$ has usually disappeared. In *C. cancrivorus*, $\frac{m.\,4}{\quad}$, $\frac{m.\,3}{\quad}$, and $\frac{\quad}{m.\,4}$ are most frequently suppressed; but $\frac{\quad}{m.\,4}$ often remains, and $\frac{m.\,3}{\quad}$ persists in one known case. In the great majority of the Canidæ, $\frac{m.\,4}{\quad}$, $\frac{m.\,3}{\quad}$, and $\frac{\quad}{m.\,4}$ are normally suppressed, while $\frac{\quad}{m.\,3}$ becomes relatively small, and, as a rule, disappears in *Cyon*. Finally, in the majority of examples of *Icticyon*, both $\frac{m.\,2}{\quad}$ and $\frac{\quad}{m.\,3}$ are wanting, and when $\frac{m.\,2}{\quad}$ is present it is very small.

The gradation will be rendered more intelligible by placing the formulæ of the cheek-teeth under one another.

	Maxilla.		Mandible.	
	pm.	*m.*	*pm.*	*m.*
Otocyon:				
Fullest dentition observed...	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4
Ordinary........................	1 2 3 4	1 2 3 *	1 2 3 4	1 2 3 4
C. cancrivorus:				
Fullest dentition observed...	1 2 3 4	1 2 3 *	1 2 3 4	1 2 3 4
Ordinary........................	1 2 3 4	1 2 * *	1 2 3 4	1 2 3 *
Most Alopecoids and Thooids	1 2 3 4	1 2 * *	1 2 3 4	1 2 3 *
Cyon.................................	1 2 3 4	1 2 * *	1 2 3 4	1 2 * *
Icticyon:				
Fullest dentition observed...	1 2 3 4	1 2 * *	1 2 3 4	1 2 * *
Ordinary........................	1 2 3 4	1 * * *	1 2 3 4	1 2 * *

In the individual teeth, the most important changes are the increase of the length in proportion to the breadth of the upper sectorial, and, in the lower sectorial, the change in the relative dimensions and position of the inner anterior cusp, which, from being on a level with the outer and higher than it in *Otocyon*, becomes smaller and shifts further and further backwards, eventually even disappearing, as in

Icticyon and *Palæocyon*. The heel of this tooth also diminishes in proportion to its blade.

IV. All the known kinds of canine animals may be arranged in two series, starting from *Otocyon* as the nearest ally of the lowest member of each series.

It is probable that when a sufficient number of specimens of each species at present recognized has been examined, it will be found that the forms with least-modified skulls and teeth are connected by insensible gradations with those with most-modified skulls and teeth, and that no absolute line of demarcation can be drawn between one species and another in cranial and dental characters.

There is no evidence that any one of these species is infertile when crossed with any other. Such evidence as exists with respect to *C. cancrivorus*, the Jackal, Dog, and Wolf tends to the conclusion that species of approximately the same size are capable of fertile unions.

V. The taxonomy of the Canidæ, under these circumstances, is very much a matter of convention. I am disposed to think that the most convenient mode of representing the facts is to regard *Otocyon* and the Thooid and Alopecoid series respectively as genera, retaining for the two latter the old names of *Canis* and *Vulpes*.

In each of these genera a lower, a middle, and a higher section may be conveniently recognized, though they are hardly susceptible of strict definition.

Thus, in the genus *Vulpes*, Baird has separated *V. littoralis* and *V. cinereo-argentatus* under the name of *Urocyon*. The Corsacine Foxes, *V. zerda*, *V. caama*, *V. bengalensis*, and *V. velox* may constitute another subgeneric section, and the most differentiated Foxes, such as *V. lagopus*, *V. fulvus*, and the rest, a third.

In the genus *Canis* we have, in like manner, as a lowest section the species of the *C. cancrivorus* and *C. vetulus* type (answering pretty much to the Aguarra Dogs of Hamilton Smith), the Sacaline section (*C. aureus*, *C. anthus*, *C. mesomelas*, *C. antarcticus*, *C. latrans*), and the Lupine section (*C. lupus* and all its varieties). *Icticyon*, *Lycaon*, and *Cyon* may probably be usefully retained as subgeneric names for the special modifications of the Thooid type which are denoted by them.

As for species, no one zoologist has ever yet agreed with the estimate of another as to what should be considered species and what local varieties among Wolves and Foxes; and, as there is no criterion by which the question can be decided, it is probable that such agreement never will be attained. The suggestion that it may be as well to give up the attempt to define species, and to content oneself with recording the varieties of pelage and stature which accompany a definable type of skeletal and dental structure in the geographical district in which the latter is indigenous, may be regarded as revolutionary; but I am inclined to think that sooner or later we shall have to adopt it.

VI. The most notable facts in the Distribution of the Canidæ are:—(1) the occurrence of the Corsacine Alopecoids and the Sacaline

Thooids, side by side, from South Africa, through Central Asia, to India and North and South America; (2) the limitation of *Otocyon* to South Africa; (3) the limitation of Aguarine Thooids to South America and North-east Asia, including Japan; (4) the limitation of the most specialized Thooids, namely the Wolves and the ordinary Foxes, to the Northern hemisphere; (5) the exclusion of Foxes from South America; (6) the distribution of *Cyon*, which curiously resembles that of the Tiger.

If provinces of distribution were marked out by the Canidæ, they would by no means correspond with those generally recognized. There is nothing peculiar about the Australian dog, while the American continent contains within itself all the chief types of Canine animals, except *Otocyon*. The presence of this form, with its ancient type of dentition, in South Africa is not improbably due to the fact that this region contains the remains of a very old Mammalian fauna.

VII. The morphological relations of the living Canidæ are such as to suggest that they result from the gradual accumulation of small variations in the general direction of increase of size and of differentiation of the teeth, superinduced upon a primitive stock which presented the full microdont dentition of *Otocyon*.

VIII. Though the palæontological history of the Canidæ is incomplete, the facts which are ascertained tend in the same direction. In skull and dentition, the older Tertiary Canidæ either, as in the case of *Cynodictis*, resemble the less-differentiated Canidæ, or, as in *Amphicyon*, present a third upper molar, such as occasionally exists in *Canis cancrivorus*. But if, as I suppose, *Cynodictis* and *Amphicyon* were preceded by forms having four molars above and below, they have yet to be discovered, as no Eocene mammals with four molars, except Opossums, have as yet been brought to light.

IX. The primitive stock of the dogs, for which we thus have to seek in older Eocene or earlier deposits, is theoretically required to have been a pentadactyle plantigrade animal provided with clavicles and possibly with bony epipubes. Such an animal, if it existed now, would probably be regarded as an Insectivore with more or less marked didelphous affinities.

In conclusion I desire to express my thanks to the President, to Dr. Günther, and to Dr. Rolleston for the ready access afforded me to the abundant materials for the study of the Canidæ in the Museum of the Royal College of Surgeons, the British Museum, and the Oxford Museum, to Sir Joseph Fayrer and to Mr. Wood-Mason, of the Indian Museum at Calcutta, for the great trouble they have been good enough to take in supplying me with specimens of Indian species, and to Professor Peters, of Berlin, for the loan of a skull of *V. corsac*.

[P.S. I ought to mention that large additions have been made to this paper since it was read before the Society; but I have deferred the consideration of the origin and relations of the domestic dogs until the evidence which I am at present collecting is more complete. July 4th, 1880.]

LIST OF WOODCUTS.

April 20, 1880.

Professor W. H. Flower, LL.D., F.R.S., President, in the Chair.

The Secretary made the following report on the additions to the Society's Menagerie during March 1880:—

The total number of registered additions to the Society's Menagerie during the month of March was 97, of which 10 were by birth, 30 by presentation, 34 by purchase, 16 received in exchange, and 7 received on deposit. The total number of departures during the same period, by death and removals, was 97.

The most noticeable addition during the month was:—

A pair of Spanish Ichneumons (*Herpestes widdringtoni*) from Andalusia, presented by J. C. Forster, Esq., F.Z.S., March 19.

Prof. Owen, C.B., F.R.S., read descriptions of various new and little-known species of Cephalopoda, amongst which was a new generic form proposed to be called *Tritaxeopus*.

This paper will be published in the Society's 'Transactions.'

Dr. M. Watson read an account of the female organs of the Proboscidea, as observed in a specimen of the Indian Elephant which he had lately dissected.

This paper will be published in the Society's 'Transactions.'

The following papers were read:—