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A MONOGRAPH

OF THE

BRITISH PLEISTOCENE MAMMALIA

VOL. II.

BRITISH PLEISTOCENE HYÆNIDÆ, URSIDÆ, CANIDÆ, AND MUSTELIDÆ.

BY

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VOL. II, PART I.

THE CAVE HYÆNA.

BY

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MONOGRAPH

ON

THE BRITISH MAMMALIA

OF THE

PLEISTOCENE PERIOD.

THE CAVE HYÆNA.

Order—CARNIVORA.

FAMILY—HYÆNIDÆ.

Genus—HYÆNA.

Species—*Hyæna crocuta*, Erxleben.

I. HISTORICAL INTRODUCTION.

THE early history of the recognition of remains of the hyæna in Europe is dealt with by Cuvier, and much use has been made of his account in the following pages.

The first evidence for their occurrence is afforded by a figure of part of the right mandibular ramus given by Kundmann in his 'Rariora Naturæ et Artis,' published in Breslau in 1737. He regarded this as similar to that of a calf, but its hyænine nature was recognised by Cuvier.

Thirty-seven years later (1774), Esper figured bones from Gailenreuth—an atlas which he regarded as hyænine, but which Cuvier says is that of a bear,—and some teeth, which he regarded as belonging to a lion, but which Cuvier says are hyænine.

Again, in 1784, Collini gave an excellent figure of a hyæna skull found near Mannheim. Unfortunately, however, he was disposed to regard it as perhaps that of a seal.

The first full account of the cave hyæna was that given by G. Cuvier in 1812.[1] He mentioned a number of Continental localities in which bones of hyænas had been found, and considered that the fossil hyæna was distinct from any living species, basing his opinion at that time mainly on the great size of many of the fossil bones.

The occurrence of the cave hyæna in England was first clearly established by Dean Buckland in his account of the Kirkdale Cave.[2] The full title of this important paper, which was published in 1822, is "Account of an Assemblage of Fossil Teeth and Bones of Elephant, Rhinoceros, Hippopotamus, Bear, Tiger, Hyæna, and sixteen other Animals discovered in a Cave at Kirkdale, Yorks, in the year 1821, with a Comparative View of five similar Caverns in various parts of England, and others on the Continent." In this paper, and in his 'Reliquiæ Diluvianæ' (1824), he clearly showed that the caves in which the hyæna bones were found were the actual dens of the animals.

Buckland's discovery of hyæna remains at Kirkdale was closely followed by Clift and Whidbey's discovery of them at Oreston, near Plymouth.[3]

Goldfuss,[4] writing in 1823, was the first to apply the distinctive name *Hyæna spelæa* to the cave hyæna. He gave a detailed comparison with figures and measurements of the bones of the cave species and of the spotted hyæna.

In the second edition of the 'Ossemens Fossiles' (1823), Cuvier, in giving a further account of the cave hyæna, referred specially to what he held to be the differences between it and the spotted hyæna, and mentioned, with regard to the metacarpals and metatarsals, that all the bones measured were, without exception, shorter and thicker in the cave hyæna than in the spotted hyæna. With regard to the teeth, however, the general tendency of his remarks implies that it is impossible to distinguish those of the one from those of the other.

Meanwhile the discovery and study of hyæna remains were actively pursued on the Continent, and a number of new species of hyæna, some allied to the living *H. crocuta* and some to the living *H. striata*, were described by Croizet and Jobert[5] (1828), and by Marcel de Serres, Dubrueil, and Jeanjean[6] (1839). Throughout the first half of the nineteenth century little doubt apparently was felt by palæontologists that the cave hyæna was distinct from the spotted hyæna. Thus de Blainville[7] (1844), Pictet[8] (1844), and Owen[9] (1846) all accepted this view. De Blainville discusses the question in detail (*vide postea*), and bases his opinion mainly on the form of the upper molar.

The first palæontologist to express strong doubts as regards the specific distinction of the cave and the spotted hyænas was Gaudry[10] (1863), but Boyd Dawkins,[11] writing in 1865, was the first definitely to conclude that no distinction could be drawn between

[1] 'Oss. Foss.,' ed. 1, iv.
[2] 'Phil. Trans.,' cxii (1), p. 171.
[3] 'Phil. Trans.,' cxiii, p. 88.
[4] 'Saüg. Vorw.,' vi.
[5] 'Oss. Foss. Puy de Dôme.'
[6] 'Oss. Lunel Viel.'
[7] 'Ostéographie,' livr. 14.
[8] 'Traité Paléont.,' i, p. 180.
[9] 'Brit. Foss. Mamm.,' pp. 138—160.
[10] 'Bull. Soc. Géol. France' (2), xx, p. 404.
[11] 'Nat. Hist. Rev.,' n. s., v, p. 80.

H. spelæa and *H. crocuta*. He laid stress on the variable character of the tubercular portion of the lower carnassial, and considered that several of the supposed species that had been founded by Croizet and Jobert, and by de Serres, Dubrueil, and Jeanjean, mainly on variations in this tooth, were not valid, but were varieties of the cave hyæna (*vide postea*). In his paper on the mammal fauna of the Creswell Crags,[1] published in 1877, the same author says that, after comparison of the skulls of *H. crocuta* and *H. spelæa*, he has been unable to detect points of difference of specific value, and definitely states that he believes the two to be identical.

Busk, however, writing in the same year,[2] while recognising the close relationship between the two forms, said that he did not consider it proved that *H. spelæa* was a mere variety of *H. crocuta*.

Since the publication of Boyd Dawkins' paper in 1863, almost all authors have accepted the view of the identity of the two forms. This has been done, for example, by Newton[3] (1883), Lydekker[4] (1884–5), Forsyth Major[5] (1885), Woodward and Sherborn[6] (1890), Gaudry[7] (1892), and Zittel[8] (1893); so that the fact of their identity may be considered to be clearly established. Schlosser,[9] however, expresses doubt as to their identity, mainly on account of the geographical distribution of *H. crocuta* at the present day.

A later phase in the study of hyænas has been the discussion of the mutual relationships of the fossil forms, and the probable ancestry of the living ones. This subject has been most fully dealt with by Lydekker,[10] Schlosser,[9] and Gaudry.[7] Lydekker, basing his opinion largely on its occurrence in the Pleistocene Caves of Karnul, in the Madras Presidency, considers that *Hyæna crocuta* originated in India, being derived from the Siwalik (Lower Pliocene) *Hyæna Colvini*, Lyd. The lower carnassials of the two forms agree closely, especially as regards the development of the cingulum, differing chiefly in the relatively large development of the hind talon in *H. Colvini*. Schlosser derives the cave hyæna, and eventually *H. crocuta*, from the Upper Pliocene *H. Perrieri* of Croizet and Jobert. He derives *H. Perrieri* from an unknown form whose nearest ally was *H. sivalensis*, and he regards *H. Colvini* as altogether off the line of descent in question. Gaudry also derives *H. crocuta* (including the cave hyæna) from *H. Perrieri*, but expressly states that he has not taken account of the Indian species, not being personally acquainted with their fossil remains. The subject of the mutual relationship of the different species of hyæna lies, however, too much beyond the scope of the present monograph to be fully dealt with.

[1] 'Q. J. Geol. Soc.,' xxxiii, p. 596.
[2] 'Trans. Zool. Soc.,' x (2), p. 53.
[3] 'Geol. Mag.,' 1883, p. 433.
[4] 'Pal. Indica,' ser. 10, ii, p. 275; 'Catal. Foss. Mamm. Brit. Mus.,' i, p. 69.
[5] 'Q. J. Geol. Soc.,' xli, p. 1.
[6] 'Catal. Brit. Foss. Vert.'
[7] 'Matér. Hist. Temps Quat.' (4), p. 116.
[8] 'Handb. Palæont.,' iv, p. 661.
[9] 'Beitr. Pal. Österreich-Ungarns,' iii, p. 29.
[10] 'Pal. Indica,' ser. 10, ii, p. 310.

It may be well here to refer to the reported occurrence of hyænoid animals in North America. In his paper on "The Extinct Dogs of North America," 1883, Cope[1] described a form from the Upper Miocene beds of Nebraska and New Mexico, which he named *Ælurodon Wheelerianus.* He grouped this with the Canidæ, but nevertheless suspected it to be the ancestor of the Hyænidæ, a view which Schlosser[2] accepts, altering Cope's name to *Prohyæna.* In 1892, Cope[3] published a brief reference to a hyæna-like form from the Pliocene of Texas, which differed from *Hyæna* proper in having a fourth premolar in the lower jaw, and probably a shorter blade to the sectorial tooth of the upper jaw. He named this *Borophagus diversidens.* Lastly, in 1895, Cope[4] founded a new species of *Hyæna* (*H. inexpectata*) on a tooth from a fissure at Port Kennedy, Pennsylvania, which Lydekker[5] suggests may prove to belong to a *Nimravus*.

II. DISTRIBUTION IN BRITAIN AND ELSEWHERE.

While a number of Tertiary species of hyæna have been recognised on the Continent, only detached teeth of this genus have hitherto been discovered below the Forest Bed in Britain.[6] From the latter horizon, however, at Corton Cliff, Suffolk, hyæna remains were described by Newton[7] in 1883. These consist of the canine, and second, third, and fourth premolars, all from the upper jaw, and all clearly referable to *H. crocuta.* It is thus evident that the animal was an immigrant from the continent of Europe in Pliocene times. In this respect it resembles the cave bear and horse, with which its remains are often associated, and differs from the lion, which does not appear to have reached England till Pleistocene times.

In these times the hyæna was extremely plentiful in England. Its remains are not infrequent in river gravels, but its almost universal occurrence in cave deposits shows that in the Pleistocene period it was essentially a cave dweller as it is at the present time. The fact that these caves were the actual dens of the hyænas, in which they lived and died, is clear from the frequent occurrence of coprolites, of splintered and gnawed bones, and of the teeth of young individuals. Referring to the state of the bones in the Robin Hood Cave, Boyd Dawkins[8] says: "With few exceptions the solid bones are alone perfect, the long bones containing marrow, and the vertebræ being represented merely by gnawed fragments. All the lower jaws have lost their angles and coronoid processes, and the number of teeth stands in a greater ratio to the number of bones than would have been the case had not their possessors fallen a prey to a bone-

[1] 'Amer. Nat.,' xvii, p. 243.
[2] 'Beitr. Pal. Österreich-Ungarns,' iii, p. 25.
[3] 'Amer. Nat.,' xxvi, p. 1028.
[4] 'Proc. Ac. Nat. Sci. Philad.,' 1895, p. 446.
[5] 'Zoöl. Record,' 1895, p. 28.
[6] *Hyæna antiqua,* Lankester, 'Ann. Mag. Nat. Hist.,' ser. 3, vol. xiii, 1864, p. 56, pl. viii, figs. 5, 6, from Red Crag, Suffolk.
[7] 'Geol. Mag.,' 1883, p. 433.
[8] 'Q. J. Geol. Soc.,' xxxii, p. 245.

destroying animal." This description would apply equally well to the state of the bones in almost all the caves in which hyæna remains occur; and the fact that the bones of the hyæna itself are often found gnawed and splintered shows that the animal was sometimes compelled to feed on its own kind.

The following is a list of British localities in which remains of hyænas have been found. Boyd Dawkins[1] published a similar list in 1869, and the number of localities has not been much added to since that date.[2]

Caves and Fissures.—Bleadon, Somerset; Boughton fissure, Maidstone; Blackrock fissure, Tenby; Bench and other caves, Brixham; Burrington, Somerset; Calay Cave; Cae Gwyn, North Wales; Cefn, near St. Asaph; Cheddar; Coygau Cave, near Laugharne, Carmarthen; Creswell Caves, Derbyshire; Durdham Down, Bristol; Ffynnon Beuno, North Wales; Gower Caves (Bacon Hole, Cat's Hole, Caswell Bay, Crow Hole, Long Hole, Minchin Hole, Paviland, Ravenscliff, Spritsail Tor); Hutton, Somerset; Hoyle; Ightham fissure, Kent; Kirby Moorside; Kirkdale, Yorkshire; Oreston, Plymouth; Raygill fissure, Yorkshire; Sandford Hill, Somerset; Torquay (Kent's Hole and Tor Bryan); Uphill, Somerset; Victoria Cave, Settle; Wookey Hole, Somerset; Yealm Bridge, Devon.

While the majority of the above were caves of occupation, in some instances, such as Uphill, the bones occur in fissures whose connection with any cave of occupation, though probable, has not been proved. In such cases the bones were probably swept into the fissures by water action.

Localities other than Caves and Fissures.—Aymestry, Brentford, Dogger Bank, Erith, Fisherton near Salisbury, Grays, Lawford near Rugby, Maidstone, Walton in Essex, Weston-super-Mare, Yarmouth.

While at the present day *Hyæna crocuta* is found only in Africa south of the Sahara, it appears from the above lists that in Pleistocene times it ranged over England and Wales as far north as Yorkshire, not, however, reaching Scotland or Ireland. It has been recorded from caves over the whole of continental Europe, from Spain and Sicily to Poland. One of the most interesting records of the occurrence of the cave hyæna is that from the Karnul Caves in the Madras Presidency.[3] The importance lies in the fact that the area of distribution of the cave hyæna is thereby connected with that of the closely allied Pliocene crocutine hyænas, such as *H. Colvini*. Hence it becomes probable that it was in India that the cave hyæna originated, spreading thence into Europe in late Pliocene times.

For the purpose of the present monograph the bones found in the Somersetshire caves, and especially the very large series from Wookey Hole, preserved in the Taunton Museum, have proved most useful. The series includes two almost complete skeletons

[1] 'Quart. Journ. Geol. Soc.,' xxv, p. 194.

[2] See also Woodward and Sherborn, 'Catal. Brit. Foss. Vert.,' 1890, p. 354.

[3] Lydekker, 'Pal. Indica,' ser. 10, iv, p. 30.

composed of associated bones. These, which are here referred to as skeletons A and B, have furnished the great majority of the bones figured, and may be briefly described.

Skeleton A.—This includes the cranium (Pl. I, and Pl. II, fig. 1), of which the occipital region, sagittal crest, palatal plate, dentition of left side, and a considerable portion of the left zygomatic arch are well preserved. The mandible is missing. The vertebral column is nearly complete, lacking only the caudal vertebræ. The left scapula is fragmentary, but the right one is fairly well preserved, having the coracoid and glenoid borders unfortunately much broken. The right anterior limb is in a remarkably perfect state except for the loss of some of the small bones of the manus; but the left limb lacks the distal end of the ulna and the proximal end of the radius. The ribs and the sternum are wanting. Both ossa innominata are in a fairly perfect state (Pl. XII). The right posterior limb is complete except for the loss of some of the small bones of the pes; but the left fibula is wanting.

Skeleton B.—The skull (Pl. II, fig. 2) is nearly perfect, the mandible (Pl. III, figs. 2, 3) being associated with the cranium. The chief parts lacking are the zygomatic arches, and the incisors and canines of the upper jaw. The posterior end of the sagittal crest is damaged. The mandible lacks nearly all the incisor teeth, and has the left condylar region in a fragmentary state. The vertebral column lacks the first thoracic and the first and second lumbar, as well as the caudal vertebræ, but is otherwise in good condition. The left os innominatum is nearly complete, but the other parts of both limb girdles are in a fragmentary state. All the long bones of both anterior and posterior limbs are well preserved, except the left femur. The left fibula shows a growth of bone (exostosis) such as one generally meets with in menagerie skeletons.

The other bones and teeth figured are from the Creswell Caves, Derbyshire, the Tor Bryan Caves, Torquay, and Kirkdale Cave, Yorkshire. All measurements are given in centimetres.

In the preparation of this monograph I have received much kind help from Professor Boyd Dawkins, Mr. Sherborn, and Dr. Smith Woodward, and to them my best thanks are tendered. I am also greatly indebted to Mr. H. St. G. Gray, to Mr. Hoyle, and to Professor Sollas for facilities in the examination and figuring of specimens preserved in the Taunton Castle, Owens College, and Oxford University Museums; and finally to Mr. J. Green for the great amount of care and trouble he has taken in drawing eight of the plates.

III. DESCRIPTION OF THE REMAINS.

A. The Skull (Plates I, II, III).

(1) *Distinctive Features of the Skull in the Genus Hyæna.*—There are many noteworthy features in which the skull of *Hyæna* contrasts markedly with that of *Felis* and

Canis, nearly all of these features being noted many years ago by Cuvier [1] and de Blainville.[2] They may be summarised as follows:

The face is short, the cranium narrow behind the orbits and below the ears, giving rise to very wide and deep temporal fossæ. The mandible is even shorter than in *Felis*, and has the salient angle more marked. The sinuses are very large, occupying the whole sagittal crest from the frontal to the supra-occipital. They are large also in the occipital crest, which is formed by the supra-occipital without the addition of any inter-parietal. The sinuses in the occipital crest often have irregular openings to the surface. The auditory bulla is simple and undivided by a septum, in this respect differing from that of *Felis*. There is no alisphenoid canal. The pterygoid is prolonged into prominent, backwardly directed, and sometimes hooked processes. The post-glenoid process of the squamosal is better marked than in *Felis* and *Canis*. In some cases processes of the premaxillæ and frontals meet and separate the nasals from the maxillæ, while in most cases the nasals and maxillæ are in contact for a short space; in the genera *Felis* and *Canis* the nasals and maxillæ are united along a wide surface.

(2) *Differences between the Skull of the Living* Hyæna crocuta *and those of* Hyæna striata *and* Hyæna brunnea.—This subject was fully dealt with by Cuvier and de Blainville, and subsequently by Busk.[3] The points of difference are as follows:

1. The space partially enclosed between the truncated ends of the nasal bones is relatively wider, and its posterior opening is less acute in *H. crocuta* than in *H. striata*.
2. In *H. crocuta* the auditory bulla is considerably more inflated than in *H. striata*.
3. The mastoid process of the periotic is more compressed in *H. striata* than in *H. crocuta*.
4. The anterior palatine foramina are relatively larger in *H. striata* than in *H. crocuta*.
5. The rotundity and fulness of the parietal region of the skull is greater in *H. crocuta* than in *H. striata*.
6. The sagittal crest, as noted by Cuvier, is more compressed and distinct in *H. striata* than in *H. crocuta*.
7. The post-orbital process of the frontal is less prominent in *H. crocuta* than in *H. striata*.
8. The pterygoid process is narrower in *H. crocuta* than in *H. striata*.
9. The zygomatic arch is less arched in *H. crocuta* than in *H. striata*.
10. The angle of the mandible is more pronounced in *H. crocuta* than in *H. striata*.
11. The jawbones and zygomatic arch are thicker in *H. crocuta* than in *H. striata*.

[1] 'Oss. Foss.,' ed. 3, iv, p. 381. [2] 'Ostéographie: Hyènes,' p. 10.
[3] 'Journ. Linn. Soc. (Zool.),' ix, p. 59.

(3) Table of Comparative Measurements of Hyæna Skulls.

	H. striata, No. 136K (Brit. Mus.), from Karachi.	*H. crocuta*, 92.8.1.4 ♀ (Brit. Mus.), Nyassa.	*H. crocuta*, No. 523 (College of Surgeons).	*H. crocuta*, No. 524 (College of Surgeons).	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta* (skull A), Wookey (Taunton Museum), fig. Pl. I and II.	*H. spelæa* = *crocuta* (skull B), Wookey (Taunton Museum), fig. Pl. II.	*H. spelæa* = *crocuta*, Creswell (Owens College Mus.).	*H. spelæa* = *crocuta*, Creswell (Owens College Mus.).	*H. spelæa* = *crocuta*, No. 28558 (Brit. Mus.), Sundwig.	*H. spelæa* = *crocuta*, No. 28557 (Brit. Mus.), Sundwig.	*H. brunnea*, out of stuffed specimen, 53.3.11.1 (Brit. Mus.).	*H. striata*, Ngaputuh Mts., Vict. Nyanza, 6.5.12.1 (Brit. Mus.).
1. Length from intercondylar notch to anterior end of skull	20·0	24·7	23·6	22 55	22·3	24·65	24·7	22·5	...	25·6	...	...	20·1
2. Extreme width across zygomatic arches	15·2	17·6	17·65	16·75	18·05	...	. .	...	...	...	19·9	17·5	14·8
3. Vertical height from suture between basioccipital and basisphenoid to top of sagittal crest	7·8	9·8	9·95	9·3	9·6	10·95	10·35	9·5	7·9	11·6	10·7	9·1	8·1
4. Width immediately above lachrymal foramen	4·6	6·1	6·55	6·1	5·35	6·65	6·75	...	5·6	6·15	6·6	5·35	4·25
5. Width between ends of post-orbital processes.............. ...	7·5	8·0	8·1	7·4	8·6	8·2	9·8	...	7·2	9·9	8·5	8·55	8·0
6. Width measured from alveolar borders immediately above last upper premolars	8·7	11·3	10·95	10·7	11·7	...	12·6	...	...	12·7	12·4	9·7	8·15
7. Minimum width below foramen lacerum anterius	0·9	1·65	1·75	1·7	1·6	1·65	1·65	2·1	2·05	1·7	1·7	0·9	1·25
8. Diameter across occipital condyles ...	4·4	5·2	4·4	5·25	5·25	5·6	5·75	...	...	5·6	...	...	4·35
9. Transverse diameter of foramen magnum	1·9	...	1·7	2·25	2·1	2·1	2·2	...	...	2·0	...	...	2·0
10. Maximum diameter of anterior narial opening	2·4	3·3	2·7	2·8	2·8	3·4	3·2	...	...	...	3·2	2·4	2·15
11. Maximum length of right mandibular ramus	16·5	19·85	19·85	18·7	18·95	...	18·85	17·65 [1]	...	21·25	...	18·45	16·15
12. Transverse measurement of one condyle	3·25	4·6	4 6	4·1	4·45	...	4·4	3·2	4·1 [1]	5·05	...	4·4	3·2
13. Height from angle to top of coronoid process	6·35	8·9	8·7	8·2	8·05	...	8·75	...	...	9·9	...	8·3	7·05

[1] I am not aware whether these mandibles belong to the crania measured.

B. Dentition (Plates IV, V).

(1) *Distinctive Features of the Teeth in the Genus Hyæna.*—The dental formula of *Hyæna* is i. $\frac{3}{3}$ c. $\frac{1}{1}$ pm. $\frac{4}{3}$ m. $\frac{1}{1}$, as compared with i. $\frac{3}{3}$ c. $\frac{1}{1}$ pm. $\frac{3}{2}$ m. $\frac{1}{1}$ in *Felis,* and i. $\frac{3}{3}$ c. $\frac{1}{1}$ pm. $\frac{4}{4}$ m. $\frac{2}{3}$ in *Canis* and *Ursus.* In the upper jaw the incisor teeth progressively increase in size, so that there is no such marked contrast between i. 3 and c.

as there is in *Felis* (see Pl. IV, fig. 1). The canines are less powerful than in *Ursus* and *Felis*, and are oval in transverse section, without any longitudinal groove or angle separating the inner third. Pm. 3, pm. 3, and pm. 4, the large and powerful bone-crushing teeth, are very characteristic, as is the form of the carnassial teeth. The features of the teeth will be now more fully described.

(2) *Permanent Dentition of the Upper Jaw* (see Pl. IV).—I. 1 and 2 show a prominent anterior cone or cusp separated by a groove from a depressed posterior area, which is divided by a second groove into right and left cusps. These teeth have wide laterally compressed and somewhat squarely truncated roots.

I. 3 is a much larger caniniform tooth, with a marked ridge specially developed antero-externally where it encroaches on the crown. The root is massive and subcylindrical.

C. The canine has the usual form. Its crown forms about one third of its length, and is not traversed by grooves, as in the Felidæ. It is thickest in the middle, and tapers nearly as rapidly towards the end of the root as towards the tip of the crown. It is not always easy to distinguish between an upper and a lower canine, but Dawkins remarks that the upper differs from the lower by the absence of the lateral curvature of the root.

Pm. 1 is a small one-rooted tooth. Its crown forms a low, somewhat incurved cone traversed by a longitudinal ridge.

Pm. 2 is a stout tooth with a low cone and small accessory cusps placed internally and posteriorly. The base of the crown is surrounded by a well-marked cingulum, and the tooth is fixed in the jaw by a pair of stout, subequal, and only slightly divergent roots.

Pm. 3 is a far larger and stronger tooth than pm. 2. The crown forms a stout, slightly incurved cone. The cingulum is strongly developed, and is much thickened posteriorly and antero-internally, sometimes forming irregular cusps from which marked ridges ascend the cone. The tooth forms a powerful bone-crusher.

Pm. 4 is the upper carnassial, and is larger than any other molar or premolar tooth in either jaw. The long trenchant blade is divisible into three lobes: an anterior one, the smallest of the three, and forming little more than a large cusp; a middle one which rises into a point; and a posterior one which is the longest of the three, and is divided from the middle one only by a deep narrow notch. On the inner side of the first lobe is a large but low inner tubercle. There are three roots, two smaller ones placed side by side anteriorly, and a very large laterally compressed posterior root.

M. 1 is not represented in the British Museum set figured on Pl. IV. Dawkins describes it as follows:[1]—"Very small, equilateral-triangular, and supported by two fangs, of which the anterior and outer is by far the smaller; the posterior supporting the two posterior angles is enclosed in an alveolus with very delicate walls, which would soon disappear by absorption after the loss of the tooth."

(3) *Permanent Dentition of the Lower Jaw* (see Pl. IV).—The three incisors are all

[1] 'Nat. Hist. Rev.,' n. s., v, 1865, p. 90.

teeth of much the same form, progressively increasing in size to a slight extent when followed backwards.

$\overline{\text{I. 1}}$ has a low crown with a simple transversely extended trenchant edge; the root is three times as long as the crown, and is laterally compressed.

$\overline{\text{I. 2}}$ differs from $\overline{\text{i. 1}}$ in being slightly larger and in bearing a small cusp on its outer side.

$\overline{\text{I. 3}}$ is again a good deal larger, and has a more conical, less transversely extended crown. It has a small but well-marked cusp on its outer side, and sometimes a slight indication of a cusp on its inner side, these features being in each case due to the enlargement of the cingulum. The root is much wider anteriorly than posteriorly, so as to be nearly triangular in section.

$\overline{\text{C.}}$ is much like that of the upper jaw, and has the inner side of the crown marked by two slight ascending ridges. The root is slightly more outwardly twisted than is the case with the upper canine, and it frequently, at any rate, tapers rather more rapidly to the point of implantation than is the case with that of the upper canine.

$\overline{\text{Pm. 1}}$ is absent.

$\overline{\text{Pm. 2}}$ is much like $\underline{\text{pm. 2.}}$ The crown forms a broad but low cone springing from a very marked cingulum. A groove separates off a posterior cusp from the main part of the cone, while sometimes a second but less distinct groove marks off an anterior cusp. Of the two roots the posterior is the larger, and the anterior has its tip bent backwards.

$\overline{\text{Pm. 3}}$ is a powerful conical tooth much resembling $\underline{\text{pm. 3.}}$ It has a very stout cone surrounded by a cingulum, least developed on the outer face, and thickened posteriorly into a fairly well-marked cusp. From this cusp, and from a slighter thickening on the anterior face, faint ridges ascend to the top of the cone. The two roots are stout, subcylindrical and subequal, the anterior being slightly the longer.

$\overline{\text{Pm 4}}$ is intermediate in character between $\overline{\text{pm. 2}}$ and $\overline{\text{pm. 3}}$ just described. The crown is traversed by a strong ridge dividing it into subequal right and left halves. At the anterior end is a small cusp; then follows a prominent cone, and lastly a large and somewhat irregular cusp.

$\overline{\text{M. 1}}$, the carnassial tooth of the lower jaw, has a very large trenchant blade divided by a deep groove into two parts, the relative proportion between which is variable, but the anterior is somewhat the larger. The cingulum is well marked, especially on the antero-outer side and posteriorly, where it merges into the much reduced tubercular portion of the tooth to form a small talon or cusp. This cusp is subject to a large amount of variation in different specimens, and upon these variations several supposed species have been based by French palæontologists. The principal variations, which are fully described by Dawkins,[1] are as follow:

1. A ridge passes obliquely across the tubercle towards the posterior part of the

[1] 'Nat. Hist. Rev.,' n. s., v, p. 92.

blade, from which it is separated by a small cleft without any cusp; this is the most common form.

2. A small cusp intervenes between the aforesaid ridge and the blade (characteristic of *H. intermedia*, de Serres, Dubrueil, and Jeanjean).

3. In place of the ridge occurring in 1 is a groove dividing the inner from the outer part of the tubercle, which thus becomes bilobed. The cusp occurring in 2 is not present (*H. Perrieri*, Croizet and Jobert).

Boyd Dawkins states that these are all to be regarded as mere variations of the typical form, and by no means as characters of specific value. In this view he has been followed by most subsequent writers.

(4) *Differences between the Teeth of the Living* Hyæna crocuta *and those of* Hyæna striata *and* Hyæna brunnea.—The many and marked differences between the teeth of *H. crocuta* and those of *H. striata* and *H. brunnea* were long ago described by de Blainville[1] and by Busk,[2] and may be summarised as follows:

1. In *H. striata* and *H. brunnea* the upper molar is triradicular[3] and tricuspid, and rarely measures less than 0·5 by 0·2 inch, being considerably larger than that of *H. crocuta*. In *H. crocuta* it is normally biradicular (occasionally monoradicular) and bicuspid, and is often absent (as in five skulls examined at the British Museum).

2. In *H. striata* and *H. brunnea* the three lobes of the upper carnassial $(\underline{\text{pm. 4}})$ are subequal antero-posteriorly, while in *H. crocuta* the last lobe is more than twice as long as the first. This fact was noted by Cuvier.[4]

3. In *H. striata* and *H. brunnea* there is a more or less distinct accessory point on the inner side of the posterior cusp of the lower carnassial $(\overline{\text{m. 1}})$, which is absent or less developed in *H. crocuta*. Cuvier noted the occurrence of this accessory point, and says it disappears with age. The lower carnassial is relatively much smaller in *H. striata* than in *H. crocuta*, whose lower carnassial approaches somewhat closely to that of the Felidæ.

4. The second upper premolar is relatively smaller and the third larger than in *H. striata*, so that the contrast between the second and third is much greater in *H. crocuta* than in *H. striata*. Busk stated that the third upper premolar is also somewhat obliquely truncated behind in *H. striata*, while in *H. crocuta* it is square behind. This, however, is not particularly apparent in the British Museum skulls. In *H. striata* the second lower premolar has an anterior accessory cusp better developed than in *H. crocuta*.

5. The first, second, and third upper premolars in *H. striata* have the anterior cusp better developed than in *H. crocuta*.

[1] 'Ostéographie, Hyènes,' p. 21.

[2] 'Trans. Zool. Soc.,' x (2), p. 77.

[3] According to de Blainville, as noted by Dawkins ('Nat. Hist. Rev.,' n. s., v, p. 81), the molar is monoradicular.

[4] 'Oss. Foss.,' ed. 3, iii (1825), p. 399.

6. In *H. striata* and *H. brunnea* the second and third premolars, both upper and lower, are placed with the long axes oblique to the line of the alveolar border, while in *H. crocuta* this is not so.

(5) Table of Measurements of the Permanent Teeth.

Hyæna spelæa = *crocuta*, Tor Bryan caves, Torquay (Brit. Mus.), fig. Pl. IV. m. 1 is from Wookey Hole.	i. 1.	i. 2.	i. 3.	c.	pm. 1.	pm. 2.	pm. 3.	pm. 4.	m. 1.	i. 1.	i. 2.	i. 3.	c.	pm. 2.	pm. 3.	pm. 4.	m. 1.
1. Antero-posterior extent at base of crown..........	0·8	1·0	1·3	1·75	0·75	1·85	2·5	4·5	0·5	0·55	0·6	0·9	1·C5	1·7	2·2	2·25	3·35
2. Maximum transverse measurement	0·65	0·7	1·0	1·35	0·7	1·4	1·7	2·1	0·5	0·4	0·55	0·8	1·35	1·3	1·55	1·35	1·4
3. Maximum length	2·4	2·7	4·15	6·3	2·05	2·95	4·6	4·55	...	2·3	2·55	3·6	6·2	2·75	4·5	3·95	4·0
4. Measurements taken from notch between roots to top of crown	...	...	...	...	...	1·2	2·7	2·4	...	..	...	...	...	1·05	2·15	1·9	...

(6) *Succession of Teeth in Hyæna.*—This subject has been dealt with by Boyd Dawkins,[1] who mentions that in the upper jaw the first tooth to appear is pm. 1. In the lower jaw, to judge by two specimens in the British Museum, c. and i. 1 appear first, followed by the large carnassial tooth m. 1, and by pm. 2; the other premolars, pm. 3 and 4, appearing somewhat later.

Boyd Dawkins mentions that the first teeth to disappear in the adult hyæna are the large bone-crushers pm. 2 and 3, and pm. 3 and 4; these teeth are always very much worn in the middle-aged adult, while pm. 1 and pm. 2 show scarcely any trace of wear.

(7) *Distinctive Features of the Deciduous Dentition of the Genus Hyæna.*—The formula for the deciduous dentition in *Hyæna* is d.i. $\frac{3}{3}$ d.c. $\frac{1}{1}$ d.m. $\frac{4}{3}$, as in *Canis* and *Ursus*, as compared with d.i. $\frac{3}{3}$ d.c. $\frac{1}{1}$ d.m. $\frac{3}{2}$ in *Felis*.

I have not had an opportunity of examining the deciduous incisors, but de Blainville notes that they differ from those of the adult in having the crown quite undivided. There is no noteworthy difference in the canines. The most distinctive teeth are the deciduous carnassials d.m. 3 and d.m. 4.

D.m. 1. The only example of this tooth that I have seen is that shown in Pl. V, fig. 5. The fragment of the upper jaw showing deciduous dentition figured in Pl. V, figs. 3, 4, bears no trace of its alveolus. Dawkins[2] describes it as follows:—"Trenchant, conical, and slightly incurved. Its anterior base, narrower than the posterior, bears a small cusp, while the posterior generally exhibits a slight thickening without the cusp. Sometimes,

[1] 'Nat. Hist. Rev.,' n. s., v.

[2] Ibid., v, p. 86.

however, the accessory cusp is developed behind and suppressed before. The crown is supported by two fangs, cylindrical and divaricant, the posterior being by far the stouter."

D.m. 2 is a simple conical tooth with no marked accessory cusps. The base is slightly wider posteriorly than anteriorly. There are two strong roots, the posterior being the larger. They do not diverge so much as do those of d.m. 1.

D.m. 3, the milk carnassial, has much the same general form as the permanent carnassial, and consists of a long sectorial portion and an inner tubercle. The sectorial portion shows two small cusps placed anteriorly and obliquely, and two large subequal blades separated from one another by a deep and narrow notch. The inner tubercle which arises from the anterior half of the blade is low, but extends a long way inwards. There are three roots, a small one supporting the inner tubercle, and two large divergent ones supporting the main part of the tooth.

D.m. 4, as noted by Dawkins, is remarkable for its size, and its resemblance to m. 1 in *Hyæna striata*. Its crown is shaped like an isosceles triangle with a broad forwardly directed base. The three angles are connected by a stout ridge, and each is supported by a divergent root.

D.m. 2 is a simple conical tooth with two marked accessory cusps, though occasionally small cusps may be developed at either end of the tooth. The base of the crown is wider posteriorly than anteriorly, and of the two roots, which diverge strongly, the posterior is the thicker.

D.m. 3 consists of a well-marked median cone and two small cusps, one placed antero-internally, the other posteriorly. On the inner side of the posterior cusp is a small accessory ridge. There are two divergent cylindrical subequal roots.

D.m. 4 is the carnassial tooth. Its cutting edge is divided into two subequal blades separated from one another by a cleft. Separated from the posterior blade by a well-marked groove is a large tubercle which usually shows indistinct division into three little cusps. Boyd Dawkins notes that occasionally all three cusps are suppressed, and the ridge which takes their place is cleft posteriorly, giving the tubercular portion a slightly bilobed appearance.

(8) Measurements of the Deciduous Teeth.

	Upper.					
	Teeth in fragment of jaw from Creswell Cave, figured in Pl. V, figs. 3 and 4.			Teeth in fragment of jaw from Brixham (Brit. Mus.).		
	d.m. 2.	d.m. 3.	d.m. 4.	d.m. 2.	d.m. 3.	d.m. 4.
Maximum antero-posterior measurement ...	1·5	2·2	0·8	1·15	2·2	0·8
Maximum transverse measurement of crown	0·6	0·75	1·4	0·7	0·8	1·35
Measurement from notch between roots to top of crown	0·75	0·9	...	...	...	...

(8) Measurements of the Deciduous Teeth (*continued*).

	Lower.					
	Teeth in jaw from Kent's Hole, Torquay, figured in Pl. III, fig. 4 (Brit. Mus. No. 1743).			Teeth in jaw from Kirkdale Cave (Brit. Mus. No. 36).		
	d.m. 2.	d.m. 3.	d.m. 4.	d.m. 2.	d.m. 3.	d.m. 4.
Maximum antero-posterior measurement ...	1·05	1·45	2·1	1·05	1·5	2·05
Maximum transverse measurement of crown	0·65	0·75	0·7	0·55	0·7	0·65
Measurement from notch between roots to top of crown	0·65	0·8	...	...	...	...

c. The Vertebral Column (Pls. VI, VII, VIII).

(1) *Distinctive Features of the Vertebral Column of the Genus Hyæna.*—There are not many distinguishing features characterising the vertebral column in *Hyæna* as compared with that in other Carnivora. Twenty is the regular number of thoraco-lumbar vertebræ in the great majority of Carnivora, but the relative proportion of thoracic to lumbar varies from thirteen thoracic and seven lumbar in *Felis, Canis,* and *Viverra,* to sixteen thoracic and four lumbar in *Arctonyx collaris.* In *Hyæna* there are fifteen thoracic to five lumbar vertebræ.

The small size of the thoracic vertebral centra, and the rapid decrease in the length of the neural spines when followed back, are features characterising *Hyæna.* The first sacral vertebra is a good deal larger than the others, causing the sides of the pelvis to converge posteriorly as in *Ursus,* instead of being approximately parallel as in *Canis.*

(2) *Distinctive Features of the Vertebral Column in the Different Species of Living Hyæna.*—There seems to be no marked difference between the vertebral columns of *H. crocuta* and *H. striata,* except that in *H. crocuta* the sacrum includes four vertebræ, while in *H. striata* there are three. There are only eighteen caudal vertebræ in *H. crocuta,* as compared with twenty-three in *H. striata.* Most of the vertebræ are more massive in *H. crocuta* than in *H. striata,* and the size of the vertebræ when followed back decreases somewhat more rapidly in the former than in the latter species.

(3) Tables of Comparative Measurements of Hyæna Vertebræ.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), skeleton A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), skeleton B.
Atlas.			
Maximum width	12·9	15·1	14·6
Median dorso-ventral diameter	3·9	4·1	3·9
Extreme width of the condylar articular surfaces	...	6·3	6·15
Maximum width of neural canal	2·6	2·8	2·55
Axis.			
Length from anterior end of odontoid process to postero-ventral extremity of centrum	7·0	7·3[1]	...
Height from roof of neural canal to top of neural spine	3·4	3·7	3·55
Transverse diameter across prezygapophyses	4·9	5·2	4·8
Transverse diameter across postzygapophyses	5·15	5·35	5·5
Length from anterior end of neural spine to notch between postzygapophyses	5·7	7·3	6·35

[1] Figured.

	3rd cervical.			4th cervical.			5th cervical.		
	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.
Maximum length of centrum taken from the dorso-anterior to the ventro-posterior edge	4·8	4·65[1]	5·0	4·95	5·0	5·1	4·9	5·1	4·95
Length from antero-dorsal to postero-dorsal extremity of the centrum	3·2	3·35	3·35	3·55	3·6	3·65	3·5	3·3	3·0
Width across transverse processes	7·5	8·1	7·2	8·65	7·8	7·4	7·45	7·9	7·7
Width across postzygapophyses	5·8	6·8	6·0	5·6	6·85	5·95	5·65	6·75	6·1
Height from roof of neural canal to top of neural spine	2·1	...	2·6	1·95	...	2·6	2·55	2·15	2·4

[1] Figured.

Note.—The letter A or B appearing after a bone indicates that it forms part of skeleton A or skeleton B described on p. 6.

Comparative Measurements of Hyæna Vertebræ (*continued*).

	6th cervical.			7th cervical.		
	H. crocuta, No 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.
Maximum length of centrum from dorso-anterior to ventro-posterior edge	4·9	5·0[1]	4·8	...	4·1[1]	...
Length from dorso-anterior to dorso-posterior edge of centrum	...	3·2	3·25	...	2·85	...
Width across transverse processes	6·35	7·45	7·4	8·2	7·6	8·0
Width across postzygapophyses	...	6·8	5·9	5·3	5·9	5·6
Height from roof of neural canal to top of neural spine	2·15	3·2	...	...	3·2	...
Length of inferior lamella of transverse process	4·25	5·25	...	...	...	...

[1] Figured.

	1st thoracic.			2nd thoracic.		3rd thoracic.			4th thoracic.		
	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.
Length from dorso-anterior to dorso-posterior edge of centrum	...	3·0	2·9	2·55	2·7	...	2·5	2·55	...	...	2·35
Width across prezygapophyses	...	5·9	5·9	4·15	4·1	...	3·35	3·3	...	3·4	2·8
Width across postzygapophyses	4·35	4·3	4·5	3·4	3·4	...	3·35	2·9	...	3·0	2·6
Width across transverse processes	7·6	7·8	7·9	7·95	6·85	6·6	6·8	6·75	6·2	6·5	6·5
Length of neural spine from notch between prezygapophyses	...	...	...	...	8·0	...	9·75	...	...	8·95	7·75

COMPARATIVE MEASUREMENTS OF HYÆNA VERTEBRÆ (*continued*).

	5th thoracic.			6th thoracic.			7th thoracic.			8th thoracic.			9th thoracic.		
	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.
Maximum length of centrum	...	2·65	2·6	...	2·45	...	...	2·5	2·5	...	2·5	2·7	...	2·65	2·6
Width across transverse processes	6·1	6·5	6·45	5·8	5·85	...	5·85	5·55	6·05	5·7	4·8	5·4	5·55	5·25	5·45
Length of neural spine from notch between prezygapophyses	...	7·75	8·7	...	7·85	...	...	7·5	...	...	6·8	7·15	...	5·95	6·35

	10th thoracic.			11th thoracic.			12th thoracic.			13th thoracic.			14th thoracic.		
Maximum length of centrum	...	2·6	2·6	...	2·65	2·65	...	2·8	2·7	...	2·7	2·8[1]	...	3·0	2·95
Width across transverse processes	5·5	...	5·25	5·55	5·0	4·8	...	4·7	4·45	...	4·45	4·25	...	4·2	4·2
Length of neural spine from notch between prezygapophyses	...	...	5·45	...	...	4·95	...	...	...	...	4·1	4·15	...	...	...

	1st lumbar.		2nd lumbar.		3rd lumbar.			4th lumbar.		5th lumbar.			
	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta* Wookey (Taunton Museum), A.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta* Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), B.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. crocuta*, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.	*H. spelæa* = *crocuta*, Wookey (Taunton Museum).	*H. spelæa* = *crocuta* Wookey (Taunton Museum), B.
Maximum length of centrum	2·85	3·05	2·75	3·1	2·9	3·35	3·45	2·95	3·4[1]	...	2·8	3·1[1]	3·15
Width across processes bearing prezygapophyses	4·6	4·2	4·5	4·15	4·15	4·10	4·3	...	3·75	...	3·6	...	3·5
Height of neural spine measured from roof of neural canal	...	4·15	...	4·4	...	...	...	4·15	3·9	...	3·6	...	2·75
Diameter across transverse processes	...	...	...	9·0	...	...	...	...	12·1	10·6	...	9·7	...

SACRAL.			
Maximum transverse diameter of 1st (true sacral) vertebra	7·95	8·9	8·8
Height of centrum	...	1·9	1·9
Height of neural canal	...	0·7	0·8

[1] Figured.

D. The Ribs and Sternum.

Hyæna possesses fifteen pairs of ribs, which are much arched, causing the cavity of the chest to be large as compared with that in *Canis*, and very large as compared with that in *Felis*. The sternum includes eight sternebræ. Neither ribs nor sternum present any features of special importance.

E. The Shoulder Girdle (Pl. IX).

The scapula in *H. crocuta* is straighter, and the postscapular fossa relatively smaller than in *H. striata*. The coracoid process is very little marked in *Hyæna*, and the clavicle, which is minute and more or less oval in outline, is entirely suspended in the muscles.

Table of Measurements of the Scapula.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Creswell (Owens College Museum).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.
Length along line of spine..................	17·8	19·55 [1]	20·95
Antero-posterior diameter of neck	4·2	5·25	4·6
Maximum length of glenoid cavity	4·45	4·5	4·5
Diameter from highest point in spine to point on inner surface of scapula immediately below	4·95	4·25	4·0
Length from end of coracoid process to surface of bone behind glenoid cavity	...	6·0	6·0

[1] Figured.

F. The Anterior Limb (Pls. X, XI).

The humerus of *Hyæna* is a well-marked bone. Its form is short and robust, with an exceptionally large great tuberosity. The condyle is larger and more pronounced than in *Canis*, the radial part being specially large. The deltoid crest extends further down the shaft in *H. crocuta* than in *H. striata*. The humerus differs from that of *Canis, Ursus*, and *Mustela* in nearly always having a supra-trochlear foramen. There is no entepicondylar foramen such as occurs in *Canis* and *Mustela*, and neither an ectepicondylar foramen nor crest occurs.

The manus of *Hyæna* differs from that of all other Carnivora in having the pollex represented by only a rudimentary metacarpal, which resembles a sesamoid bone. The metacarpals are longer and less enlarged above the phalangeal articulation than in *Felis*.

TABLES OF COMPARATIVE MEASUREMENTS.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.	*H. spelæa = crocuta*, Creswell (Owens College Museum).
HUMERUS (right).				
Extreme length ...	21·6	22·3	23·8 [1]	...
Diameter of proximal end passing across centre of articulating surface and greater tuberosity ...	6·4	...	6·7	...
Vertical diameter of shaft at middle of deltoid ridge ...	3·2	3·8	4·3	...
Transverse diameter at same point ...	2·2	2·2	2·4	...
Maximum transverse diameter at distal end ...	5·65	5·9	5·85	5·6
Maximum width of trochlea ...	4·65	4·7	4·55	4·4

[1] Figured.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.	*H. spelæa = crocuta*, Creswell (Owens College Museum).
RADIUS (right).				
Extreme length ...	21·65	21·9	21·9 [1]	...
Right and left or transverse measurement at humeral articulation ...	3·1	3 0	3·3	3·0
Antero-posterior or vertical measurement at humeral articulation ...	...	2·05	2·25	2·1
Transverse diameter at carpal articulation	4·1	3·95	4·55	...
Vertical diameter at carpal articulation ...	2·7	2·5	2·65	...
Transverse diameter at middle of shaft ...	2·65	2·25	2·65	2·35
Vertical diameter at middle of shaft ...	1·2	1·4	1·6	1·6
ULNA (right).				
Extreme length ...	24·15	25·65	25·3	..
Maximum vertical measurement ...	4·7	4·6	5·1	4·3
Maximum transverse measurement of olecranon ...	2·55	2·15	2·95	...
Transverse diameter at carpal articulation	1·15	1·1	1·2	...
Vertical diameter at carpal articulation ...	1·8	1·8	1·6	...

[1] Figured.

Table of Comparative Measurements (*continued*).

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Tor Bryan, Torquay (Brit. Mus.).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum).
Length of first metacarpal..................	2·35	3·35 [1]	...
„ second metacarpal	7·5	7·6	7·7
„ third metacarpal	9·2	8·15	8·95
„ fourth metacarpal	9·0	8·6	8·75
„ fifth metacarpal	7·6	7·45	7·1

[1] Figured.

The above measurements tend to confirm Cuvier's observation that the metacarpals of the cave hyæna are relatively shorter than those of the living spotted hyæna.

g. The Pelvic Girdle (Pl. XII).

The pelvis of *Hyæna* is characterised by its shortness, its comparatively large size, and its obliquity with regard to the sacrum. The ilium is decidedly larger in proportion to the size of the animal than in bears, and is prolonged into an anterior downwardly directed hook.

Tables of Measurements.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa* = *crocuta*, Wookey (Taunton Museum), A.
Right Innominate Bone.		
Maximum length	19·55	22·5 [1]
Length from acetabulum to border of ilium	11·1	12·6
Vertical measurement of ilium	10·55	10·9
Thickness of ilium at middle of surface......	0·95	0·95
Antero-posterior diameter of acetabulum ...	3·25	3·55
Length from acetabulum to posterior border of ischium	4·85	6·5
Left Innominate Bone.		
Maximum diameter of obturator foramen ...	4·1	5·15 [1]
Measurement along ischium from symphysis to end of ischial spine	7·5	...

[1] Figured.

h. The Posterior Limb (Pls. XIII, XIV).

The intercondylar notch of the femur is less deep than in *Canis*. The cnemial crest of the tibia gradually dies away instead of being strongly truncated as in *Canis*. The hallux in *Hyæna*, as in *Canis* and *Felis*, is represented only by a vestigial metatarsal.

TABLES OF MEASUREMENTS.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), A.	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.
RIGHT FEMUR.			
Maximum length	23·7	25·7 [1]	26·0
Transverse diameter at condyles	5·1	5·5	5·3
Antero-posterior diameter of head	3·25	3·15	3·15
Vertical or antero-posterior diameter of shaft at middle	1·8	1·9	1·9
Transverse or right to left diameter of shaft at middle	2·5	2·35	2·35
Transverse diameter at proximal end measured across head and great trochanter	6·35	6·9	6·55
RIGHT TIBIA.			
Maximum length	18·9	20·1	19·9 [1]
Transverse or right to left diameter at proximal end	5·3	5·3	5·5
Vertical or antero-posterior diameter at proximal end measured from notch between articulating surface for femur and top of crest	5·25	5·4	5·25
Transverse diameter at distal end	4·05	3·9	4·2
Vertical diameter at distal end	2·45	2·6	2·85
Transverse diameter at narrowest part of shaft	1·75	1·8	2·15

[1] Figured.

	H. crocuta, No. 522 (College of Surgeons).	*H. spelæa = crocuta*, Wookey (Taunton Museum), B.	*H. spelæa = crocuta*, Tor Bryan, Torquay (Brit. Mus.).
RIGHT FIBULA.			
Maximum length	17·8	17·85	...
Transverse diameter at distal end	1·25	1·25	...
Vertical diameter at distal end	2·10	2·15	...
Transverse diameter at proximal end	1·0	0·9	...
Vertical diameter at proximal end	1·4	1·4	...
CALCANEUM.			
Length	5·9	...	6·7
Maximum transverse diameter	2·8	...	2·8
ASTRAGALUS.			
Right to left diameter	3·15	...	3·7
METATARSALS.			
Length of first metatarsal	1·75	...	...
" second metatarsal	7·35	...	7·8
" third metatarsal	8·4	...	8·0
" fourth metatarsal	8·2	...	7·95
" fifth metatarsal	7·2	...	6·75

IV. CONCLUSIONS.

The evidence for the view that the *Hyæna* from the caves is a species distinct from the modern *H. crocuta* may now be more fully considered.

Cuvier,[1] writing in 1825, mentions the following features as characteristic of *H. spelæa*:

1. The upper surface of the skull is less arched than in *H. crocuta,* and the temporal ridges do not unite so quickly to form a sagittal crest.

2. All the bones of the metacarpals and metatarsals measured are without exception shorter and thicker than in *H. crocuta.*

Reference is also made to the relatively thick character of the bones in the cave hyæna by Gaudry,[2] who concludes that the animal was more thick-set than its living representative, and suggests that it may have had a more crouching gait.

Cuvier remarks, however, with regard to the teeth, that it is impossible to distinguish those of *H. spelæa* from those of *H. crocuta.*

De Blainville[3] gives the following features as characteristic of *H. spelæa*:

1. The form of the upper carnassial with the large size of the third lobe (talon).[4]
2. The absence of the inner cusp on the tubercular portion of the lower carnassial.
3. The size, which is $\frac{1}{5}$ larger than in *H. crocuta.*
4. The greater extension and compression of the occipital crest.
5. The increased thickness and shortness of the muzzle.
6. The increased thickness and shortness of the limb bones.

He remarks that of these characters the least important is the increased relative size, and the most important the increased thickness of the limbs and elevation of the occipital crest. Relative size depends on conditions of life, and comparisons as regards size have too often been made between fossil individuals at the maximum of their development, owing to savage life, and individuals raised in menageries. The character of the occipital crest also differs much, according to the age of the animal.

Owen[5] states that the upper true molar in *H. spelæa* is monoradicular, and quotes this as a character distinguishing *H. spelæa* from *H. crocuta.* Dawkins,[6] on the other hand, shows that the tooth in question is sometimes mono-, sometimes bi-radicular, and that the method of implantation cannot be quoted as a character of specific value.

The modern view that there is no specific distinction between *H. spelæa* and *H. crocuta* was first clearly stated by Boyd Dawkins in 1865,[6] and is now almost universally accepted.

[1] 'Oss. Foss.,' ed. 3, iv, p. 396.

[2] 'Matér. Hist. Temps Quat.' (4), 1892, p. 118. [3] 'Ostéographie, Hyènes,' p. 39.

[4] I cannot trace any difference as regards the form of the upper carnassial or the size of the third lobe between *H. spelæa* and *H. crocuta.*

[5] 'Brit. Foss. Mamm.,' p. 150. [6] 'Nat. Hist. Rev.,' n. s., v.

The measurements quoted above, however, show that some of the skulls of the cave hyæna, especially those from the German caves, are considerably larger than those of any modern hyæna measured. They also show that it is true that the metacarpals of the cave hyæna tend to be shorter than those of the modern form, hence it seems reasonable to follow Gaudry[1] in regarding the cave hyæna as a distinct race of *H. crocuta*.

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PLATE I.

CAVE HYÆNA.

Cranium.

(Two thirds natural size.)

FIG.

1. Palatal view }
2. Dorsal view } Skull A from Wookey Hole, now in the Taunton Museum.

a. Supra-occipital.

b. Occipital condyle.

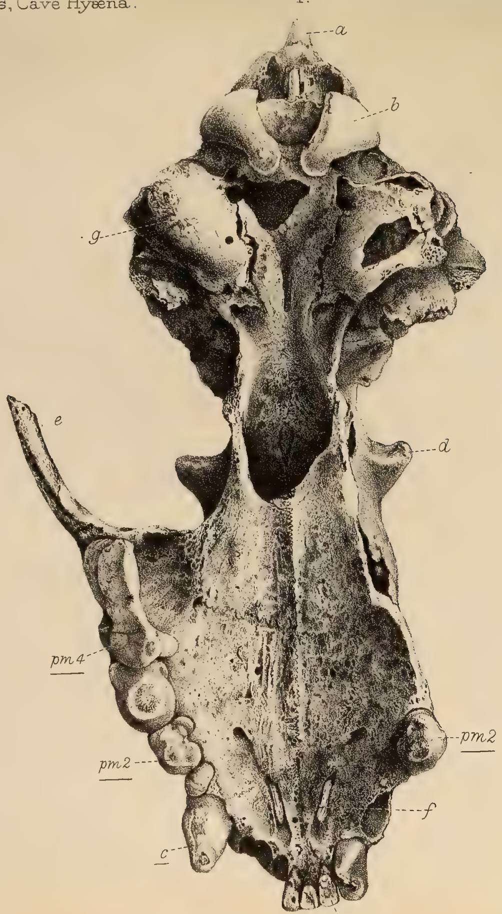
d. Post-orbital process of frontal.

e. Jugal.

f. Anterior palatine foramen.

g. Auditory bulla.

1.



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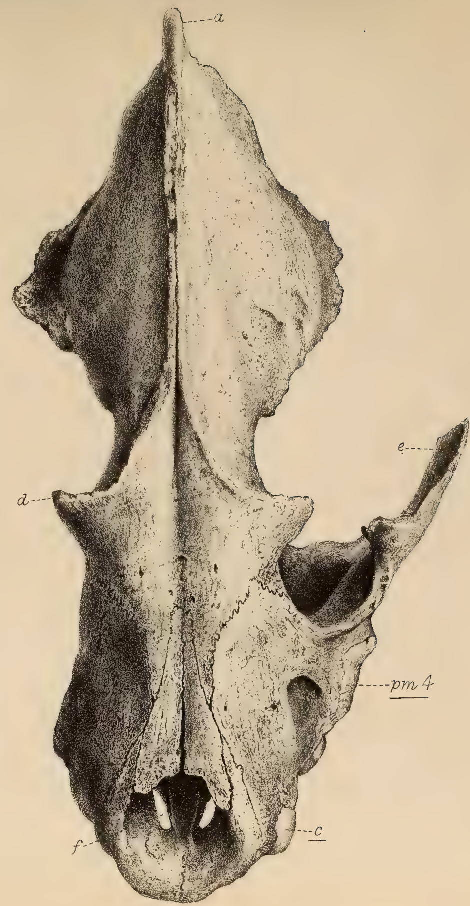


J. Green del et lith.

Mintern Bros. imp.

Cranium.

PLATE II.

Cave Hyæna.

Cranium and Mandible.

(Two thirds natural size.)

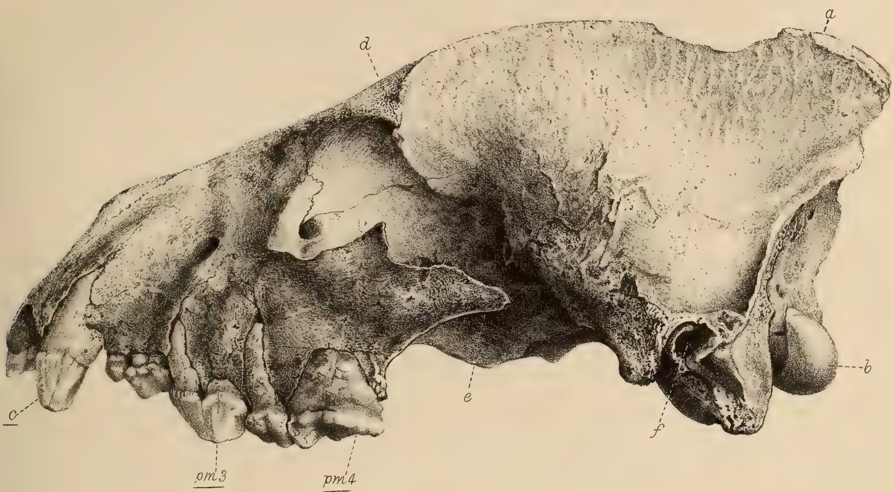
Fig.

1. Cranium A seen from the left side.
2. Cranium and mandible B seen from the right side.

a. Sagittal crest.
b. Occipital condyle.
d. Post-orbital process of frontal.
e. Jugal.
f. External auditory meatus.
g. Angle of mandible.

Both the above specimens are from Wookey Hole, and are now preserved in the Taunton Museum.

1.



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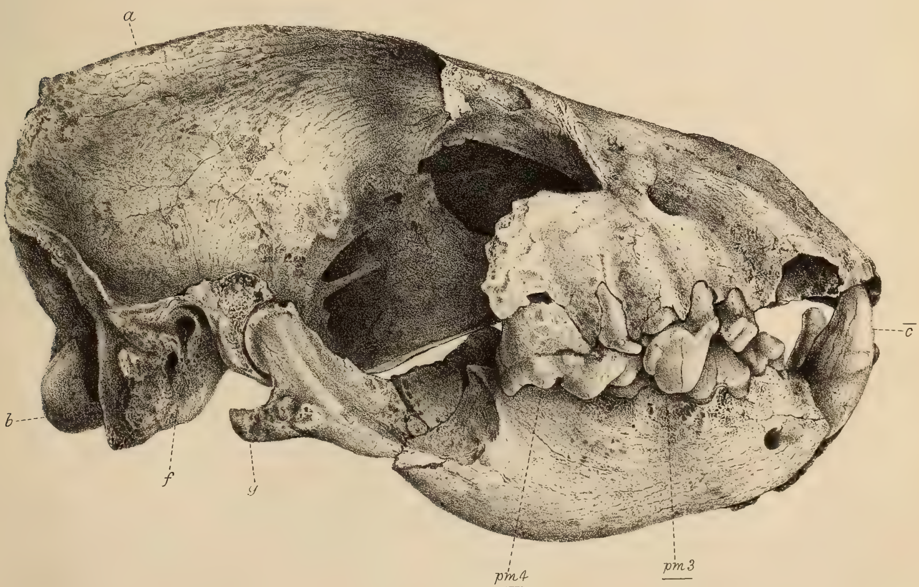


J. Green del. et lith. Mintern Bros. imp.

Cranium & mandible.

PLATE III.

Cave Hyæna.

Cranium and Mandible.

(Two thirds natural size.)

Fig.

1. Posterior view of Cranium A (Skeleton A).
2. Mandible seen from the left side (Skeleton B).
3. Palatal view of the same mandible (Skeleton B).
4. Inner view of the left mandibular ramus of a young individual showing the milk dentition.

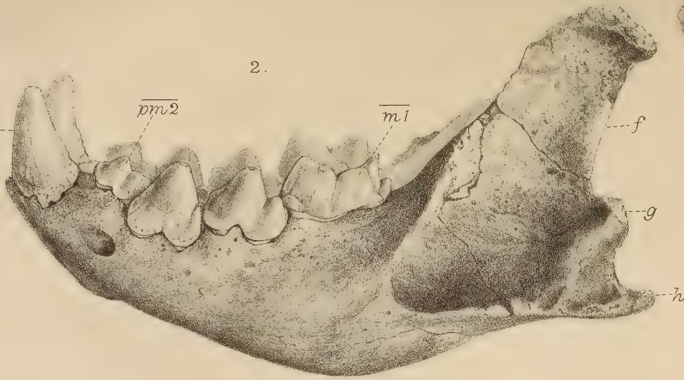
a. Sagittal crest.
b. Post-orbital process of frontal.
d. Jugal.
e. Occipital condyle.
f. Coronoid process.
g. Condyle of mandible.
h. Angle of mandible.

The specimen shown in fig. 4 is from Kent's Hole, Torquay, and is now preserved in the British Museum (Nat. Hist.) at South Kensington. The other specimens are from Wookey Hole, and are now in the Taunton Museum.

Reynolds, Cave Hyæna.

Pl. III.

2.



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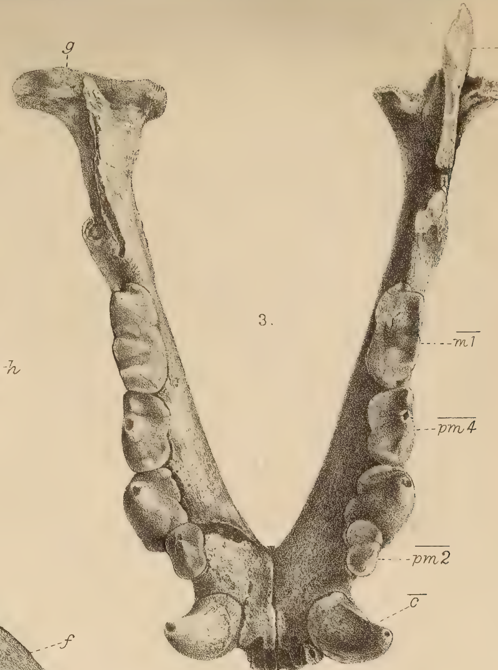

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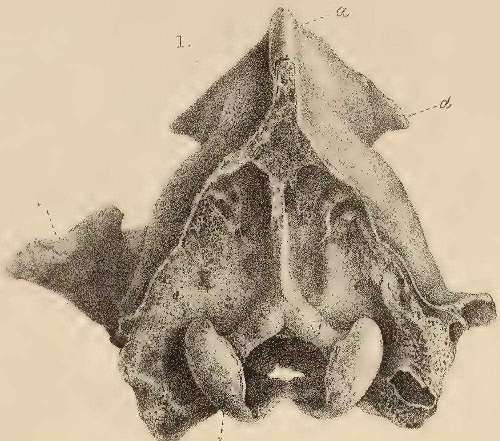

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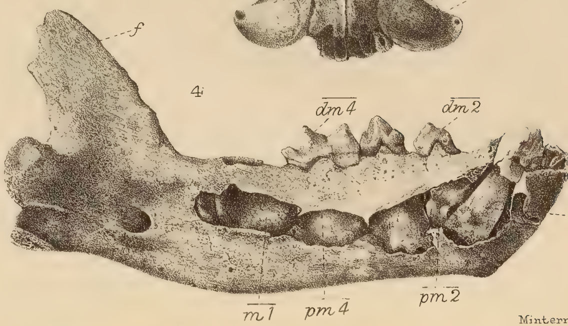


J. Green del. et lith.

Mintern Bros. imp.

Cranium & mandible.

PLATE IV.

CAVE HYÆNA.

Permanent Dentition.

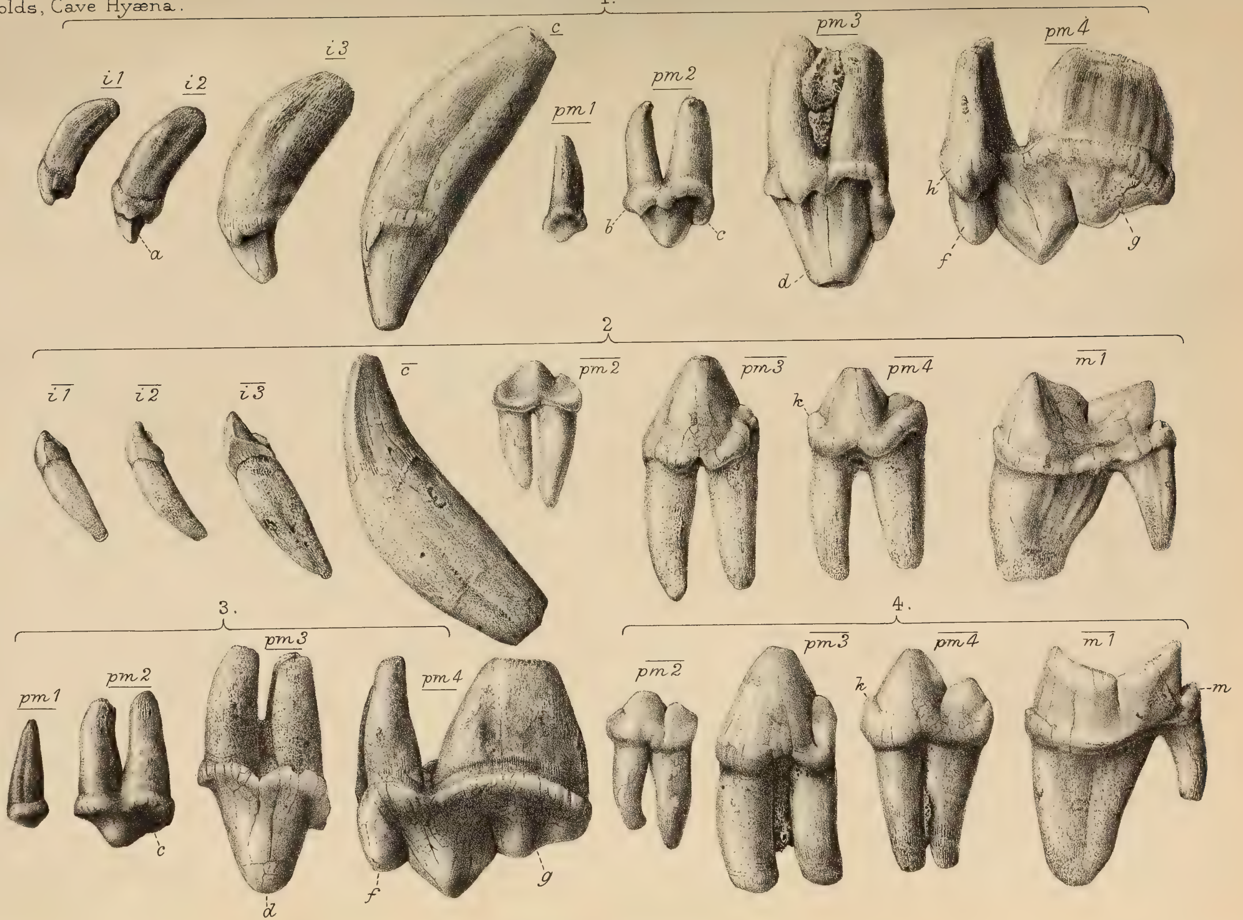
(Natural size.)

FIG.

1. Right upper teeth, seen from the inner side.
2. Right lower teeth, seen from the inner side.
3. Left upper premolars, seen from the outer side.
4. Left lower premolars and molar, seen from the outer side.

- *a.* Cone of $\underline{\text{i. 2}}$.
- *b.* Anterior cusp of $\underline{\text{pm. 2}}$.
- *c.* Posterior cusp of $\underline{\text{pm. 2}}$.
- *d.* Cone of $\underline{\text{pm. 3}}$.
- *f.* Anterior lobe of blade of $\underline{\text{pm. 4}}$.
- *g.* Posterior lobe of blade of $\underline{\text{pm. 4}}$.
- *h.* Inner tubercle of $\underline{\text{pm. 4}}$.
- *k.* Anterior cusp of $\overline{\text{pm. 4}}$.
- *m.* Posterior cusp of $\overline{\text{m. 1}}$.

The above specimens are from the Tor Bryan caves, near Torquay, and are now preserved in the British Museum (Nat. Hist.).



J. Green del. et lith.

Permanent dentition.

Mintern Bros. imp.

PLATE V.

Cave Hyæna.

Dentition.

(Natural size.)

Fig.

1. Left upper permanent teeth which had not yet cut the jaw, seen from the inner side.
2. Left lower permanent teeth which had not yet cut the jaw, seen from the inner side.
3. Inner aspect of fragment of right half of upper jaw showing deciduous dentition.
4. Palatal aspect of the same fragment.
5. Inner aspect of part of left half of upper jaw.
6. Anterior view of $\underline{\text{m. 1.}}$
7. Inner aspect of $\underline{\text{m. 1.}}$
8. Outer aspect of right $\overline{\text{m. 1.}}$
9. A deciduous canine, probably from the upper jaw.
10. Outer aspect of left $\underline{\text{dm. 2.}}$
11. Inner and outer aspect of right $\underline{\text{dm. 3.}}$
12. Lower deciduous molars: $\overline{\text{dm. 2}}$ and $\overline{\text{dm. 4}}$ are seen from the outer side; $\overline{\text{dm. 3}}$ from the inner side.

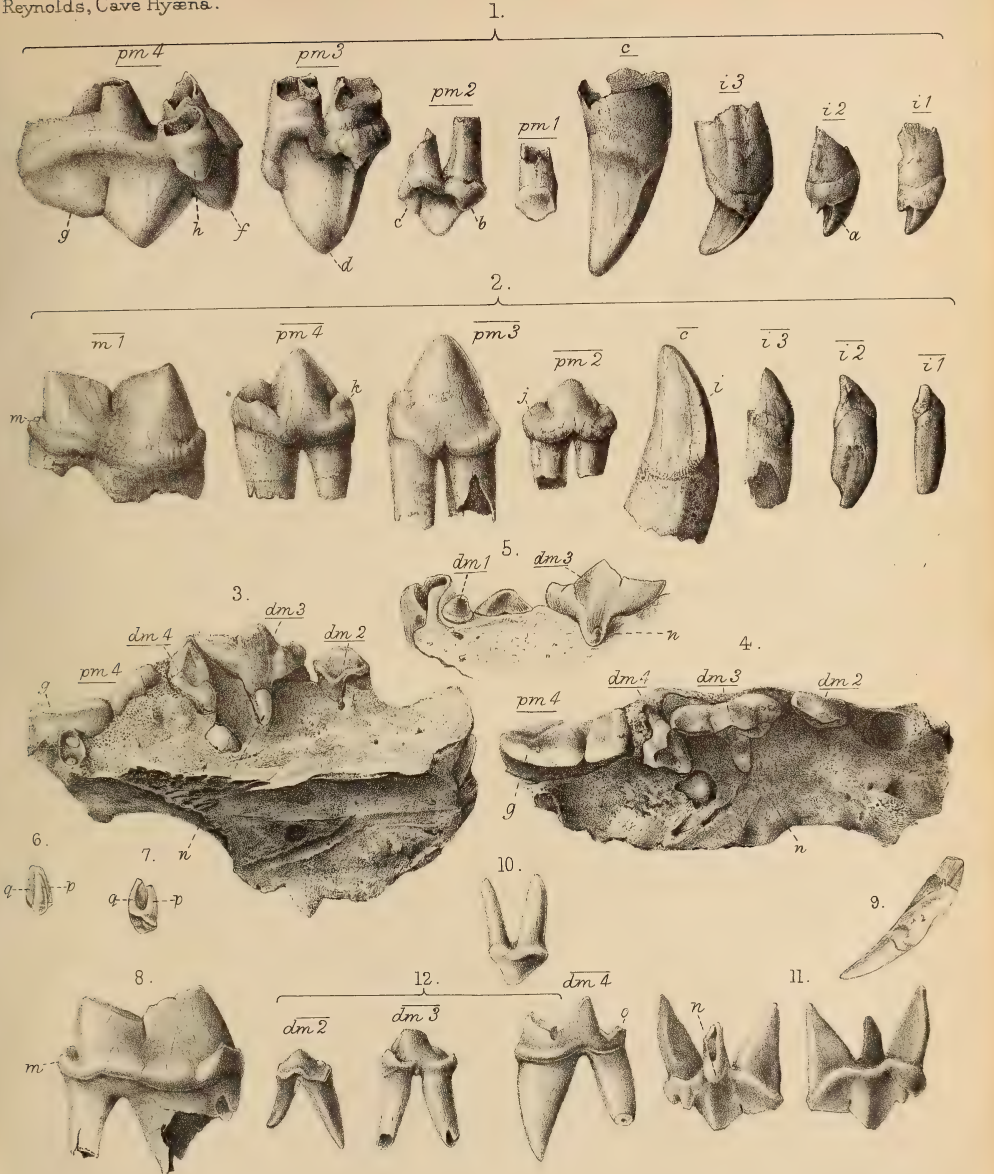
Lettering as on Pl. IV, with the addition of—

i. Ridge on inner side of crown of $\overline{\text{c.}}$
j. Posterior cusp of $\overline{\text{pm. 2.}}$
n. Inner tubercle of $\underline{\text{dm. 3.}}$
o. Tubercle of $\overline{\text{dm. 4.}}$
p. Anterior root of $\underline{\text{m. 1.}}$
q. Posterior root of $\underline{\text{m. 1.}}$

The teeth shown in figs. 1 and 2 are from the Tor Bryan caves, near Torquay, and are now in the British Museum (Nat. Hist.). The other specimens, with the exception of those shown in figs. 5, 6, 7, and 9, are from the Creswell caves, Derbyshire, and are now in the Owens College Museum, Manchester. The tooth shown in fig. 9 is from Kirkdale cave, while the two shown in figs. 5, 6, and 7 are from Wookey Hole. These three latter specimens are all preserved in the Oxford Museum.

Reynolds, Cave Hyæna.

Pl. V.



J. Green del. et lith.

Mintern Bros. imp.

Dentition.

PLATE VI.

Cave Hyæna.

Vertebræ.

(Natural size.)

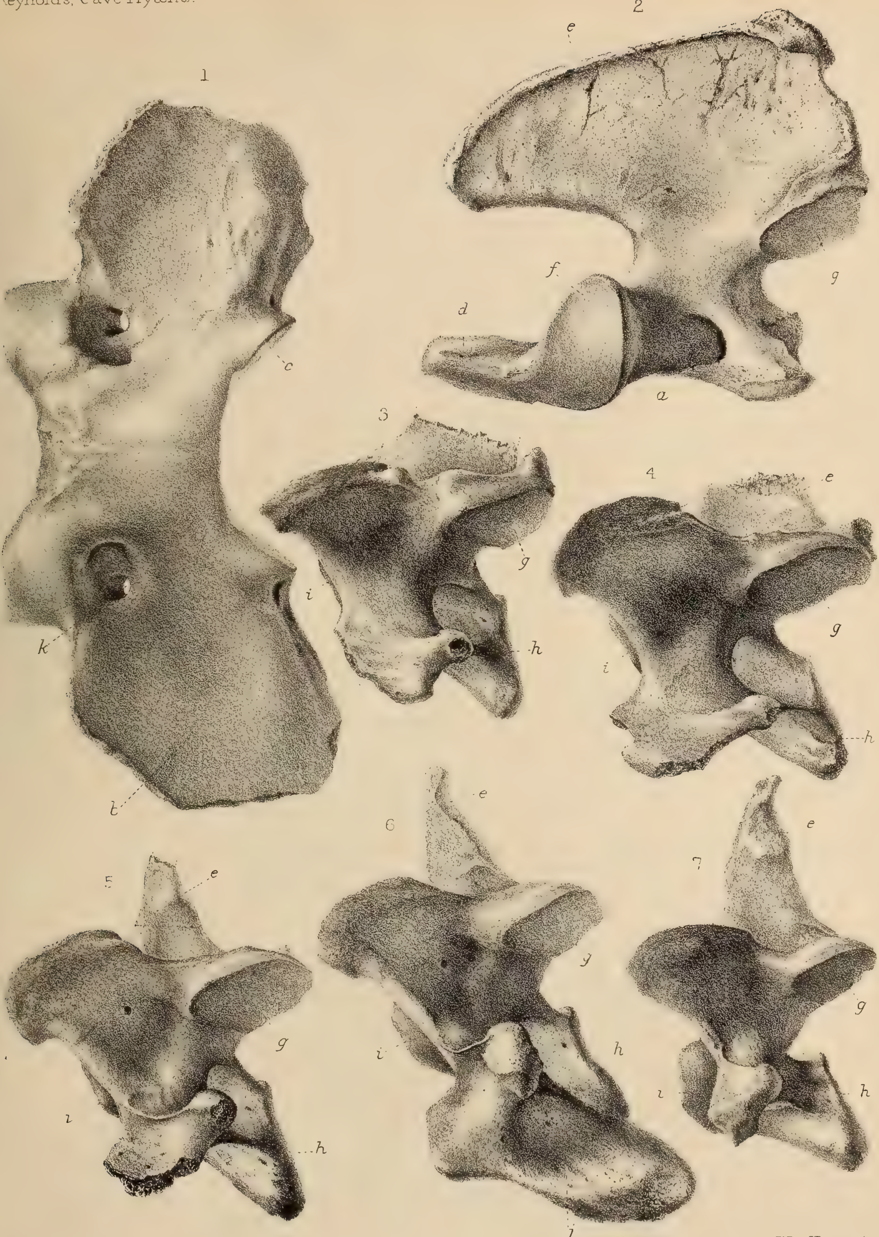
Fig.

1. Atlas, dorsal aspect.
2. Axis.
3. Third cervical.
4. Fourth cervical.
5. Fifth cervical.
6. Sixth cervical.
7. Seventh cervical.

(Figs. 2–7) All viewed from the left side.

a. Vertebrarterial canal.
b. Transverse process of atlas.
c. Posterior articulating surface of atlas.
d. Odontoid process.
e. Neural spine.
f. Anterior articulating surface of axis.
g. Postzygapophysis.
h. Posterior face of centrum.
i. Anterior face of centrum.
j. Inferior lamella of sixth vertebra.
k. Foramen for exit of spinal nerve.

All the above specimens are from Wookey Hole, Somerset, and are now preserved in the Taunton Museum. All except the atlas are from Skeleton A.



W. Bidgood del. et lith.

West Newman imp

Vertebræ

PLATE VII.

Cave Hyæna.

Vertebræ.

(Natural size.)

Fig.

1. First thoracic, front view.
2. Second thoracic, seen from the left side.
3. Third thoracic, seen from the left side.
4. Fifth thoracic, front view.
5. Sixth thoracic, seen from the left side.
6. Tenth thoracic, front view.
7. Eleventh thoracic, seen from the left side.

a. Neural spine.

b. Neural canal.

c. Prezygapophysis.

d. Transverse process.

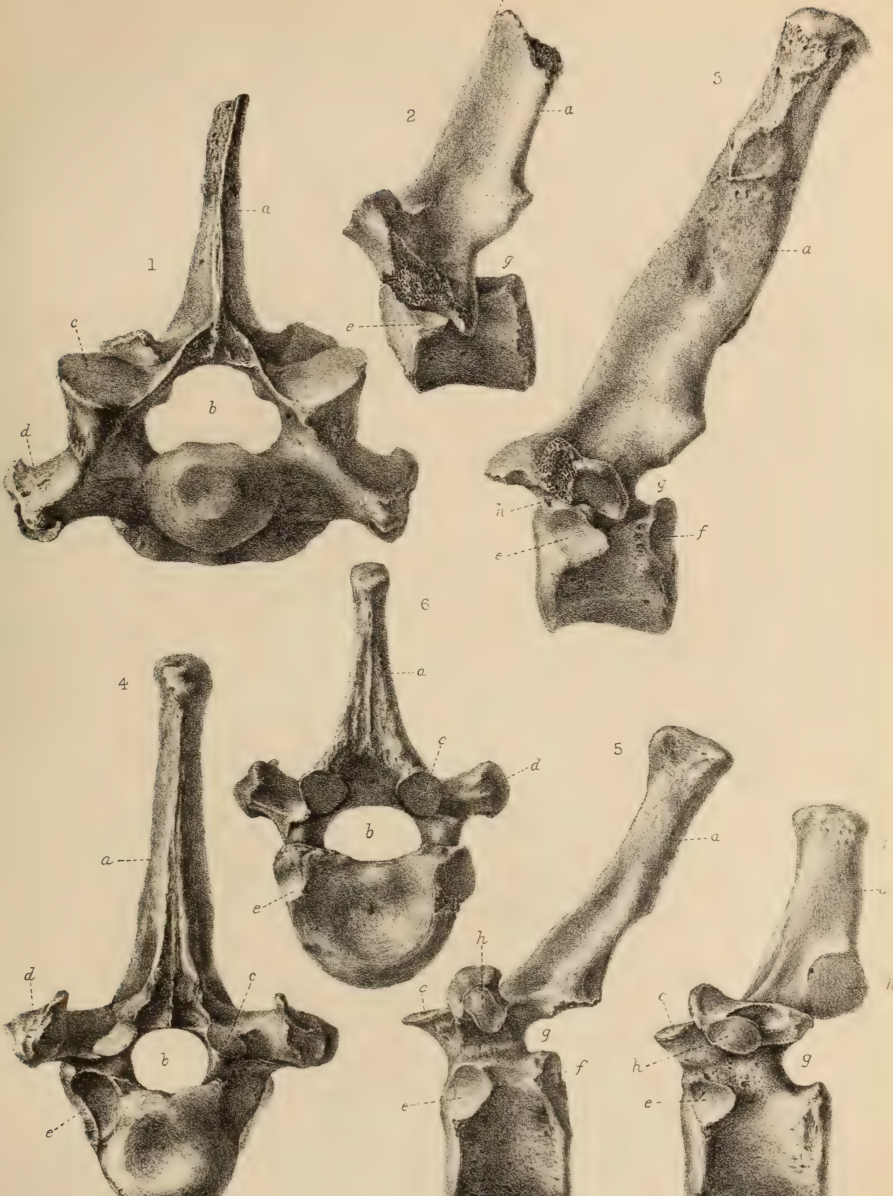
e. Anterior facet for articulation with capitulum of rib.

f. Posterior facet for articulation with capitulum of rib.

g. Notch for exit of spinal nerve.

h. Facet for articulation with tuberculum of rib.

All the above specimens are from Wookey Hole, and are now preserved in the Taunton Museum. Those shown in figs. 2, 3, and 5 are from Skeleton A; those shown in figs. 4, 6, and 7 are from Skeleton B.



W. Bidgood del. et lith.

West, Newman imp.

Vertebræ.

PLATE VIII.

Cave Hyæna.

Vertebræ.

(Natural size.)

Fig.

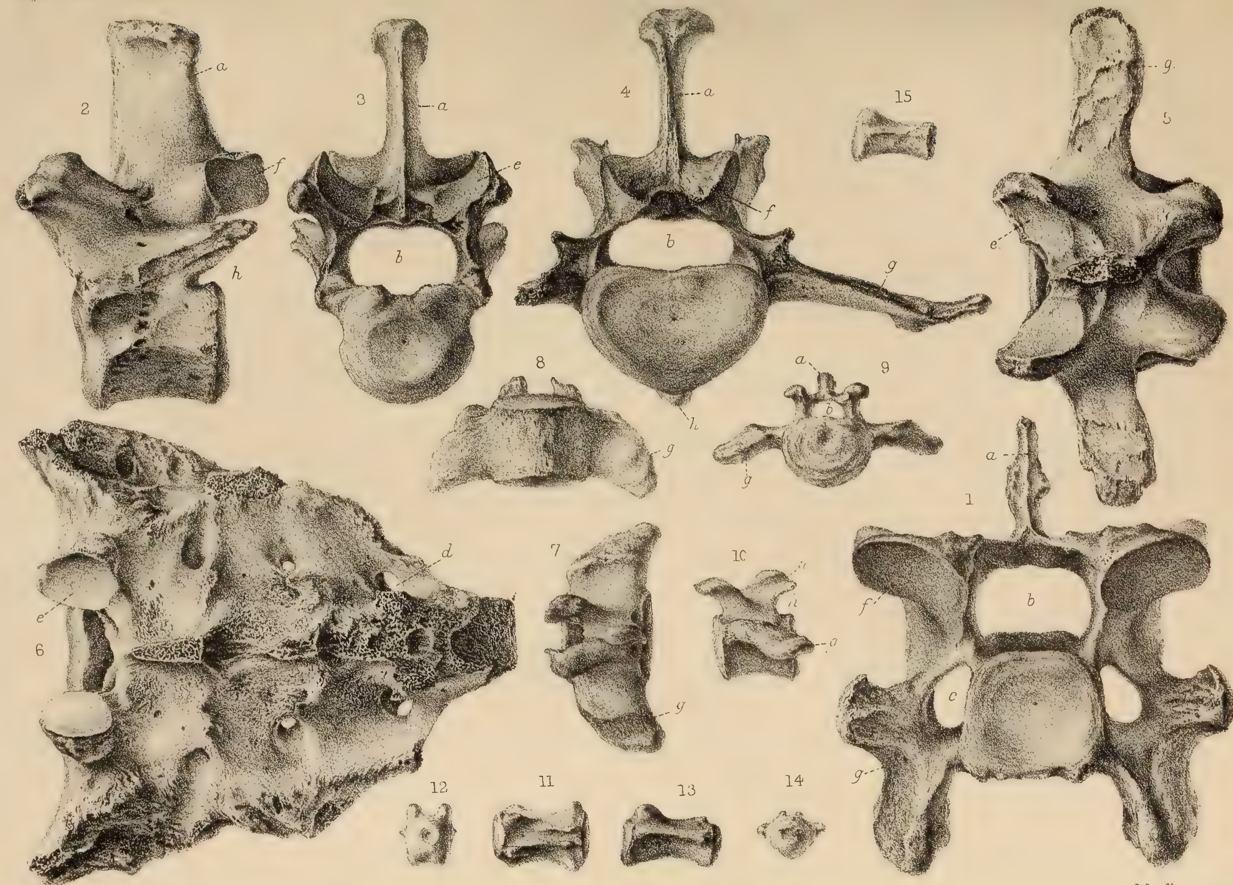
1. Sixth cervical, posterior view.
2. Thirteenth thoracic, seen from the left side.
3. Thirteenth thoracic, front view.
4. Fourth lumbar, posterior view.
5. Fifth lumbar, dorsal view.
6. Sacrum, dorsal view.
7. Dorsal }
8. Ventral } view of the first free caudal vertebra.
9. Anterior }
10. The same vertebra seen from the left side.
11. Dorsal }
12. Anterior } view of probably the ninth free caudal vertebra.
13. The same vertebra seen from the left side.
14. Anterior view of a late caudal vertebra, perhaps the twelfth.
15. The same vertebra seen from the left side.

a. Neural spine.
b. Neural canal.
c. Vertebrarterial canal.
d. Foramen in sacrum for exit of spinal nerve.
e. Prezygapophysis.
f. Postzygapophysis.
g. Transverse process.
h. Notch for exit of spinal nerve.

The specimens shown in figs. 1—6 are from Wookey Hole, and are preserved in the Taunton Museum. The other specimens figured are also without doubt from Wookey Hole, but I was unable to find them in the Taunton Museum. Figs. 1 and 4 are from Skeleton A; figs. 2, 3, and 6 from Skeleton B.

Reynolds. Cave Hyæna

Pl. VIII.



W Bidgood del. et lith

West, Newman imp

Vertebræ.

PLATE IX.

CAVE HYÆNA.

Scapula.

(Natural size.)

FIG.

1. Outer aspect } of left scapula.
2. Posterior aspect } of left scapula.

a. Glenoid cavity.

b. Acromion.

c. Prescapular fossa.

d. Postscapular fossa.

e. Glenoid border.

This specimen is from the Creswell caves, Derbyshire, and is now preserved in the Museum of Owens College, Manchester.

1.

2.

J. Green del. et lith.

Mintern Bros. imp.

Scapula.

PLATE X.

Cave Hyæna.

Humerus, Ulna, and Radius.

(Natural size.)

Fig.

1. Right humerus,
2. Right ulna, } all anterior aspect.
3. Right radius,

a. Head of humerus.

b. Great tuberosity.

c. Lesser tuberosity.

d. Deltoid ridge.

e. Supra-trochlear foramen.

f. Trochlea.

g. External condyle.

h. Internal condyle.

i. Olecranon.

j. Sigmoid notch.

k. Surface for articulation with radius.

l. Distal end of ulna.

m. Surface for articulation with humerus.

n. Distal end of radius.

The three bones are all from the Skeleton B found at Wookey Hole, and now preserved in the Taunton Museum.

W. Bidgood del. et lith.

West, Newman imp.

Humerus, Ulna, and Radius.

PLATE XI.

Cave Hyæna.

Manus.

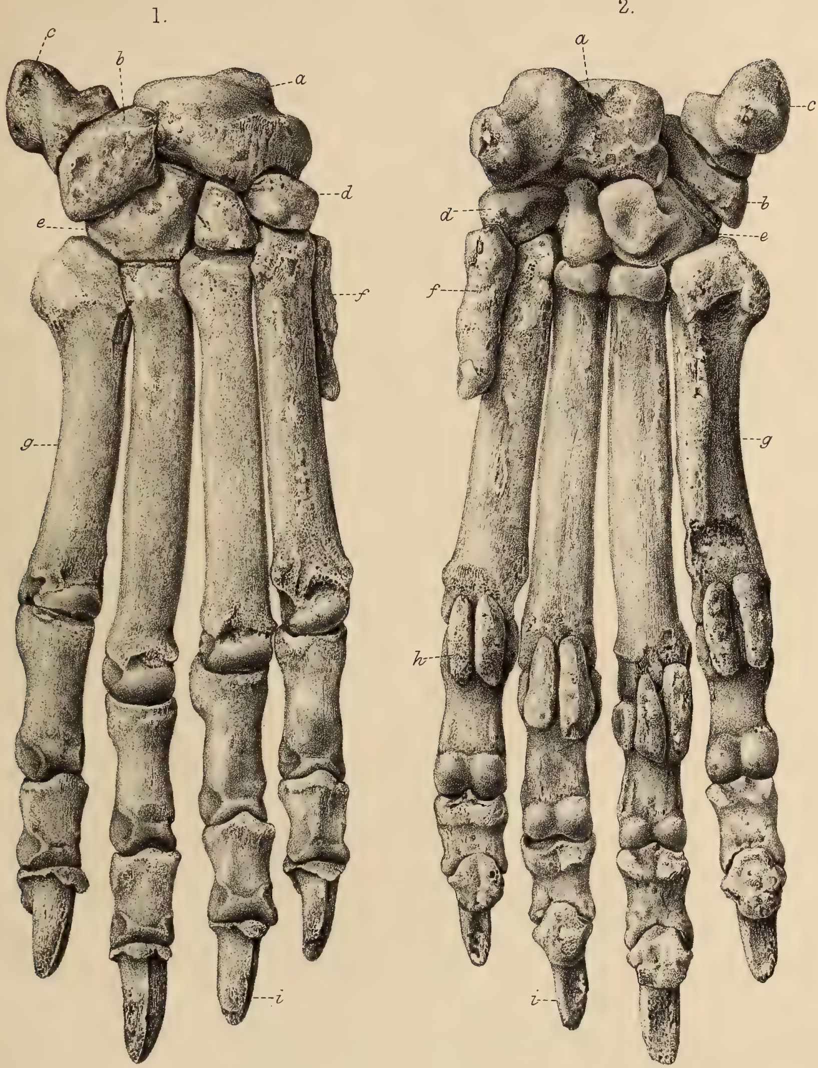
(Natural size.)

Fig.

1. Dorsal or anterior view of right manus.
2. Ventral or posterior view of right manus.

- *a.* Bone representing the fused scaphoid, lunar, and centrale.
- *b.* Cuneiform.
- *c.* Pisiform.
- *d.* Trapezoid.
- *e.* Unciform.
- *f.* First metacarpal.
- *g.* Fifth metacarpal.
- *h.* Sesamoid bone at metacarpo-phalangeal articulation of second digit.
- *i.* Ungual phalanx of third digit.

The specimens from which these figures were drawn are from the Tor Bryan caves, near Torquay, and are now in the British Museum (Nat. Hist.).



J. Green del. et lith. Mintern Bros. imp.

Manus.

PLATE XII.

CAVE HYÆNA.

Pelvis.

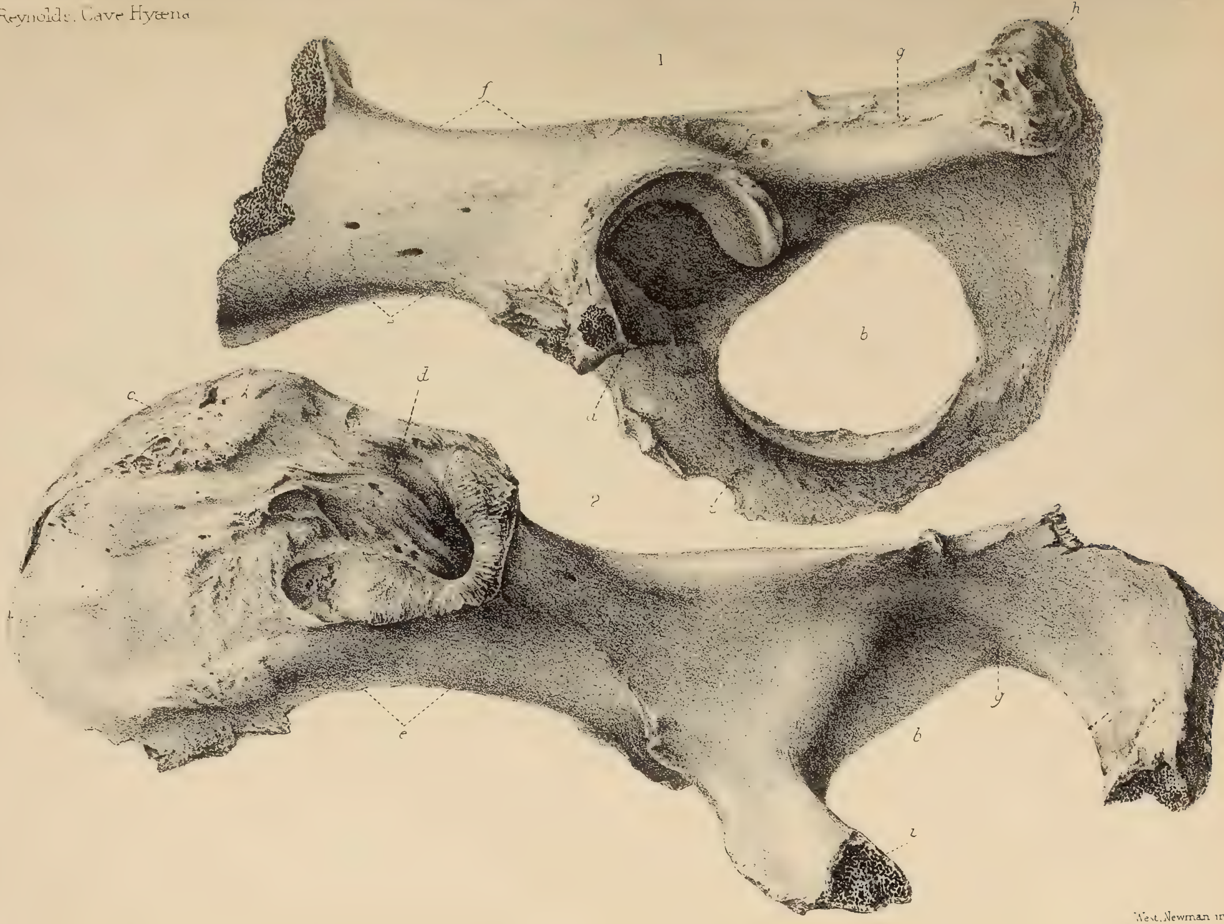
(Natural size.)

FIG.

1. Left innominate bone, seen from the outer side.
2. Right innominate bone, seen from the inner or sacral side.

a. Acetabulum.
b. Obturator foramen.
c. Supra-iliac border of ilium.
d. Sacral surface.
e. Pubic border.
f. Ischial border.
g. Ischium.
h. Ischial tuberosity.
i. Pubis.

Both the above specimens belong to Skeleton A, found at Wookey Hole, and now in the Taunton Museum.



W. Bidgood del et lith.

West, Newman imp.

Pelvis.

PLATE XIII.

Cave Hyæna.

Femur, Tibia, and Fibula.

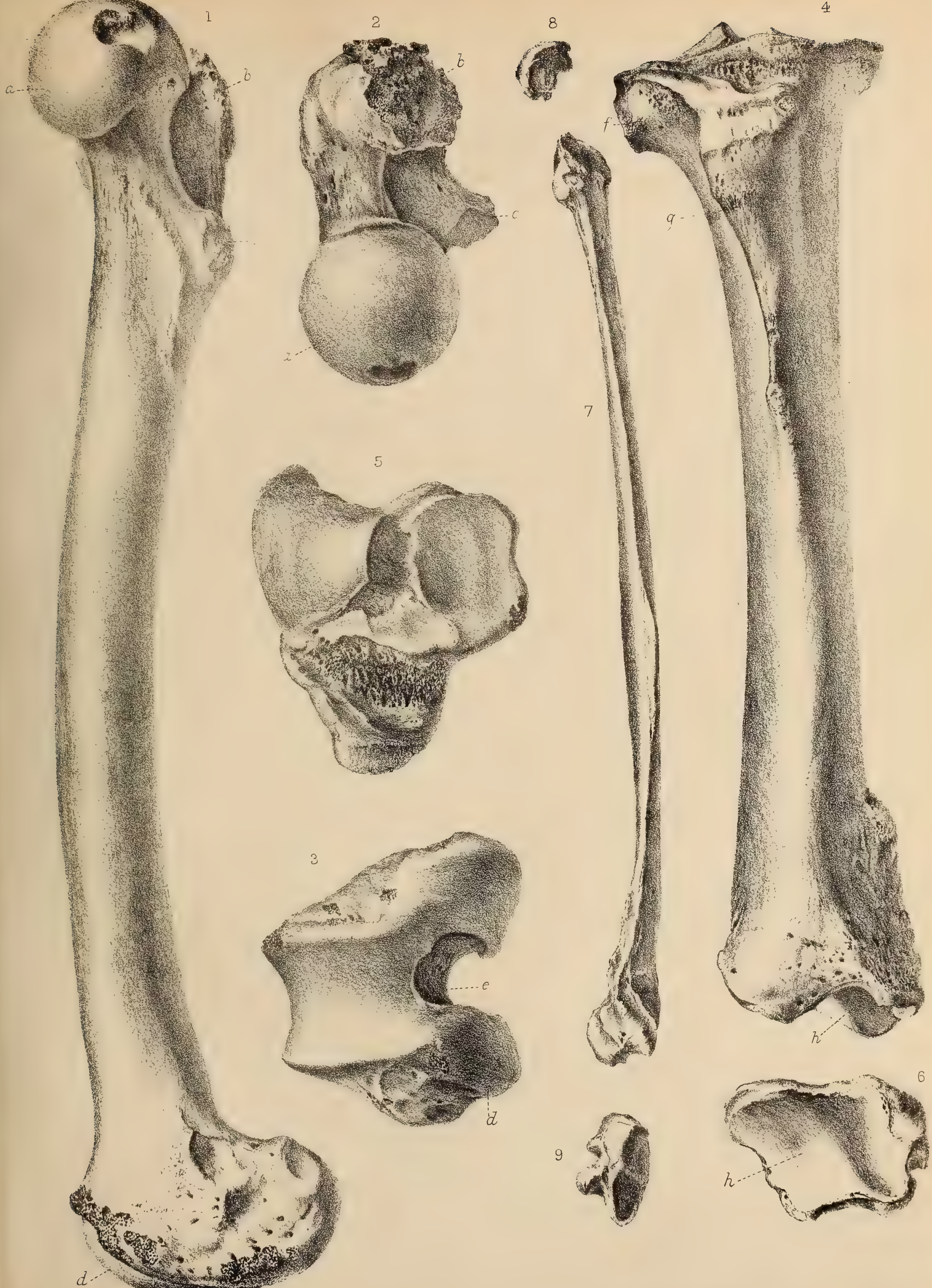
(Natural size.)

Fig.

1. Right femur, viewed from the left side.
2. The same, proximal end.
3. The same, distal end.
4. Right tibia, anterior aspect.
5. The same, proximal end.
6. The same, distal end.
7. Right fibula, anterior aspect.
8. The same, proximal end.
9. The same, distal end.

a. Head of femur.
b. Great trochanter.
c. Lesser trochanter.
d. Outer condyle of femur.
e. Intercondylar notch.
f. Surface for articulation with fibula.
g. Cnemial crest.
h. Surface for articulation with astragalus.

All the above specimens are from Wookey Hole, Somerset, and are now preserved in the Taunton Museum. The specimen from which figs. 1, 2, and 3 were drawn forms part of Skeleton A; the remainder are from Skeleton B.



W. Bidgood del et lith.

West, Newman imp.

Femur, Tibia and Fibula.

PLATE XIV.

Cave Hyæna.

Pes.

(Natural size.)

Fig.

1. Dorsal or anterior view of right pes.
2. Ventral or posterior view of the same.

a. Astragalus.

b. Calcaneum.

c. Cuboid.

d. Navicular.

e. External cuneiform.

f. Middle cuneiform.

g. First metatarsal.

h. Fifth metatarsal.

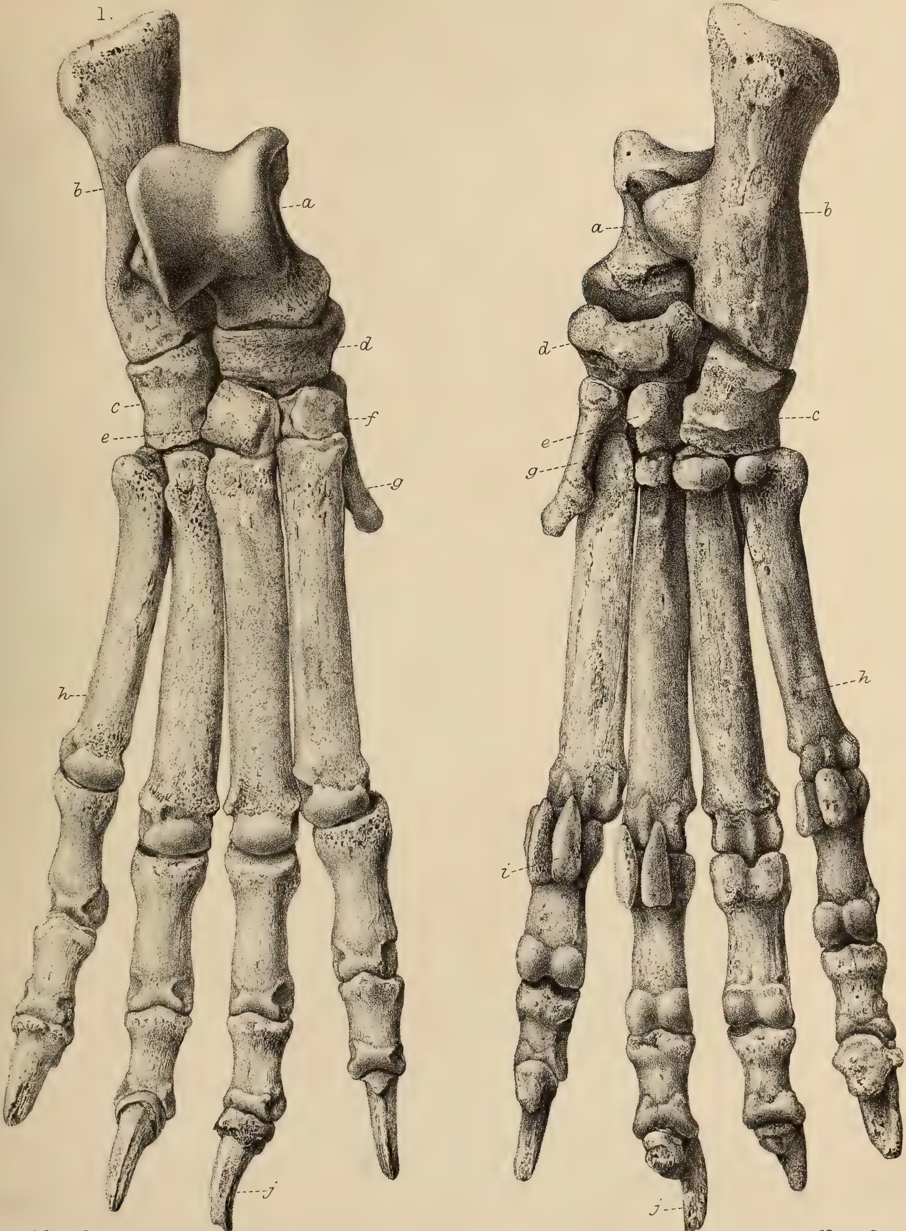
i. Sesamoid at metacarpo-phalangeal articulation of second digit.

j. Ungual phalanx of third digit.

The specimens from which these figures were drawn are from the Tor Bryan caves, near Torquay, and are now in the British Museum (Nat. Hist.).

Reynolds, Cave Hyæna.

Pl. XIV.



J. Green del. et lith.

Mintern Bros. imp.

Pes.

Palæontographical Society, 1906.

A MONOGRAPH

OF THE

BRITISH PLEISTOCENE MAMMALIA

VOL. II, PART II.

THE BEARS.

BY

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PAGES 1—35; PLATES I—VIII.

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MONOGRAPH

ON

THE BRITISH MAMMALIA

OF THE

PLEISTOCENE PERIOD.

THE BEARS.

Order—CARNIVORA.

Family—URSIDÆ.

Genus—Ursus.

I. HISTORICAL INTRODUCTION.

The fossil bears form a group of animals whose study is by no means easy, not from any scarcity of their remains, but from the difficulty of coming to a decision about the mutual relationship of the various living and fossil forms. Very divergent opinions have been expressed with regard to the number of species of bears, and the literature dealing with the subject is remarkably extensive. Cuvier[1] and de Blainville[2] treat of the early discoveries of fossil bears very fully, and their accounts have been freely used in the following pages.

Fossil bones, which eventually proved to be those of bears, were first mentioned by J. Paterson Hayn[3] (1672), who considered them to be the bones of dragons. He obtained representatives of nearly all parts of the skeleton from a cave in Mount Krapacks, Hungary. H. Vollgnad[4] (1673) referred to the same bones, again considering them to be the remains of dragons.

[1] 'Oss. Foss.,' ed. 1, 1812, tom. iv, part iv.

[2] 'Ostéographie,' tom. ii, K.

[3] 'Éphém. Curieux de la Nature,' dec. i, an. iii, obs. cxxxix, p. 220.

[4] Ibid., an. iv, obs. clxx, p. 226.

F. E. Brückmann[1] (1732) was the first to compare these cave-bones with those of bears. J. F. Esper[2] (1774) gave figures of a large number of bear-bones found in a cave in Franconia, but in default of material for comparison was unable to decide definitely that they belonged to bears, though he noted the resemblance. Later on Esper[3] (1784), having obtained the skull of a polar bear, adopted the view that the cave remains were to be attributed to the same species.

In 1794 John Hunter[4] compared a fossil skull, which had been referred to the polar bear, with the skull of the last-mentioned species, and noted various differences, though cautiously observing that great changes in the shape of the skulls of Carnivora occur during their growth to maturity and old age.

In 1795 J. C. Rosenmüller[5] recognised differences between the brown, white, and cave bears, and gave a table of comparison between the skulls of these three forms printed in parallel columns. He was also the first to apply the name *Ursus spelæus* to the cave bear.

In 1804 Rosenmüller[6] published a folio volume in French and German dealing solely with the cave bears, and fully described their remains, concluding with a suggestive chapter on the conditions under which bones found in caves might have accumulated. He also emphasised the fact that differences in skulls depend not only on age (as noted by Hunter), but also on sex.

Meanwhile, the study of fossil bears was undertaken by Blumenbach and Cuvier. The former[7] arrived at the conclusion that the German caves contained not only *Ursus spelæus*, which he regarded as distinct from all living species, but also another form which he named *U. arctoideus*, intending thus to indicate its relationship to the brown bear. Cuvier[8] (1806) confirmed Blumenbach's statement that some of the larger bones from the German caves indicated specific differences from all living bears, and also agreed with the suggestion that they represented two extinct forms—*U. spelæus* with the forehead arched, *U. arctoideus* with the forehead flat—the latter approaching living species more closely than the former.

1 'Breslauer Samml.,' 1732, p. 628; and 'Epist. Itin.,' 32.

2 'Ausführliche Nachricht zoolith. Bayreuth.'

3 'Écrits Soc. nat. Berlin,' v, p. 56.

4 'Phil. Trans.,' lxxxiv, 1794, p. 407.

5 'Beitr. Geschicht. foss. Knochen,' p. 44 (German reprint of the same author's 'De Oss. foss.,' Leipzig, 1794).

6 Abbild. u. Beschreib. der foss. Knochen des Höhlenbären,' Weimar.

7 Quoted by Cuvier, 'Bull. Sci., Soc. Philomath.,' no. 50. This reference is taken from de Blainville, 'Ostéographie,' Carnassiers, p. 46. It is quoted apparently from him by Owen, 'Brit. Foss. Mamm.,' p. 86, and by other subsequent writers. In the official catalogue of Cuvier's papers the title appears without any reference as to where the paper can be found. The paper cannot be traced, and was probably suppressed.

8 'Annales du Muséum,' vii, p. 324.

In 1810 Goldfuss[1] published a memoir in which he attempted to distinguish a third species of fossil bears, named *U. priscus*. This was accepted by Cuvier.[2] Meanwhile the fossil bones of bears were being discovered in several localities in England, notably in the caves of Kirkdale, Yorkshire (whence Buckland[3] described rare fragments), and Oreston, near Plymouth (Clift and Whidbey).[4]

In 1825 Cuvier in the third edition of 'Ossemens Fossiles' reverted[5] to the conclusion that the forms called *U. spelæus* and *arctoideus* were only varieties of the same species. De Blainville, however, remarked[6] that Cuvier's unfortunate establishment of a new species on insufficient evidence gave an impulse to this practice, which was exaggerated in the hands of less skilful palæontologists. In proof of this he referred to Croizet and Jobert[7] (1828) who believed they could recognise *U. cultridens* by a single canine, and sought to establish a new species *U. arvernensis* on a fragment of the anterior part of the skull, a humerus and other isolated bones. The work of M. de Serres[8] is an instance of the same method.

P. C. Schmerling[9] (1833), although he corrected certain mistakes of Cuvier, was led by his example to establish several new species on material more or less incomplete. He concluded that no less than five species of bears lived in the Liège district—viz., *U. spelæus* and *arctoideus*, Blum., *U. priscus*, Goldf., and two new species, *U. giganteus* and *leodiensis*. In 1842 Owen[10] described a fine skull of the brown bear from Manea fen, Cambridge.

With the increase of knowledge and facilities for comparison, the extreme difficulty of recognising specific distinctions between the various bears began to be apparent, with a tendency to group together several forms which had previously been regarded as distinct species. This tendency was first shown by de Blainville[11] who in 1844 gave a detailed and critical account of the different kinds of fossil bears with splendid illustrations. Further reference to his conclusions follows later, but it may be mentioned here that he considered all the bears, living and fossil, found in Europe to belong to one species, but thought there were two races of fossil bears, a larger race the male of which was represented by *U. giganteus* and *U. spelæus major* and the female by *U. arctoideus* and *U. leodiensis*, and a smaller race in which the male was represented by *U. spelæus minor* and the female by *U. priscus*. He considered that a second small species was represented by *Ursus*

[1] 'Verhandl. kaiserl. Leopold.-Karolin. Akad. der Naturforscher,' x, 2, p. 260.

[2] 'Oss. Foss.,' ed. 3, 1825, iv, p. 380.

[3] 'Reliquiæ diluvianæ,' ed. 2, p. 17; and 'Phil. Trans.,' 1822, p. 171.

[4] 'Phil. Trans.,' cxiii, 1823, p. 88.

[5] Tom. iv, p. 358.

[6] 'Ostéographie,' Carnassiers, p. 50.

[7] 'Rech. Oss. foss. Puy de Dome,' p. 628.

[8] 'Bull. univ. des Sci. Nat.,' 1830, xii, no. 19, p. 161.

[9] 'Recherches Oss. foss. Cavernes de Liège.'

[10] 'Rep. Brit. Assoc.,' 1842, p. 69.

[11] 'Ostéographie,' Carnassiers, p. 38.

arvernensis. He doubted the distinction of the bears of north-western America (*i.e.* the grizzly bear) from the European species. This view was also accepted by Middendorff (1851),[1] who concluded that all the bears of the *arctos* group from both eastern and western hemispheres were varieties of one species.

On the other hand, Owen in 1846 in his 'British Fossil Mammals and Birds' dealt fully with the British fossil bears, recognising three species, *U. spelæus*, *U. arctos*, and *U. priscus*, Goldf., to which species he attributed a lower jaw from Kent's Cavern. J. A. Wagner[2] also (1851) agreed with Owen in recognising more than one species among the bears of the *arctos* group and considered de Blainville's views on the subject to be retrogressive. Gray[3] (1864) went farther in the process of subdivision than anyone else, separating the living bears not only into a number of species, but also into several genera.

The descriptions of the bones of bears from a number of Irish localities now commenced—*e.g.* by R. Ball,[4] A. Carte,[5] and H. Denny.[6] Some of the bones found were even attributed to the polar bear.

Müller[7] (1872), in a beautifully illustrated work on certain bears' skulls from Russia, doubted the possibility of distinguishing between the different species of fossil bears even by their teeth.

In 1867 appeared the first of a series of important communications from Busk dealing with the fossil bears. In this paper, of which, unfortunately, only an abstract was published,[8] he mentioned that the teeth on which reliance was to be placed in distinguishing the different species of fossil bears were $\overline{\text{pm. 4}}$, $\underline{\text{pm. 4}}$, $\underline{\text{m. 2}}$, $\overline{\text{m. 3}}$. He expressed the opinion that *U. priscus* was identical with *U. ferox*. In 1873 appeared his very important paper[9] on the animal remains found in the Brixham cave, in which he fully discussed the mutual relationship of the various species of fossil bears. He established the fact that *U. priscus*, Cuv., was identical with *U. fossilis*, Goldf., and *U. ferox*, the modern grizzly, and considered that all the Irish specimens were referable to the latter species. He thought that *U. ferox (priscus)* was commoner even in England than *U. spelæus*. He discussed the differences by which, according to Owen, the teeth of *U. spelæus*, *U. arctos*, and *U. ferox* could be distinguished, but thought that these differences were not all constant and considered that it would be impossible to distinguish between the

[1] 'Untersuch. Schädeln des gemeinen Landbaren,' etc., St. Petersburg.

[2] 'Abhandl. k. bay. Akad. Wissensch.,' vi, I Abth., 1851, p. 193.

[3] 'Cat. Carniv. Pachyderm. and Edentate Mamm. in Brit. Mus.,' p. 217.

[4] 'Proc. R. Irish Acad.,' iv, 1849, p. 146.

[5] 'Journ. R. Dublin Soc.,' ii, 1860, p. 344; and 'Journ. R. Geol. Soc. Dublin,' x, 1864, p. 114.

[6] 'Proc. Yorks. Geol. and Polyt. Soc.,' iv, 1864, p. 347.

[7] 'Drei in der Provinz Preussen ausgegrabene Bärenschädel.'

[8] 'Q. J. Geol. Soc.,' xxiii, 1867, p. 342; and 'Phil. Mag.,' xxxiv, 1867, p. 399.

[9] 'Phil. Trans.,' clxiii, p. 532.

three species in respect of the teeth. He returned to the subject four years later in his 'Report on the Ancient or Quaternary Fauna of Gibraltar,'[1] in which he discussed minutely the characters of the cave, brown, and grizzly bears as based upon their teeth, stating his belief that no character of specific importance could be drawn from any part of the bear's skeleton except the teeth.

The question of the relationship of the fossil bears was further considered by R. Hensel[2] (1876). Basing his view on a study of the teeth, he urged the distinction of the cave bear, but did not express a clear opinion as to whether the other Pleistocene bears represented more than one species. In 1877 Boyd Dawkins,[3] who had already[4] commented on the extreme difficulty of distinguishing between the brown and grizzly bears by means of their hard parts, adopted the view of their identity.

About this time A. L. Adams commenced a series of important papers in which he discussed the Irish specimens. In the earliest[5] of these (1878) he referred the specimen described by Carte as *U. maritimus* to *U. ferox*, and in the second[6] he gave a critical account of all the Irish bear-remains, referring them all to *U. ferox*, the grizzly bear, which he concluded was the only bear whose remains had been proved to occur in Ireland. In a later paper[7] the same author, in describing further remains of Irish bears, was the first to suggest that those known as *U. spelæus* might be only those of large individuals of *U. ferox*. He confirmed Busk's and his own previously expressed opinion, that all the remains of Irish bears were referable to *U. ferox*. The paper included a table of dimensions of bears' crania. The following year (1881) Adams published another paper[8] further developing his suggestion that the differences between fossil bear-remains may be racial, sexual, or even individual, dependent on mode of life or character of food, and that the different British fossil bears may best be regarded as races of one species.

Later writers have also discussed fully the mutual relationship of the bears, and very varying opinions have been reached.

Lydekker,[9] writing in 1884, gave dental characters by which the brown and grizzly bears might be distinguished, but a year later doubted[10] whether a valid distinction of this kind was possible. In 1897 he separated[11] *U. spelæus* as a species, grouping all the bears of the *arctos* group (*i. e.* all those of the northern

[1] 'Trans. Zool. Soc.,' x (2), 1877, p. 60. [2] 'Sitzb. Naturf. Freunde, Berlin,' p. 49.
[3] 'Q. J. Geol. Soc.,' xxxiii, 1877, p. 598. [4] Ibid., xxxii, 1876, p. 248.
[5] 'Proc. R. Irish Acad.,' 2nd series, iii, 1878, p. 94.
[6] 'Journ. R. Geol. Soc. Ireland,' iv, 1877, p. 247.
[7] 'Sci. Proc. R. Dublin Soc.,' ii, 1880, p. 49.
[8] 'Trans. Roy. Dublin Soc.' (2), i, 1881, p. 201.
[9] 'Palæont. Indica,' ser. 10, ii, 1884, p. 202.
[10] 'Cat. Foss. Mamm. Brit. Mus.,' pt. i, p. 173.
[11] 'Proc. Zool. Soc.,' 1897, p. 412.

hemisphere except the polar bear, the American black bear, and the blue bear of Thibet) as one species. A. E. Brown[1] (1894) went farther than this, including even the American black bear as a subspecies of *U. arctos.* In this view he was in accordance with that previously reached by Allen,[2] who, however, afterwards changed his opinion[3] with regard to this point. In the paper just referred to[3] he gave a valuable table of measurements showing the great individual variability in bears' skulls from the same locality, and considered that, though *U. americanus* might be distinct, there was a complete passage between the brown and grizzly bears.

The remarkable individual variability was still more impressively shown by E. Schäff[4] (1889) in a paper on a collection of thirty-five skulls all obtained from a limited area in Russia. The variability of the European bears was shown to be more than paralleled by those of America in C. H. Merriam's paper,[5] which was based on a study of more than two hundred skulls, a series of as many as ninety-five having been obtained from one locality. The conclusions which he drew were, however, widely different from those drawn by Brown and Allen; for he not only considered that the American "brown" bears (of which he made a number of new species) were specifically distinct from the European, but separated the black bear subgenerically.

The difficulty of distinguishing between the different species of fossil bears is further illustrated by the important papers by Gaudry and Boule,[6] and E. T. Newton.[7] The former authors showed that even the loss of the three anterior upper premolars is not absolutely characteristic of the cave bear, as individuals of the smaller race from Gargas retain $\underline{\text{pm. 3}}$. The close connection between the bears of the brown and grizzly types is illustrated by the fact that they considered *U. priscus* to come nearer to *U. arctos*, especially as regards the humerus, than to *U. horribilis*, with which it is usually thought to be identical.

Newton, in describing the Vertebrata from the Forest Bed, agreed with Owen in assigning the jaw figured in the 'British Fossil Mammals,' p. 106, to *U. spelæus*, in spite of its small size, while he assigned another specimen to *U. spelæus* in spite of its retaining $\overline{\text{pm. 1}}$.

1 'Proc. Acad. Nat. Sci. Philad.,' xlvi, 1894, p. 119.

2 'Bull. Mus. Comp. Zool.,' i, 1869, p. 184.

3 'Bull. U. S. Geol. Surv. of Territories,' ii, no. 4, 1876, p. 334.

4 'Archiv für Naturgeschichte,' 1889, p. 244.

5 'Proc. Biol. Soc. Washington,' x, 1896, pp. 65–83.

6 'Mat. pour l'histoire des temps quaternaires,' fasc. iv, p. 105 (1892).

7 "Vertebrata of Forest Bed Series," 'Mem. Geol. Surv.,' p. 5 (1882).

II. DISTRIBUTION IN BRITAIN AND ELSEWHERE.

The oldest British formation from which the fossil remains of bears have been described is the Suffolk Crag. Owen,[1] writing in 1846, says "the oldest fossil referable to the genus *Ursus* from British strata is the crown of a molar tooth, which was found at Newbourn, near Woodbridge, Suffolk. The bear's tooth is the antepenultimate grinder of the right side, upper jaw; it is smaller than the corresponding tooth in *U. spelæus*." Newton[2] was, unfortunately, unable to verify this determination, and suggests that the tooth may be attributable to *Sus*. In 1864 Lankester[3] described and figured a slender canine tooth, also said to have come from the Red Crag of Newbourn, near Woodbridge. This specimen, which is in the Reed collection at York, he referred with little hesitation to *U. arvernensis*. Boyd Dawkins, and Newton[2] have both doubted the correctness of this identification, the latter saying "it seems more probable it will prove to be an anterior tooth of *Squalodon* and, therefore, cannot be taken as evidence of the occurrence of *Ursus* in the Red Crag."

The Forest Bed is the oldest British formation in which undoubted bears' bones have been found. The best specimens were originally described by Owen,[4] and they have been re-examined and described by Newton.[5] The specimens found were at first attributed to as many as four species of bears—*U. spelæus*, *arvernensis*, *etruscus*, and *priscus* (= *horribilis*). The best specimen described by Owen is a small mandible,[6] which, in spite of its small size, is referred to *U. spelæus* for the following reasons: (1) There is a long diastema between the canine and the first tooth of the molar series, $\overline{\text{pm. 4}}$; (2) $\overline{\text{pm. 4}}$ has a complicated form; (3) $\overline{\text{m. 3}}$ is broad as compared with the same tooth in the brown and grizzly bears. Owen's identification is endorsed by Newton. Another specimen[7] has $\overline{\text{pm. 1}}$ present, but in spite of this fact is referred by Newton to *U. spelæus*, while a third and larger specimen[8] agrees with the normal *spelæus* in the complete absence of the anterior premolars. Of the sixteen specimens found in the Forest Bed, nine are referred by Newton without hesitation to *U. spelæus*, and probably two more belong to this species.

The supposed occurrence of *U. arvernensis* is based on a fragment of the right maxilla with two teeth, now in the Museum of Practical Geology. It has been regarded by Dawkins as probably referable to *U. arvernensis*. Newton considered that there was no evidence to show the correctness of this attribution, and regarded

[1] 'Brit. Foss. Mamm. and Birds,' p. 105 (1846).

[2] 'Mem. Geol. Surv.,' "Vert. of Pliocene Deposits," p. 15 (1891).

[3] 'Ann. Mag. Nat. Hist.' (3), xiv, p. 358.

[4] 'Brit. Foss. Mamm. and Birds,' p. 89 (1846).

[5] 'Mem. Geol. Surv.,' "Vert. of Forest Bed Series," pp. 5—16 (1882).

[6] Fig., ibid., pl. i (1).

[7] Fig., ibid., pl. i (2).

[8] Fig., ibid., pl. i (3).

the size of the teeth as too great, *U. arvernensis* being a small species. He considered it far more probable that the fragment was to be referred to the grizzly bear. Newton summarised his views with regard to the occurrence of *U. arvernensis* as follows[1]: "No description of a specimen of *U. arvernensis* from these deposits has ever been published, although the name has been admitted in the list of mammals. If such a specimen is in existence its resting place is not known and one is compelled, therefore, to omit the species until evidence of its existence is

TABLE SHOWING THE DISTRIBUTION OF THE BRITISH PLEISTOCENE BEARS.

River Deposits, etc.	Cave.	Brown.	Grizzly.
Acton	...	...	*
Ballymahon on borders of Longford and Westmeath	...	*	...
Ballinamore, co. Leitrim	...	...	*
Barrington	*	*	...
Bedford	?	...	...
Bourne, Lincoln	...	*	...
Burwell Fen	...	*	...
Clonburne, King's co.	...	...	*
Copford	...	...	?
Crayford	...	*	...
Dumfries	...	*	...
Grays, Essex	...	*	*
Ilford	...	...	?
Ipswich	...	...	*
Kew Bridge	...	...	*
Kilrathmurray, co. Kildare	...	*	*
King's co.	...	...	*
Longford	...	...	*
Lough Gur, co. Limerick	...	...	*
Manea Fen	...	*	...
Murston	?	?	?
Newbury, Berks.	?	...	?
Stonehouse	...	...	*
Tewkesbury	...	...	?
Walton, Essex	...	...	?
Waterford	...	...	*
Westmeath	...	*	*
Whitesand Bay, St. David's	...	?	...
Whitstable	...	...	?
Windsor	?	...	...
Woodbridge	...	...	*
Great Yeldham, Essex	...	*	...

Caves and Fissures.	Cave.	Brown.	Grizzly.
Bacon Hole, Gower	*	...	...
Ballynamintra, co. Waterford	...	...	*
Banwell	*	...	...
Bleadon	*	*	...
Bosco's Hole, Gower	*	...	...
Brixham	*	*	*
Burrington	*	...	...
Cae Gwyn, Clwyd Vale	?	...	...
Cefn, near St. Asaph	*	...	*
Chudleigh	...	...	?
Clevedon	...	?	...
Cresswell Crags, Derbyshire	...	?	?
Crow Hole, Gower	*	...	...
Deborah Den, Gower	?	*	?
Durdham Down	*	*	...
Edenvale, co. Clare	...	*	...
Enniskillen	...	...	*
Hoe Grange, Longcliffe, Derbyshire	...	...	*
Hutton	*	*	...
Ightham fissure	...	?	...
Kent's Hole, Torquay	*	*	*
Kesh, Sligo	...	*	...
Kirby Moorside	*	...	...
Kildare	...	...	*
Kirkdale	*	*	*
Llandeilo	...	*	...
Long Hole, Gower	*	...	...
Minchin Hole, Gower	*	...	*
Oreston	...	*	*
Paviland, Gower	*	*	...
Pinxies Cave	?	...	...
Ravenscliff, Gower	*	...	...
Sandford	*	*	...
Shandon Cave, Dungarvon	...	...	*
Spritsail Tor, Gower	*	*	*
Uphill	*	...	...
Windy Knoll, Castleton	*	...	*
Wookey Hole	*	*	*
Yealm Bridge	*	...	...

NOTE.—In each case the attribution of the bones, whether to the cave, brown, or grizzly bear, has simply been copied from previous authors, and does not imply an expression of opinion on the part of the present writer.

[1] "Vert. of Forest Bed Series," p. 16 ('Mem. Geol. Surv.,' 1882).

forthcoming." With regard to the fourth species, *U. etruscus*, the evidence for its inclusion is even slighter. It was doubtfully included in the list of the Forest Bed mammals by Prestwich in 1872 on the authority of Boyd Dawkins, but the specimen has not been described or figured.

During Pleistocene times bears were very plentiful in England, ranging also into North and South Wales, and occurring at a number of localities in Ireland. They do not appear to have been met with in Scotland north of Dumfries. But while very widespread in England, their remains are not, as a rule, so plentiful as those of the hyæna, and they are by no means so abundant as in some parts of the continent, such as the limestone districts of Belgium and Moravia.

The table of localities on the previous page is based on that of Boyd Dawkins[1], published in 1869, but the bones of bears have, as was to be expected, been found in several fresh localities since his list was prepared.

The most noteworthy point about the above list from Pleistocene river deposits is the large number of records of the grizzly bear especially from Ireland, while of the cave bear the records are few and mostly of a doubtful character. Till recently none of the bones found in Irish caves were attributed to the brown bear, but Scharff, who has been unable to recognise valid distinctions between *U. arctos* and *U. horribilis*, has applied the former name to the remains of bears from the caves of Kesh,[1] co. Sligo, and Edenvale,[2] co. Clare. An interesting point about the Irish bear-remains is their relatively perfect and uninjured character. Adams suggests that this may be due to the non-occurrence of the bone-crushing hyæna in Ireland.

The cave bear has been recorded from twenty-six British caves, as compared with seventeen records of the occurrence of the brown, and fourteen of the grizzly bear. Busk considered that the grizzly was more abundant than the cave bear, even in England, and was the only bear met with in Ireland.

No large and associated series of bones of bears from British localities occurs in any museum comparable with the series of hyæna bones at Taunton; and the specimens figured are preserved in several collections. I am much indebted to Mr. H. A. Allen, Mr. H. St. G. Gray, Prof. T. Mc K. Hughes, Dr. R. F. Scharff, and Dr. A. Smith Woodward, for facilities in the figuring of specimens preserved in the Museum of Practical Geology, the Taunton Castle Museum, the Sedgwick Museum, the National Museum of Science and Art, Dublin, and the British Museum (Natural History) respectively.

I wish also to thank Dr. Smith Woodward, Dr. Andrews, and Mr. C. D. Sherborn for help and advice, and Mr. J. Green for the great care and skill he has shown in drawing the plates and figures.

[1] 'Quart. Journ. Geol. Soc.,' xxv, 1869, p. 192.

[2] 'Trans. Roy. Irish Acad.,' xxxii, B, pt. 4, p. 201.

[3] Ibid, xxxiii, B, pt. 1, p. 43.

III. DESCRIPTION OF THE REMAINS.

It may be well to begin with a statement of the distinctive osteological characters of bears. They agree with the other Arctoidea in the following respects [1]: (1) there are five well-developed digits; (2) the auditory bulla is simple with no trace of a dividing septum, and the inferior lip of the auditory meatus is considerably prolonged; (3) the paroccipital process of the exoccipital is more or less triangular and is directed backwards, outwards, and downwards, standing quite apart from the bulla; (4) the mastoid process of the periotic is widely separated from the paroccipital and generally very prominent; (5) the carotid foramen is large and placed on the inner margin of the bulla, usually near the middle, but occasionally more posteriorly; (6) the condyloid foramen is distinct and exposed and never sunk into a common opening with the foramen lacerum posterius; (7) the glenoid foramen is always present and usually conspicuous; (8) a large penial bone occurs.

The family Ursidæ is characterised by the following features:[2] In existing forms the true molars are $\frac{2}{3}$ and have broad flat tuberculated crowns. The three anterior premolars of both jaws are rudimentary and often deciduous. The fourth upper premolar, the carnassial tooth, has no third or inner root. An alisphenoid canal is present. The auditory bulla is depressed and scarcely at all inflated. The feet are plantigrade. There is no entepicondylar foramen to the humerus.

As noted by de Blainville, a bear's skeleton presents certain resemblances to that of man, dependent partly on the animal's habit of sitting on the ischia, partly on the plantigrade method of walking.

A. The Skull (Plates I—V).

(1) *Distinctive Features of the Skull in the Genus* Ursus.—The skull is more or less elongated. The orbits are small and the post-orbital bar is incomplete. The palate is prolonged considerably behind the last molar tooth. An alisphenoid canal is present. The pterygoid has a well-developed hamular process.

The following are the features in the skulls and teeth of bears, in which the greatest amount of variation takes place, and to which special attention should be paid in attempting to discriminate between the different species:

(1) The presence or absence of the anterior premolars;

(2) The length of the interspace between $\underline{\text{c.}}$ and $\underline{\text{pm. 4}}$, and between $\overline{\text{c.}}$ and $\overline{\text{pm. 4}}$;

(3) The form of $\overline{\text{pm. 4}}$ and $\overline{\text{m. 3}}$;

(4) The width of the posterior narial opening;

(5) The shape of the jugal arcade;

[1] Flower and Lydekker, 'Mammals Living and Extinct,' p. 586.

[2] Ibid., p. 556.

(1) TABLE OF COMPARATIVE MEASUREMENTS OF BEAR SKULLS.

	U. spelæus, Banwell, Beard coll. (Taunton Mus.).	*U. spelæus*, Banwell (Taunton Mus.).	*U. spelæus*, Sandford (Taunton Mus.).	*U. spelæus*, Sundwig, Westphalia, No. 28544 (Brit. Mus.).	*U. spelæus*, Jersmanowice, Rus. Poland (Brit. Mus.).	*U. priscus*=*horribilis*, Muggendorf, Baireuth (Brit. Mus.).	*U. horribilis*, Clonburne, King's Co. No. 214 (Brit. Mus.).	*U. horribilis*, Ballinamore, Leitrim (Brit. Mus.).	*U. arctos*, Burwell fen (Sedgwick Mus., Cambridge).	*U. arctos*, Bourne, Lincoln (Jermyn St. Mus.).	*U. arctos*, Manea fen, Cambs. (Sedgwick Mus., Cambridge.)	*U. horribilis*, Yellowstone River, Montana, No. 854, (R. Coll. of Surgeons Mus.).	*U. horribilis*, No. 58.6.18.10. (Brit. Mus.).	*U. horribilis* var. *horriæus*, No. 67.2.23.3. (Brit. Mus.).	*U. arctos* No. 218e (Brit. Mus.	*U. arctos*, Kamtchatka, No. 91.12.18.13 (Brit. Mus.).	*U. arctos* var. *piscator*, N.W. Asia, No. 93.9.10.1. (Brit. Mus.).
1. Length from intercondylar notch to anterior end of skull	...	42·0	35·5	44·3	43·3	31·5	32·2	35·8	36·0	33·6	29·55	30·5	34·85	30·1	32·2	34·7	35·9
2. Length of space between c. and pm. 4...	...	...	...	4·65	5.05	3·1	3·7	3·25	...	3·1	...	...	3·6	2·65	2·85	3·7	4·1
3. Length of space between c. and pm. 4...	...	...	...	...	...	4·1	...	...	...	...	...	...	4·65	3·9	3·95	4·2	5·25
4. Extreme width across zygomatic arches	...	...	21·3	31·5	31·9	19·4	22·0	25·4	19·5	24·25	19·9	21·0	20·9	22 4	25·1	26·0	25·1
5. Vertical height from suture between basi-occipital and basi-sphenoid to top of sagittal crest	...	14·35	...	13·45	14·7	9·2	10·25	11·75	8·4	10·9	8·1	9·6	11·45	9·4	11·1	11·2	11·9
6. Width immediately above lachrymal foramen	12·55	...	8·1	9·7	10·8	7·1	7·8	9·4	7·9	8·65	7·65	8·15	8·5	7·55	9·8	9·1	9·1
7. Width between ends of post-orbital processes	19·8	...	...	15·15	14·15	10·6	10·65	13·45	10·5	12·6	11·15	11·5	12·7	12·5	14·85	13·8	15·35
8. Width measured from alveolar border immediately above second upper premolars	12·55	...	9·65	12·1	12·8	9·45	9·45	10·0	9·0	9·1	8·3	8·65	8·7	8·4	9·0	10·05	9·3
9. Minimum width in front of foramen lacerum anterius	...	...	...	3·8	...	3·9	4·3	4·4	3·65	3·6	3·3	3·7	4·5	3·3	4·15	4·8	3·4
10. Transverse measurement across occipital condyles	...	9·0	7·35	8·9	8·65	7·1	7·1	8·1	6·5	7·45	6·7	6·2	7·2	6·5	6·7	7·55	7·5
11. Transverse measurement across external auditory meatus	22·6	...	14·1	18·4	16·85	13·4	13·2	15·2	12·0	14·05	12·55	13·6	14·75	13·7	15·55	15·5	16·45
12. Transverse measurement across mastoid process of periotic	29·0	...	16·9	21·9	20·8	14·3	16·9	20·8	14·55	15·95	14·3	15·25	17·25	15·95	19·3	18·8	20·6
13. Transverse diameter of foramen magnum	...	3·95	3·2	3·7	3·75	3·25	3·7	4·05	2·9	3·3	3·0	...	2·7	2·7	2·6	3·4	3·3
14. Maximum diameter of anterior narial opening	6·7	...	5·35	6·45	7·0	4·2	5·35	5·3	4·45	4·35	4·55	...	5·8	4·8	4·95	5·45	4·9
15. Width of posterior narial opening at pterygoid suture	...	...	...	3·0	...	3·7	3·05	3·15	3·0	2·6	2·6	...	3·65	2·5	3·6	3·3	3·4
16. Maximum length of mandibular ramus measured to end of condyle	...	...	27·0	...	...	23·2	...	...	23·9	...	...	...	27·2	24·0	24·2	26·25	26·0
17. Height from angle to top of coronoid process	...	...	...	...	...	9·55	...	...	9·5	...	...	...	12·35	9·8	11·2	12·2	13·0

(6) The shape of the forehead; and

(7) The form and size of the mastoid process of the periotic.

Although the conclusion arrived at is, that it is impossible to separate *U. horribilis* (*ferox*) from *U. arctos* by the study of the skeleton, it has been thought advisable in the tables of comparative measurements to quote without comment the name previously assigned to any specimen.

B. Dentition (Plate VI).

(1) *Distinctive Features of the Teeth in the Genus Ursus.*—The dental formula is i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{4}$, m. $\frac{2}{3}$, as in the dog. In *Hyæna* it is i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{3}$, m. $\frac{1}{1}$, and in *Felis* i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{3}{2}$, m. $\frac{1}{1}$. Although the upper incisors increase somewhat in size from the first to the third, *Ursus* agrees with *Felis* and differs from *Hyæna* in presenting a marked contrast in size between c. and i 3. The canine is distinguished from that of the lion by the more massive character of the root. The three anterior premolars above and below are very small, one-rooted, and often early deciduous, especially the second, which is rarely present in the adult animal. Pm. 1 is situated close to the canine, pm. 3 close to pm. 4, which is the upper carnassial. This tooth lacks the antero-internally placed inner tubercle supported by a distinct root, which is so characteristic of *Felis*, *Hyæna*, and *Canis*. Pm. 4 possesses, however, a postero-internally placed inner cusp which, as in other Ursidæ, is not supported by a distinct root. The sectorial characters of pm. 4 are very little marked, and it is much smaller than m. 1. The crowns of both the upper true molars are longer than broad, and have flattened tuberculated grinding surfaces; the second has a large backward prolongation or heel. The lower carnassial (m. 1) has a small and indistinct blade and a greatly developed tubercular heel. The second molar is of about the same length as the carnassial, but with a broader and more flattened tubercular crown. The third is smaller. The milk-teeth are comparatively simple and shed at an early age.

The following descriptions are of teeth of *Ursus spelæus*, but in each case the differences presented by the teeth of bears of the *arctos* type are noted.

It has been thought best when describing the teeth not to use terms involving assumptions of homology and requiring long explanatory prefixes. The terms *cusp* and *tubercle* are regarded as synonyms for small elevations on the surface of a tooth. The terms *cone* or *lobe* are used as denoting a rather larger elevation, and the terms *talon* or *heel* for posteriorly placed segments of a tooth.

(2) *Permanent Dentition of the Upper Jaw* (see Pl. VI).—I. 1 and 2 are very similar teeth showing a prominent anterior, pointed, and somewhat backwardly directed cone or cusp, and a depressed triangular posterior area not bearing any

definite cusp. The marginal portion of the triangular area is slightly raised. The root, which in each case is rather more than twice as long as the crown, is considerably laterally compressed.

In bears of the *arctos* type the posterior area is more sharply marked off from the cone than in the cave bear.

I. 3 is a larger and more caniniform tooth, with a prominent, sharply reflected cone. There is no depressed posterior area as in I. 1 and 2, but a slight cusp is developed on the inner side, and from it a cingulum extends along the inner and posterior margin of the crown. The root is not so much laterally compressed as in I. 1 and 2.

In bears of the *arctos* type this tooth differs only in size and in the slight development of the cingulum.

C. The canine has the form usually met with in Carnivora. Its crown constitutes about one third of its length, and is frequently, though not invariably, marked by a wide, shallow groove along its inner face, and by a slight ridge along its posterior face. The crown is slightly longer and more recurved and pointed than in *Hyæna*, and the root tapers more than in that animal, and is more massive than in *Felis*. Size constitutes the only difference between the canine of the cave bear and that of bears of the *arctos* type.

Pm. 1 and 2, which are almost invariably absent in the cave bear and irregular in their occurrence in bears of the *arctos* type, are small and simple teeth, with a low crown and long cylindrical root.

Pm. 3, which is absent as a rule in the cave bear, is in bears of the *arctos* type a small tooth with well-developed cone and slight indications of anterior and posterior cusps. The cingulum is slightly developed on the inner side.

Pm. 4, the upper carnassial, has the blade divided into a prominent anterior cone (*a*)[1] and a less elevated posterior cone (*b*), behind which is commonly a slight additional cusp. Lying postero-internally to the blade is a large inner cone or lobe (Pl. VI, fig. 1, *c*), which shows considerable variation. The cingulum is often strongly marked, especially antero-internally. There are two roots, a smaller anterior one supporting the anterior cone of the blade, and a larger posterior one supporting the posterior cone of the blade and the inner lobe.

In bears of the *arctos* type the cingulum is not so strongly marked, the inner cone or lobe tending to be relatively larger than in *U. spelæus*, and often having a slight additional cusp cut off from its posterior edge, sometimes also from its anterior edge. This inner cone or lobe, which is posteriorly placed, must not be confused with the inner tubercle characteristic of the upper carnassial in *Felis*, *Canis*, and *Hyæna*, which is anteriorly placed.

M. 1 has a large, somewhat quadrangular crown with the surface raised into

[1] This and the following letters refer to Plate VI.

a double row of low cusps lying along the inner and outer edges of the tooth. Of the four cusps along the outer border, the anterior and posterior are very small, the second from the anterior end being the largest. The cingulum is well marked along the inner surface. The tooth is fixed in the jaw by three roots, one lying internally and the other two antero- and postero-externally.

In bears of the *arctos* type the cingulum is less marked, and the two principal cusps along the outer border do not appreciably differ in size.

$\underline{\text{M. 2}}$ is the largest tooth belonging to the molar series. The grinding surface is completely tuberculated, the two most prominent cusps or elevations (*d*) occupy the anterior half of the outer border, and behind them a third and much smaller cusp is often found. The anterior cusp tends to be the largest. There are four roots, one placed anteriorly, one near the middle of the outer surface, one postero-internally, and one on the inner surface near the anterior end.

In bears of the *arctos* type the two antero-external cusps tend to be equal in size, and the tooth to narrow posteriorly more than in the cave bear. These distinctions, however, do not always hold, and are of little practical value.

(3) *Permanent Dentition in the Lower Jaw* (see Pl. VI).—$\overline{\text{I. 1}}$ is a small tooth with both root and crown much laterally compressed. The crown forms a single very slightly recurved cone, with a small tubercle on the outer side. I can detect no valid difference in bears of the *arctos* type.

$\overline{\text{I. 2}}$ has the root similar to that of $\overline{\text{I. 1}}$, but the crown is not so much compressed and the tubercle on the outer side is larger and placed lower down the crown than in $\overline{\text{I. 1}}$. There is also an indication of a tubercle on the inner side of the crown, while from each tubercle a slight ridge runs downwards and backwards to meet its fellow at the base of the crown.

In bears of the *arctos* type the outer tubercle is relatively more prominent than in *U. spelæus*, while the inner tubercle and pair of downwardly and backwardly directed ridges are not present.

$\overline{\text{I. 3}}$ is a slightly larger tooth with the root triangular in section, the apex of the triangle being directed backwards. The outer tubercle (Pl. VI, fig. 2, *e*) is very prominent and sharply divergent from the crown. A slight ridge passes backwards and downwards from it to meet another bounding the inner side of the crown. In bears of the *arctos* type the tooth differs only in its smaller size, and in the slighter development of the ridges.

$\overline{\text{C}}$. This tooth differs from the corresponding one in the upper jaw in having sometimes at any rate, both crown and terminal part of the root slightly inwardly inflected on the main part of the tooth. The smaller size is the only respect in which $\bar{\text{c}}$. of bears of the *arctos* type differs from the corresponding tooth of the cave bear.

$\overline{\text{Pm. 1, 2, 3}}$, which are absent as a rule in the cave bear, are all small conical teeth with low crowns and rather long cylindrical roots, $\overline{\text{pm. 1}}$ being the largest and the one which most commonly persists.

$\overline{\text{Pm. 4}}$ is a small tooth showing much variation. As a rule, in addition to the principal cone, one or more of three little cusps may be developed, two placed respectively at the antero-internal (Pl. VI, fig. 6, 1) and postero-internal (Pl. VI, fig. 6, 3) edges, and the third (Pl. VI, fig. 6, 2) slightly behind and to the inner side of the principal cone.

In bears of the *arctos* type the development of inner cusps is not so great as in the cave bear, and in many cases the tooth is entirely without them.

$\overline{\text{M 1.}}$ This is an elongated tooth, divided by a constriction into a posterior square portion (*g*) whose length is about one third of that of the entire tooth, and an anterior more elongated portion. The posterior portion, which represents the greatly enlarged heel or talon of the corresponding tooth in *Canis*, has the surface raised into a series of low cusps, the two most marked of which lie on the inner border and are nearly equal in size. The anterior portion generally shows two prominent cusps, one forming the anterior extremity of the crown, one farther back and on the outer side of the tooth. There are several smaller and generally ill-defined cusps along the inner border. Each portion of the tooth is supported by a strong root. The angle of divergence between the two roots varies much.

In bears of the *arctos* type the constriction between the two portions of the tooth is not so marked as in the cave bear, and the cusps are less prominent. The hinder of the two, lying on the inner border of the posterior square portion of the tooth, tends to be larger than the anterior. The cusp forming the anterior end of the tooth is less marked than in the cave bear, and often has a small accessory cusp on its inner side.

$\overline{\text{M. 2.}}$ The sides of this tooth are parallel, and the length is nearly twice the breadth. A slight constriction divides the tooth into anterior and posterior halves. The surface is somewhat uniformly tuberculated, the greatest elevation lying antero-internally. The tooth is fixed in the jaw by two stout roots, the posterior being the larger.

I cannot detect any difference from the above in teeth of bears of the *arctos* type.

$\overline{\text{M. 3.}}$ The crown, which has parallel sides, is slightly rounded in front and more markedly rounded behind. The length as compared with the breadth is about 5—4. The posterior border is sometimes rounded, sometimes more or less obliquely truncated externally. The surface of the crown is very uniformly covered with low tubercles (Pl. VI, fig. 5), the largest being placed at the antero internal angle. There are three roots, one placed anteriorly and two posteriorly, but all three roots sometimes coalesce.

In bears of the *arctos* type the tooth is rather longer in proportion to its width than in the cave bear, and is as a rule rather more contracted posteriorly. The surface of the crown tends to be ridged rather than tuberculated.

It proved impossible to obtain anything approaching a complete series of milk-teeth, and it therefore seemed best not to attempt a description of them.

(2) Table of Measurements of the Series of Permanent Teeth from Torbryan, near Torquay, figured on Plate VI.

	i.1.|	i.2.|	i.3.|	c.|	pm. 3.|	pm. 4.|	m. 1.|	m. 2.|	|i.1.	|i.2.	|i.3.	|c.	|pm. 4.	|m. 1.	|m. 2.	|m. 3.
1. Antero-posterior extent at base of crown	1·0	1·1	1·1	2·1	0·75	2·0	2·5	3·95	0·9	0·9	0·95	2·1	1·55	2·7	3·05	2·55
2. Maximum transverse measurement	0·9	0·9	1·05	1·6	0·55	1·5	1·8	1·9	0·5	0·75	1·05	1·4	0·95	1·2	1·8	1·85
3. Maximum length measured along a straight line from root to crown	2·9	3·0	3·7	8·9	...	...	...	...	2·9	3·3	3·4	8·25	...	...	...	...

c. The Vertebral Column (Plates VII, VIII).

The vertebral column of bears shows few characters distinguishing it from that of other Carnivora. Probably the most noteworthy feature is the tendency to ankylosis in the sacral region in old animals, which may have as many as five sacral and pseudo-sacral vertebræ (see Text-fig. 1, p. 19). There are fourteen thoracic and six lumbar vertebræ as compared with thirteen thoracic and seven lumbar in *Felis, Canis and Viverra*, and fifteen thoracic and five lumbar in *Meles*.

(3) Tables of Comparative Measurements of Bear Vertebræ.

	U. spelæus, Banwell (Taunton Mus.).	*U. horribilis*, Sandford (Taunton Mus.).	*U. horribilis*, No. 854 (College of Surgeons).	*U. arctos*, No. 218 *d* (Brit. Mus.).
Atlas.				
1. Maximum width	...	...	17·3	19·6
2. Median dorso-ventral diameter	...	5·2[1]	4·4	5·35
3. Extreme width of the condylar articular surfaces	...	8·1	6·5	8·2
4. Maximum width of neural canal	...	3·55	3·1	4·0
Axis.				
1. Length from anterior end of odontoid process to postero-ventral extremity of centrum	8·9	8·15[1]	6·9	8·1
2. Height from roof of neural canal to top of neural spine	6·35	3·55	4·2	4·4
3. Transverse diameter across prezygapophyses	8·4	6·85	5·6	6·8
4. Transverse diameter across postzygapophyses	7·65	5·5	5·35	5·9
5. Length from anterior end of neural spine to notch between postzygapophyses	6·3	6·7	6·1	7·1

[1] Figured.

Comparative Measurements of Bear Vertebræ (*continued*).

	3rd cervical.		4th cervical.		5th cervical.	
	U. horribilis, No. 854 (College of Surgeons).	*U. arctos*, No. 218 *d* (Brit. Mus.).	*U. horribilis*,[1] Sandford (Taunton Museum).	*U arctos*, No. 218 *d* (Brit. Mus.).	*U. horribilis*, No. 854 (College of Surgeons).	*U. arctos*, No. 218 *d* (Brit. Mus.).
1. Maximum length of centrum... measured from dorso-anterior to ventro-posterior edge	4·75	4·8	4·5	4·55	4·35	5·0
2. Width across transverse processes	10·7	12·6	...	13·35	12·5	13·3
3. Width across postzygapophyses	6·0	6·25	7·8	6·95	6·35	7·0
4. Height from roof of neural canal to top of neural spine	2·15	1·35	...	4·4	3·7	4·45

[1] Figured.

	6th cervical.		7th cervical.		
	U. horribilis, No. 854 (College of Surgeons).	*U. arctos*, No. 218 *d* (Brit. Mus.).	*U. horribilis*,[1] Sandford (Taunton Museum).	*U. horribilis*, No. 854 (College of Surgeons).	*U. arctos*, No. 218 *d* (Brit. Mus.).
1. Maximum length of centrum from dorso-anterior to ventro-posterior edge	4·3	5·0	...	4·0	4·5
2. Length from dorso-anterior to dorso-posterior edge of centrum............................	3·2	3·7	3·15	2·95	...
3. Width across transverse processes	11·6	12·95	....	12·0	12·15
4. Width across postzygapophyses	6·15	6·45	7·0	6·3	6·7
5. Height from roof of neural canal to top of neural spine	3·6	4·85	11·4	4·6	6·6

[1] Figured.

COMPARATIVE MEASUREMENTS OF BEAR VERTEBRÆ (*continued*).

	1st thoracic.		2nd thoracic		3rd thoracic.	4th thoracic.
	U. horribilis, Sandford (Taunton Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).	*U. horribilis*, Sandford (Taunton Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).
1. Length from dorso-anterior to dorso-posterior edge of centrum	3·1 [1]	2·9	3·15 [1]	2·65	2·8 [1]	2·9
2. Width across postzygapophyses	6·55	4·35	4·7	3·45	3·1	3·0
3. Width across transverse processes ...	12·8	10·0	11·0	8·85	8·4	8·25
4. Length of neural spine from notch between prezygapophyses	...	6·9	...	8·35	8·2	8·35

	5th thoracic.		6th thoracic.		13th thoracic.	14th thoracic.
1. Maximum length of centrum	...	3·0 [1]	...	3·0	3·95	4·1 [1]
2. Width across transverse processes ...	...	7·75	...	7·9	...	...
3. Length of neural spine from notch between prezygapophyses	...	8·45	...	8·55	4·45	4·5

[1] Figured.

	2nd lumbar	3rd lumbar		4th lumbar.	5th lumbar.	6th lumbar.
	U. arctos, Burwell Fen (Sedgwick Museum).	*U. horribilis*, Sandford (Taunton Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).	*U. arctos* Burwell Fen (Sedgwick Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).	*U. arctos*, Burwell Fen (Sedgwick Museum).
1. Maximum length of centrum	4·35	4·45 [1]	4·35	4·45	4·45	4·0
2. Width across processes bearing pre-zygapophyses..............................	5·5	8·3	5·8	5·45	5·9	6·35
3. Height of neural spine from notch between postzygapophyses............	4·8	6·5	5·15	5·25	5·1	4·4
4. Width across transverse processes ...	11·4	...	13·0	14·7	14·3	13·4

[1] Figured.

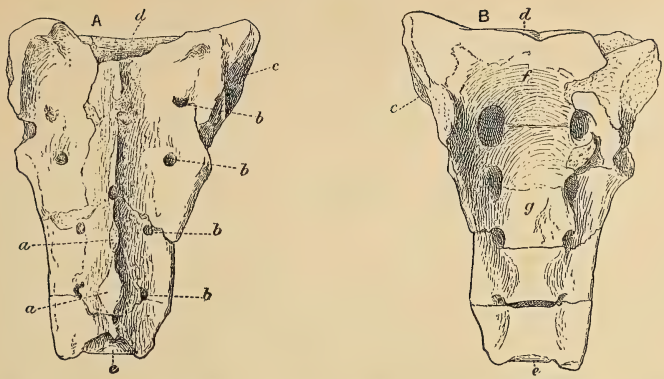

FIG. 1.—A dorsal, B ventral view of a sacrum (No. 48827), from Brixham, preserved in the British Museum; *a*, neural spine; *b*, foramen for exit of spinal nerve; *c*, articular surface for ilium; *d*, anterior face of centrum of first sacral vertebra; *e*, posterior face of centrum of third caudal or pseudosacral vertebra; *f*, ventral surface of centrum of first sacral vertebra; *g*, ventral surface of centrum of first caudal or pseudosacral vertebra.

D. THE SHOULDER GIRDLE.

The scapula in bears (Text-fig. 2) does not present any features of special interest. The British fossil specimens are almost invariably in a very fragmentary state.

(4) TABLE OF MEASUREMENTS OF THE SCAPULA.

	U. horribilis, No. 854 (R. Coll. of Surgeons Mus.).	*U. arctos*, No. 218 *d* (Brit. Mus.).
1. Length along line of spine measured from acromion	26·6	31·85
2. Maximum width	20·1	23·8
3. Maximum length of glenoid cavity	5·95	6·1
4. Height from top of acromion to inner edge of glenoid cavity	8·35	10·9
5. Length from end of coracoid process to surface of bone behind glenoid cavity	7·35	...

E. THE ANTERIOR LIMB.

The humerus (Text-fig. 3) has a strong deltoid ridge. A supra-condylar foramen is not present.

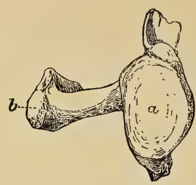

FIG. 2.—Articular view of a portion of the left scapula (N.H. 93), from the Newhall Caves, Edenvale, Co. Clare, now preserved in the National Museum, Dublin. *a*, glenoid cavity; *b*, acromion.

FIG. 3.—(1) Back view of right humerus, Sandford (Taunton Mus.). (2) Front view of left humerus, Grays, Essex (Brit. Mus.). (3) Antero-internal view of right ulna, Sandford (Taunton Mus.). (4) Front view of right radius, Sandford (Taunton Mus.). All the above specimens are attributed to *Ursus horribilis*, and are drawn $\frac{1}{3}$ natural size.

(5) TABLE OF COMPARATIVE MEASUREMENTS OF BONES OF ANTERIOR LIMB.

	U. spelæus, Banwell (Taunton Mus.).	*U. spelæus*, Sandford (Taunton Mus.).	*U. ferox fossilis = horribilis*, Grays, Essex, No. 21287 (Brit. Mus.).	*U. arctos*, No. 218*a* (Brit. Mus.).	*U. horribilis*, No. 854 (R. Coll. of Surgeons Mus.).
HUMERUS.					
1. Extreme length	...	...	[3]37·3[1]	39·15[1]	34·0
2. Diameter of proximal end passing across centre of articulating surface and greater tuberosity..................................	...	...	9·0	8·15	8·3
3. Vertical diameter of shaft at middle of deltoid ridge	6·35[1]	[3]6·8[2]	4·4	4·95	3·8
4. Transverse diameter at same point	5·5	5·85	3·9	4·05	3·7
5. Maximum transverse diameter at distal end	16·8	16·75	11·3	10·8	...
6. Maximum width of trochlea ...	...	...	...	...	7·1
RADIUS.					
1. Extreme length	42·4[1]	[3]37·8[2]	...	33·9[1]	30·3[2]
2. Right and left or transverse measurement at humeral articulation	5·55	6·1	...	4·6	4·1
3. Antero-posterior or vertical measurement at humeral articulation	4·4	4·8	...	3·65	3·05
4. Transverse diameter at carpal articulation	8·1	9·2	...	6·85	5·9
5. Vertical diameter at carpal articulation	4·8	5·45	...	4·4	3·5
6. Transverse diameter at middle of shaft	5·1	5·3	...	2·9	...
7. Vertical diameter at middle of shaft	2·8	2·5	...	2·1	...

[1] Left. [2] Right. [3] Figured.

	U. spelæus, Banwell (Taunton Mus.).	*U. horribilis*, Kew Bridge, No. 24361 (Brit. Mus.).	*U. ferox fossilis = horribilis*, Ilford, No. 38512 (Brit. Mus.).	*U. horribilis*, No. 854 (R. Coll. of Surgeons Mus.).	*U. arctos*, No. 218*a* (Brit. Mus.).
ULNA.					
1. Extreme length	46·5	44·0	38·6[1]	34·15	38·45[1]
2. Antero-posterior or vertical measurement at distal end of sigmoid notch	10·3	9·35	7·7	6·4	7·3
3. Maximum transverse measurement of olecranon..................	10·7	9·75	8·25	6·8	7·8
4. Transverse diameter at carpal articulation	3·4	3·25	3·0	2·2	2·1
5. Vertical diameter at carpal articulation	4·8	...	4·8	3·9	3·9
Length of 1st metacarpal	...	...	...	...	8·1
„ 2nd „	...	...	...	...	8·8
„ 3rd „	...	...	...	...	9·0
„ 4th „	...	...	...	...	9·3
„ 5th „	...	...	...	...	9·4

[1] Left.

F. The Pelvic Girdle.

This is characterised by the shortness of the ilia and their evertion above. The British fossil specimens are almost always in a very fragmentary state.

(6) Table of Comparative Measurements.

	U. horribilis, No. 854 (R. Coll. of Surgeons Mus.).	*U. arctos*, No. 218*d* (Brit. Mus.).
Innominate Bone.		
1. Maximum length	31·85	37·5
2. Length from edge of acetabulum to dorsal or anterior border of ilium	15·1	18·65
3. Vertical measurement of ilium at widest point...	12·1	14·7
4. Thickness of ilium at middle of surface	...	...
5. Antero-posterior diameter of acetabulum	5·05	5·3
6. Length from acetabulum to posterior border of ischium	11·25	11·7
7. Maximum diameter of obturator foramen	8·2	...
8. Measurement along ischium from symphysis to end of ischial spine	12·2	16·9

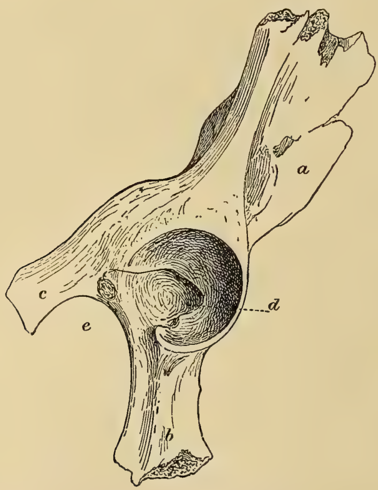

Fig. 4.—Ventral view of left innominate bone (N.H. 197), from the Newhall Caves, Edenvale, Co. Clare, preserved in the National Museum, Dublin ($\frac{1}{3}$ nat. size). *a*, ilium; *b*, ischium; *c*, pubis; *d*, acetabulum; *e*, obturator foramen.

G. The Posterior Limb.

This, as noted by Gaudry and Boule, tends to be somewhat shorter in proportion to the size of the animal in *U. spelæus* than in the bears of the *arctos* type.

The tibia is specially short, and Gaudry and Boule have suggested that this is perhaps a disposition favourable for descending into the caves in which the animal lived. Owen[1] attempts to discriminate between the femur of the different species of fossil

FIG. 5.—(1) Front view and (2) right side view of left femur attributed to *U. horribilis*, from Sandford (Taunton Mus.) ($\frac{1}{3}$ nat. size).

bears. He says that in the brown and grizzly bears the femur is broader in proportion to its length, and the tuberosity above the internal condyle is larger than in the cave bear. He also states that in the cave bear the lesser trochanter projects a little beyond the inner margin, while in the grizzly and brown bears it is thrown wholly on the posterior surface of the bone.

[1] 'Brit. Foss. Mamm.,' p. 97.

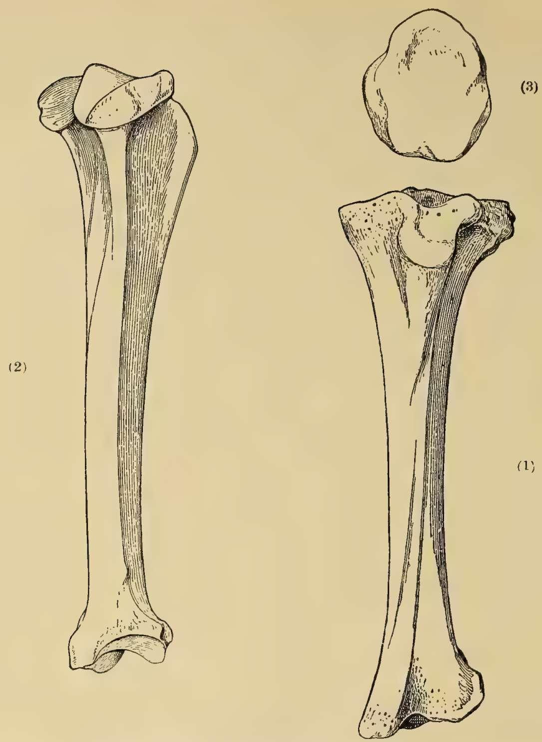

Fig. 6.—(1) Front view of right tibia, from Sandford (Taunton Mus.). (2) Postero-external view of right tibia, from Ilford, Essex (Brit. Mus.). (3) Patella, from Banwell (Taunton Mus.). All are drawn $\frac{1}{3}$ natural size. The patella is attributed to *U. spelæus*, the tibiæ to *U. horribilis*.

(7) Table of Comparative Measurements of Bones of Posterior Limb.

	U. horribilis, Sandford (Taunton Mus.).	*U. horribilis*, Sandford (Taunton Mus.).	*U. horribilis*, No. 854 (R. Col. of Surgeons Mus.).	*U. arctos* No. 218*a*, (Brit. Mus.).
Femur.				
1. Maximum length	[3] 52·5 [1]	...	40·2 [2]	46·0 [1]
2. Transverse diameter at condyles	11·5	11·7 [2]	7·3	8·3
3. Antero-posterior diameter of head	5·6	...	4·5	4·85
4. Vertical or antero-posterior diameter of shaft at middle	4·0	4·3	2·8	2·95
5. Transverse or right to left diameter of shaft at middle	5·0	5·2	3·4	4·85
6. Transverse diameter at proximal end measured across head and great trochanter	13·45	...	9·8	...

[1] Left. [2] Right. [3] Figured.

TABLE OF COMPARATIVE MEASUREMENTS—*continued.*

	U. horribilis, Sandford (Taunton Mus.).	*U. horribilis*, Sandford (Taunton Mus.).	*U. ferox fossilis* = *horribilis*, Ilford, No. 44928 (Brit. Mus.).	*U. horribilis*, No. 854 (R. Col. of Surgeons Mus.).	*U. arctos*, No. 218*a* (Brit. Mus.).
TIBIA.					
1. Maximum length	36·5	31·5 [2]	34·25 [1]	28·9 [2]	33·2
2. Transverse or right to left diameter at proximal end	11·35	9·85	8·9	7·9	8·25
3. Vertical or antero-posterior diameter at proximal end measured from notch between articulating surface for femur and top of crest	7·3	...	8·3	6·55	6·95
4. Transverse diameter at distal end	8·1	7·1	5·95	6·45	6·7
5. Vertical diameter at distal end measured across elevation between articular faces for calcaneum	5·1	4·25	...	2·95	...
6. Transverse diameter at narrowest part of shaft	4·0	3·5	3·0	2·45	2·65

[1] Figured. [2] Right.

	U. horribilis, Sandford (Taunton Mus.)	*U. horribilis*, Sandford (Taunton Mus.).	*U. horribilis*, No. 854 (R. Col. of Surgeons Mus.).	*U. arctos*, No. 218*a* (Brit. Mus.).
FIBULA.				
1. Maximum length	27·2	...	26·25	30·45
2. Transverse diameter at distal end	1·7	2·85 [2]	2·7	...
3. Vertical diameter at distal end	3·4	3·8	1·45	2·6
4. Transverse diameter at proximal end	1·75	...	1·7	...
5. Vertical diameter at proximal end	2·5	...	2·05	...
CALCANEUM.				
1. Length	11·25	11·4	8·3	9·1
2. Maximum transverse diameter	7·15	7·5	5·7	5·55
ASTRAGALUS.				
Right to left diameter	8·8	...	5·3	4·6
METATARSALS.				
Length of 1st metatarsal [1]	...	...	6·45	7·2
„ 2nd „	...	...	7·25	8·65
„ 3rd „	...	...	7·3	9·05
„ 4th „	...	...	8·3	10·25
„ 5th „	...	...	8·8	10·5

[1] All measured along plantar surface. [2] A large bone lacking proximal end.

IV. COMPARISON OF THE CAVE, BROWN, AND GRIZZLY BEARS.

The subject of the mutual relations of the Pleistocene bears is one of very great difficulty, and very varying opinions have been expressed as to the number of species. Most palæontologists have recognised three species, viz., *U. spelæus*, *U. horribilis* (= *ferox*, = *ferox fossilis*, = *priscus*), and *U. arctos*. Owen, Busk, Boyd

Dawkins (previous to 1877), Lydekker (when writing in 1885), Woodward and Sherborn, adopt the above three-fold division of the Pleistocene bears.

With very few exceptions palæontologists have considered *U. spelæus* to be distinct from the rest, but as early as 1844 de Blainville expressed doubts on this head, considering that the differences between the fossil bears were merely racial. Adams too, in 1880 and also in 1881, suggested that the bones attributed to *U. spelæus* might be only those of larger individuals of the same species as *U. ferox*, and that all the British fossil bears might be regarded as races of one species.

Comparison of the Cave Bear with Bears of the *arctos* Type.

The following characters have been quoted by various palæontologists, principally Owen,[1] Busk,[2] and Lydekker,[3] as distinguishing the cave bear from those of the *arctos* type :

(*a*) *Distinguishing Characters drawn from the Teeth.*

Cave Bear.	Bears of *arctos* Type.
(1) The three anterior premolars of both jaws are generally lost very early, all traces of their alveoli commonly disappearing.	The three anterior premolars, especially pm. 1 and pm. 3 of both jaws are far more persistent.

The complete loss of the three anterior premolars is undoubtedly almost or quite universal in the large cave bear skulls, but is not universal in the case of smaller individuals attributed to the cave bear. Thus Gaudry and Boule[4] have shown that in the small race from Gargas pm. 3 is not always lost, and Owen[5] mentions a jaw from Torquay which retains pm. 1. Newton[6] too attributes to *U. spelæus* a small jaw from the Forest Bed in spite of the retention of pm. 1.

Cave Bear.	Bears of the *arctos* Type.
(2) M. 2. has a more or less oblong form, the sides being nearly parallel, and the hind end not much narrower than the middle, and never or hardly ever pointed. The grinding surface when unworn is comparatively flat. On the outer border are three cusps of which the hindmost is very low and soon worn off (Busk).	M. 2 is more constricted behind, and the grinding surface of the unworn tooth is more compressed from side to side than in *U. spelæus*. Of the three outer cusps the two anterior are more nearly equal in size than in *U. spelæus* (Busk).

[1] 'Brit. Foss. Mamm. and Birds,' p. 86, *et seq.*

[2] 'Trans. Zool. Soc.,' x, 1877, p. 60.

[3] 'Palæont. Indica,' ser. 10, vol. ii, p. 210 ; and 'Proc. Zool. Soc.,' 1897, pp. 412—426.

[4] 'Matériaux pour l'histoire des temps quaternaires,' p. 109.

[5] 'Brit. Foss. Mamm. and Birds,' p. 91.

[6] "Vert. of Forest Bed" ('Mem. Geol. Surv.'), p. 5.

I cannot detect any constant differences between m. 2 in the two cases, though in some instances there is a tendency for the crown of the tooth to show less posterior contraction in the cave bear than in the others.

Cave Bear.	Bears of *arctos* Type.
(3) In pm. 4 besides the principal cone there are usually on the inner side two and always one smaller cusp, of which one is anterior in position to the principal cusp (Busk). Hensel[1] and Owen make similar statements, and Owen also mentions a ridge extending along the outer and back part of the base of the crown as characteristic. Lydekker[2] says pm. 4 is relatively short, the inner tubercles are very large and the first is placed more on the inner side than in *U. arctos.*	Pm. 4 has either only the principal cusp or at most a very small internal tubercle corresponding to the hinder of those met with in *U. spelæus* (Busk).

It is undoubtedly the fact that there is a greater development of accessory tubercles in the case of the tooth in the cave bear than in bears of the *arctos* type, and this tooth probably affords better characters for the separation of the cave bear than any other part of the skeleton. An examination of a large series of skulls, recent and fossil, of bears of the *arctos* type, shows that although very often pm. 4 is without any internal cusps or possesses only one small one, and though they never show the development that occurs in *U. spelæus*, yet that in some cases two or even three may be present. Further information with regard to the development of these cusps is given in the table on p. 31 ; cf. also Pl. VI, fig. 6.

Cave Bear.	Bears of *arctos* Type.
(4) M. 3 is broader in proportion to its length than in bears of the *arctos* type. The outer surface is divided into two distinct but low cusps by a deep sulcus. The grinding surface is minutely tuberculated (Busk) (*cf.* Pl. VI, fig. 5 *a*).	M. 3 is subtriangular and narrower behind than in *U. spelæus.* In typical examples there is no sulcus on the outer border. The grinding surface is coarsely ridged, not tuberculated (Busk) (*cf.* Pl. VI, fig. 5 *b*).

Great stress is laid especially by Busk on the structure of this tooth. It is certainly somewhat broader in proportion to its length in the cave bear than in bears of the *arctos* type. While no example of m. 3 from a bear of the *arctos* type

[1] 'Sitzb. Naturf. Freunde Berlin,' 1876, p. 49.
[2] 'Proc. Zool. Soc.,' 1897, pp. 412—426.

was met with showing the peculiar uniform tuberculation of some of the cave bear specimens, some of the small mandibles attributed to this species have the surface of $\overline{\text{m. 3}}$ wholly or partially ridged as in bears of the *arctos* type.

(5) Boyd Dawkins[1] states that the canine is on the whole more massive in the cave bear than in the grizzly, especially as regards the root. "It is also generally but not always absolutely larger in the crown, as Prof. Busk has remarked in his description of the teeth from the Brixham Cave."

(*b*) *Distinguishing Characters drawn from Parts other than the Teeth.*

(1) *The relatively enormous size of the cave bear.*—The size of the cave bear's skull, though as a rule much greater than that of the fossil representatives of the brown and grizzly bears, is not so much greater than that of the huge grizzlies of Alaska and brown bears of Kamtchatka. Also, as pointed out by Owen, a mandible from the Forest Bed which he figures,[2] and which on account of the complete absence of the anterior premolars he attributes to *U. spelæus,* is a good deal smaller than a second mandible from Manea fen, which, owing to the large alveoli for $\overline{\text{pm. 1, 3,}}$ he regards as belonging to *U. arctos.*

(2) *The relatively great length of the interspace between* $\underline{\text{c.}}$ *and* $\underline{\text{pm. 4}}$ *in the cave bear.*—This certainly is subject to a very large amount of variation, as the table of measurements on p. 11 shows (*cf.* also Pl. V). Busk says it is a feature distinguishing the cave from the brown bear but not from the grizzly. Owen quotes it as also distinguishing the cave bear from the grizzly.

(3) *The relative narrowness of the posterior narial opening in the cave bear.*—This, again, is a feature showing much variability (see the measurements on p. 11).

(4) *The arched character of the frontal region in the cave bear's skull.*—In many of the huge skulls from French, German, and Belgian caves this is very marked, the skull rising into two considerable bosses at the junction of the frontals and nasals owing to the enlargement of the frontal sinuses. In some of the smaller cave bear skulls, on the other hand, it is scarcely more noticeable than in those of the brown and grizzly bears. It is probably a character which increased with age and became specially marked in the old males. Owen refers to de Blainville's suggestion, that the development of the frontal sinuses depended on the cave bear's breathing a fresher, dryer, and more invigorating atmosphere than its present-day allies.

(5) *The rapid approach of the temporal crests so as to form an obtuse angle posteriorly.*

[1] 'Quart. Journ. Geol. Soc.,' xxxi, 1875, p. 251.

[2] 'Brit. Foss. Mamm. and Birds,' p. 106.

(6) *The convex character of the lower jaw* (Owen and Falconer).—Neither of the characters 5 or 6 seems to be constant.

(7) *The relative shortness of the limb bones, especially of the tibia in the cave bear* (Gaudry and Boule).—This appears to be a constant character.

(8) *The relative weakness of the hind limbs* (Gaudry and Boule).—Gaudry and Boule's suggestion in this connection has been referred to on p. 22.

(9) *The relative narrowness of the femur in proportion to its length, the small size of the tuberosity above the internal condyle, and the projection of the lesser trochanter a little beyond the inner margin in the cave bear* (Owen).

Comparison of the various Bears of the *arctos* Type.

With regard to the distinction between the brown and grizzly bears, there is by no means such a consensus of opinion as there is concerning the distinction of the cave bear. Not only de Blainville (1844), but Middendorff (1851), Müller (1872), Busk (1873), Boyd Dawkins (1877), Lydekker (1884 and 1885), and Brown (1894), doubt whether the brown and grizzly bears can be separated from one another.

The points of difference, whether valid or otherwise, have been noted as follows, and are mainly due to Owen and Busk.[1]

U. arctos.	*U. horribilis.*
1. $\underline{\text{m. 2}}$. The unworn crown is much compressed; there are only two cusps on the outer border of the tooth, of which the anterior is considerably the larger, and the posterior has in most cases a small portion in front constricted off so as to form an accessory tubercle between the two cusps (Busk).	The unworn crown is less compressed, and there are occasionally three outer cusps; the anterior two are more nearly equal in size than *U. arctos*, and the third is always small and often wanting. There is no accessory tubercle cut off from the anterior border of the posterior cusp (Busk).
2. $\underline{\text{pm. 4}}$ tends to be relatively long.	$\underline{\text{pm. 4}}$ tends to be relatively shorter, and there is more of a shelf-like projection of the cingulum at the antero-internal corner (Brown).[2]
3. There is a relatively narrow space between $\underline{\text{c.}}$ and $\underline{\text{pm. 4}}$.	There is a relatively wide space between $\underline{\text{c.}}$ and $\underline{\text{pm. 4}}$.
4. The inner posterior cusp or tubercle of $\overline{\text{pm. 4}}$ is very small or absent, and if present there is no bifid posterior talon projecting from it (Busk).	The inner posterior cusp of $\overline{\text{pm. 4}}$ is better developed than in *U. arctos*, and the posterior talon is commonly bifid or marked by two longitudinal ridges running back from it to the end of the tooth (Busk).

[1] 'Trans. Zool. Soc.,' x, 1877, p. 60.

[2] 'Proc. Acad. Nat. Sci. Philad.,' 1894, p. 119.

5. The crown of $\overline{\text{m. 3}}$ is usually more angular behind than in *U. horribilis*. There is usually no sinus or constriction on the outer border. The grinding surface presents a few coarse folds, but is never tuberculated in the slightest degree (Busk).	The crown of $\overline{\text{m. 3}}$ is usually less angular behind than in *U. arctos*. In teeth of the typical triangular form there is no sulcus on the outer border. When the tooth is more elongated it presents a shallow sinus dividing the outer border. The grinding surface is coarsely ridged, rarely tuberculated (Busk).
6. The jugal arcade is more circular (Busk and Adams).	The jugal arcade is more elliptical (Busk and Adams).
7. The posterior narial openings are wide (Busk and Adams).	The posterior narial openings are of medium width (Busk and Adams).
8. The angular crotchet is less thick and incurved than in *U. horribilis* (Busk). The coronoid process is rather less broad and high (Owen).	The angular crotchet is thicker and more incurved than in *U. arctos* (Busk). The coronoid process is rather broader and higher (Owen).
9. The claws are less long and straight (Merriam).	The claws are longer and straighter (Merriam).

The constancy and importance of the above supposed distinctions may now be considered.

(1) The differences to which Busk refers are very slight, and so far as my own observation goes, quite inconstant and unreliable.

(2) The skulls of *U. horribilis* in the Zoological Department of the British Museum do not show any marked projection of the cingulum at the antero-internal corner of $\underline{\text{pm. 4}}$, or that the tooth tends to be shorter than in *U. arctos*.

(3) Busk considered that the relative length of the interspace between $\underline{\text{c.}}$ and $\underline{\text{pm. 4}}$, on which Owen laid stress, was not constant. This is also shown by the measurements in the table on p. 11.

(4) Nearly all palæontologists have laid stress on the structure of $\overline{\text{pm. 4}}$, this being specially the case with Busk. Lydekker considered that Busk attached undue importance to the structure of the talon. Brown, too, remarks that two skulls of *U. horribilis* in the British Museum do not possess the longitudinal ridges considered by Busk to be characteristic of $\overline{\text{pm. 4}}$ in this animal, while on the other hand a skull of the Isabelline bear, a variety of *U. arctos*, possesses them.

(6) The elliptical character of the jugal arcade is variable. In the case of two grizzly bear skulls in the College of Surgeons' Museum, in No. 856, the jugal arcade is more elliptical than in the brown bear skull No. 836, while in the grizzly bear skull No. 854 it is not more elliptical. The skull from Ballymahon in the British Museum, attributed by Adams to the grizzly bear, has the jugal arcade not more elliptical than the brown bear skull No. 218*e* in the British Museum.

(7) It is generally the fact that the posterior narial opening is wider in the

brown than in the grizzly bear, but this difference does not always hold, and skulls sometimes show a remarkable amount of variation in this respect.

Dr. H. Woodward[1] quotes Dupont as stating that skulls of brown and grizzly bears may be distinguished by the fact that *U. arctos* has only the last small upper premolar (*i. e.* pm. 3), while the grizzly has also pm. 1. Whether this were a true distinction could only be determined by reference to recent skulls, and in these it emphatically does not hold. The following table shows the distribution of the small premolar teeth in a number of bears' skulls, recent and fossil, and it will be seen that all the recent skulls of the brown bear referred to, show pm. 1 in addition to pm. 3; in one case also pm. 2 is present.

(8) TABLE SHOWING DEVELOPMENT OF SMALL PREMOLARS AND OF CUSPS ON PM. 4 IN BEARS OF THE *arctos* TYPE.

	pm. 1.	pm. 2.	pm. 3.	pm. 1.	pm. 2.	pm. 3.	Cusps on pm. 4.
CRANIUM AND MANDIBLE.							
U. arctos, Kamtchatka, No. 91.12.18.13 (Brit. Mus.)	+	+	+	+	...	...	No cusps.
U. arctos, Jesso, No. 96.4.27.1 (Brit. Mus.)......	+	...	+	+	One side	...	1, 2, 3.
U. arctos var. *piscator*, N.W. Asia, No. 93.9.10.1 (Brit. Mus.)	+	...	+	+	...	...	2 (small).
U. arctos, No. 61.4.1.3 (Brit. Mus.)	Alv. one side	...	Alv.	Alv.	...	...	No cusps.
U. horribilis, No. 78.6.18.1 (Brit. Mus.)	+	...	+	...	...	...	2
U. horribilis, No. 58.6.18.10 (Brit. Mus.)	+	...	One side	+	...	...	No cusps.
U. horribilis var. *horriæus*, No. 67.2.23.3 (Brit. Mus.)	+	...	+	+	+	+	No cusps.
U. horribilis, Muggendorf (Brit. Mus.)	+	...	+	+	...	...	No cusps.
U. horribilis,[1] Ballynamore (Brit. Mus.)	Alv.	Alv.	Alv.	...	...	...	...
U. horribilis, Clonburne (Brit. Mus.)	Alv.	...	Alv.	...	...	...	...
U. horribilis, Ballymahon (Leeds, cast Brit. Mus.)	Alv.	...	Alv.	...	...	...	...
U. arctos,[1] Bourn, Lincoln (Mus. Pract. Geol.)	+	...	+	Alv.	...	...	...
U. arctos,[1] Burwell fen (Sedgwick Mus.).........	...	...	+	+ rt. side	...	Alv. rt. side	No cusps.
U. arctos,[1] Manea fen (Sedgwick Mus.)	Alv.	+	+	...	...	...	...
U. arctos[1] (labelled *U. spelæus*), Crayford, No. M.5041 (Brit. Mus.)	Alv.	Alv.	+	...	...	...	...
MANDIBLE.							
U. arctos, Manea fen (Fig. Owen, p. 106, fig. 35*a*), No. M.231 (Brit. Mus.)	...	...	...	Alv.	...	Alv.	1
U. arctos, St. David's (Brit. Mus.)	...	...	...	"	...	...	No cusps.
U. arctos, Gower, No. 859 (Coll. Surgeons Mus.)	...	...	...	"	...	...	2 (small).
U. horribilis, Grays, No. 22030 (Brit. Mus.) ...	...	...	...	"	...	...	1, 3.
U. horribilis, Deborah Den, No. 40949 (Brit. Mus.)	...	...	...	"	...	Alv.	Tooth wanting.

NOTE.—The position of the small cusps to which the figures 1, 2, 3 in the last column of the above table refer, is indicated in Fig. 6 on Pl. VI. In the other columns a + indicates that the tooth is present; if the tooth has been lost, but its socket is present, "Alv." is written.

[1] Figured.

[1] 'Geol. Mag.,' viii, 1871, p. 197.

Personally I am in agreement with the majority of zoologists referred to above, in being unable to find valid and constant characters enabling one to distinguish between the skeletal parts of the various bears of the *arctos* type. This conclusion has been stated by A. E. Brown[1] in the following forcible manner: "A critical survey of the cranial and dental characters shows little that is constant except variation, and absolutely forces the conclusion that there is not one [character] sufficiently stable and uniform to be of specific value. The European bear and grizzly run into one another so regularly that, except in extreme cases, there is no possibility of distinction apart from geographical considerations."

The differences separating the cave bear from the others are certainly greater than those between the different bears of the *arctos* type, but, unless perhaps in the case of $\overline{\text{pm. 4}}$, it is doubtful whether they are sufficiently marked and constant to afford specific distinctions. Certainly all the species of Pleistocene bears are closely allied and tend to run into one another, and it is perhaps not a matter of much practical importance whether they are grouped as one, two, or three species. On the whole it has seemed most satisfactory to recognise the specific distinction of *U. spelæus*, while grouping all the other Pleistocene bears as *U. arctos*.

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[1] 'Proc. Acad. Nat. Sci. Philad.,' 1894, p. 119.

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PLATE I.

Pleistocene Bears (*U. spelæus*).

Cranium and Mandible.

Fig.

1. Lateral view of a skull from Banwell (one quarter natural size).

2. Dorsal } view of a cranium from Sandford (one third natural size).
3. Lateral }

Both specimens are in the Taunton Museum.

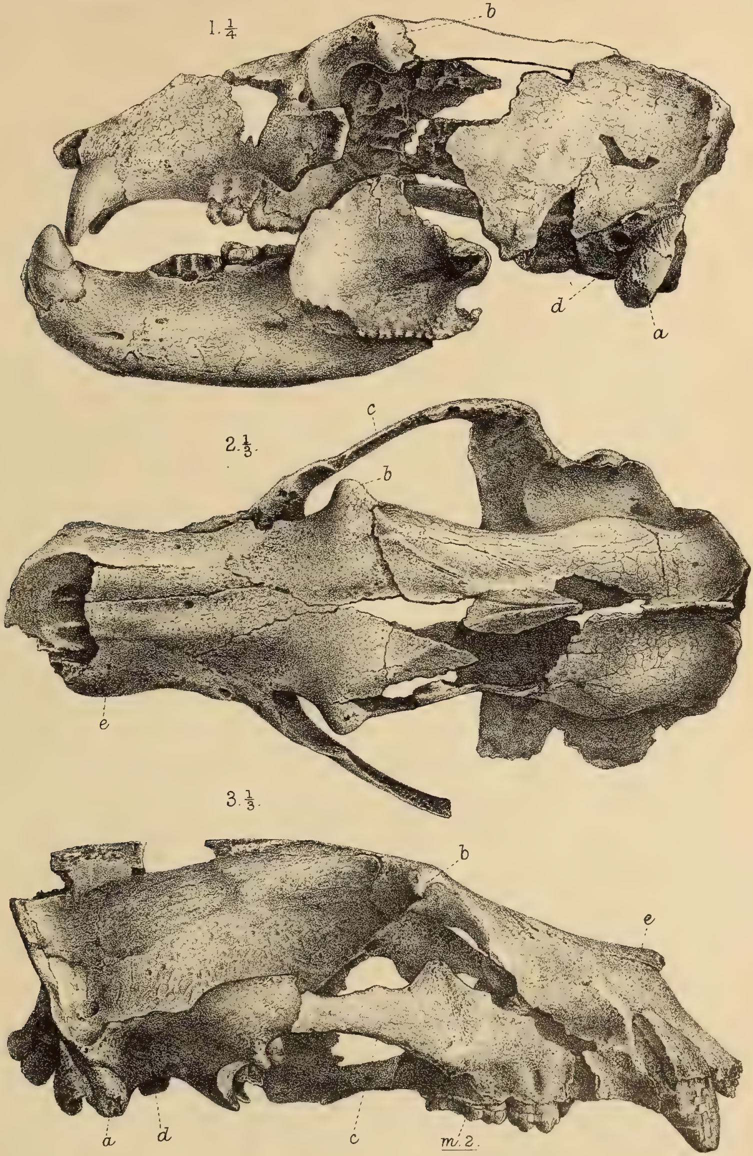
a. Mastoid process of periotic.

b. Post-orbital process of frontal.

c. Jugal.

d. External auditory meatus.

e. Nasal.



J. Green del. lith. et imp.

URSUS SPELÆUS.
Cranium & mandible.

PLATE II.

Pleistocene Bears.

Cranium and Mandible.

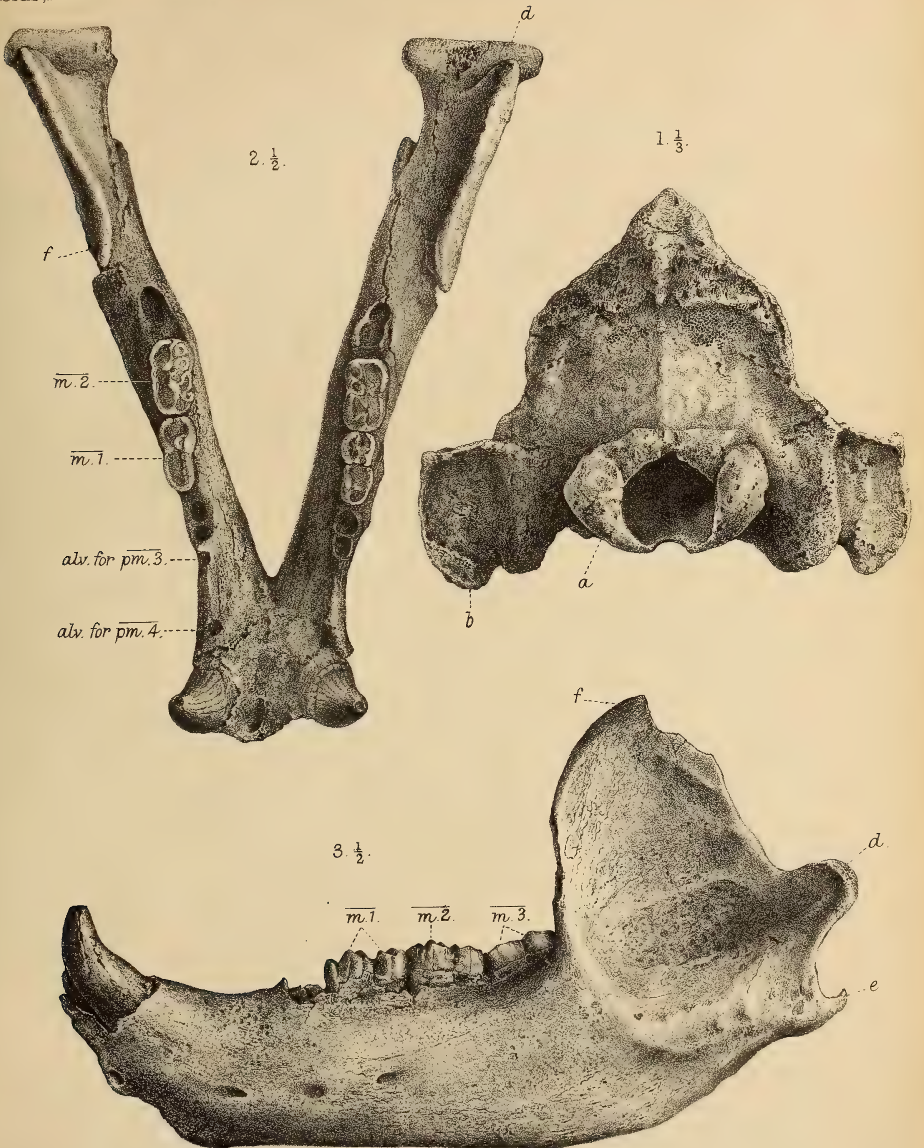
(The cranium one third, the mandibles one half natural size.)

Fig.

1. Posterior view of cranium of *U. spelæus* from Banwell.
2. Palatal view of mandible from Banwell.
3. Left mandibular ramus from Sandford, seen from the outer side.

All these specimens are preserved in the Taunton Museum. The mandibles are attributed to *U. spelæus*.

a. Occipital condyle.
b. Mastoid process of periotic.
d. Condyle of mandible.
e. Angle of mandible.
f. Coronoid process.



J. Green del. lith. et imp.

URSUS SPELÆUS.
Cranium & mandible.

PLATE III.

Pleistocene Bears (*U. arctos*).

Cranium.

(One third natural size.)

Fig.

1. Dorsal view.
2. Lateral view.
3. Ventral view.

a. Post-orbital process of frontal.

b. Occipital condyle.

c. Post-orbital process of jugal.

d. Mastoid process of periotic.

e. Anterior palatine foramen.

f. Post-glenoid process of squamosal.

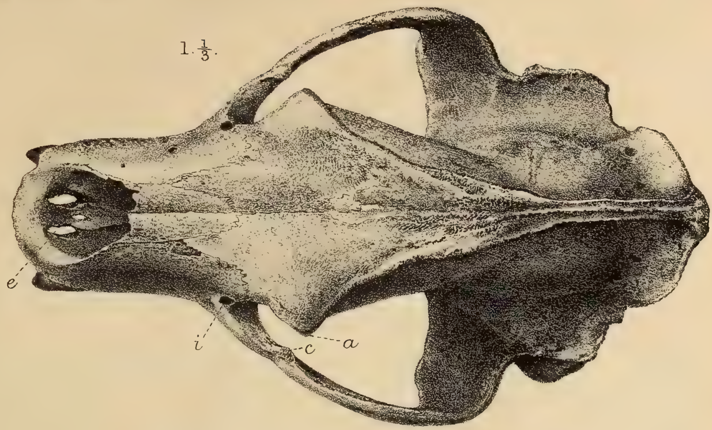
g. Post-glenoid foramen.

h. Infra-orbital foramen.

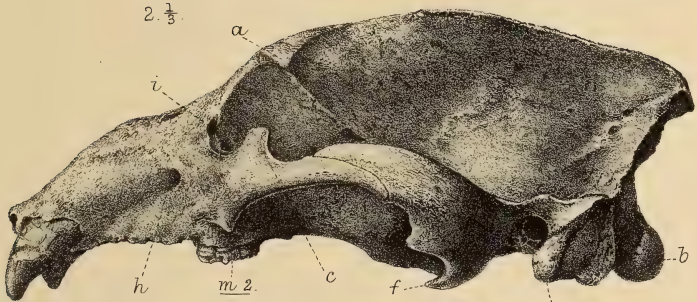
i. Lachrymal foramen.

This specimen, which is preserved in the British Museum (Nat. Hist.), was found near Ballinamore, co. Leitrim. It is referred to as *U. ferox fossilis* by Busk, 'Phil. Trans.,' clxiii, p. 543 (1873), and Leith Adams, 'Trans. Roy. Irish Acad.,' xxvi, p. 225 (1879).

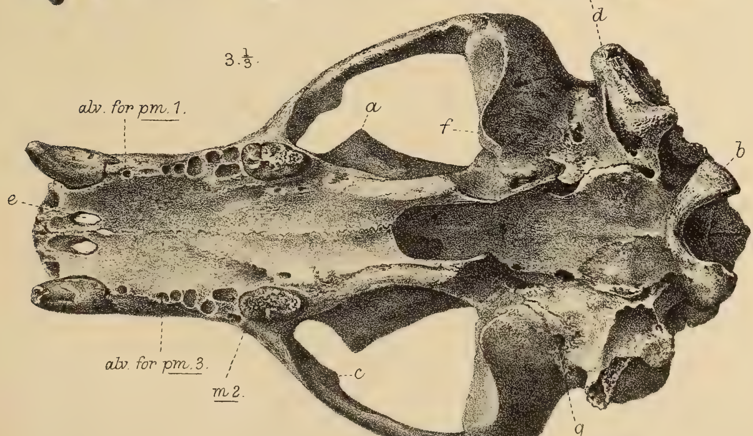
1. $\frac{1}{3}$.



2. $\frac{1}{3}$.



3. $\frac{1}{3}$.



J. Green del. lith. et imp.

URSUS ARCTOS.
Cranium.

PLATE IV.

PLEISTOCENE BEARS (*U. arctos*).

Cranium and Mandible.

(Two fifths natural size.)

FIG.

1. Dorsal view of the cranium.
2. The skull seen from the left side.
3. Ventral view of the cranium.

This specimen was found in the peat of Burwell fen, and is preserved in the Sedgwick Museum, Cambridge.

Lettering as in Plate III, with the addition of—

j. Condyloid foramen.
k. End of sagittal crest.
l. Foramen lacerum posterius.
m. Carotid foramen.
n. External auditory meatus.
o. Eustachian canal.
p. Posterior aperture of alisphenoid canal.
q. Paroccipital process of exoccipital.
r. Angle of mandible.

J. Green del. lith. et imp.

URSUS ARCTOS.
Cranium & mandible.

PLATE V.

PLEISTOCENE BEARS (*U. arctos*).

Mandible and Portions of Cranium.

(Fig. 3 one half, the others two thirds natural size.) Each figure shows the palatal aspect.

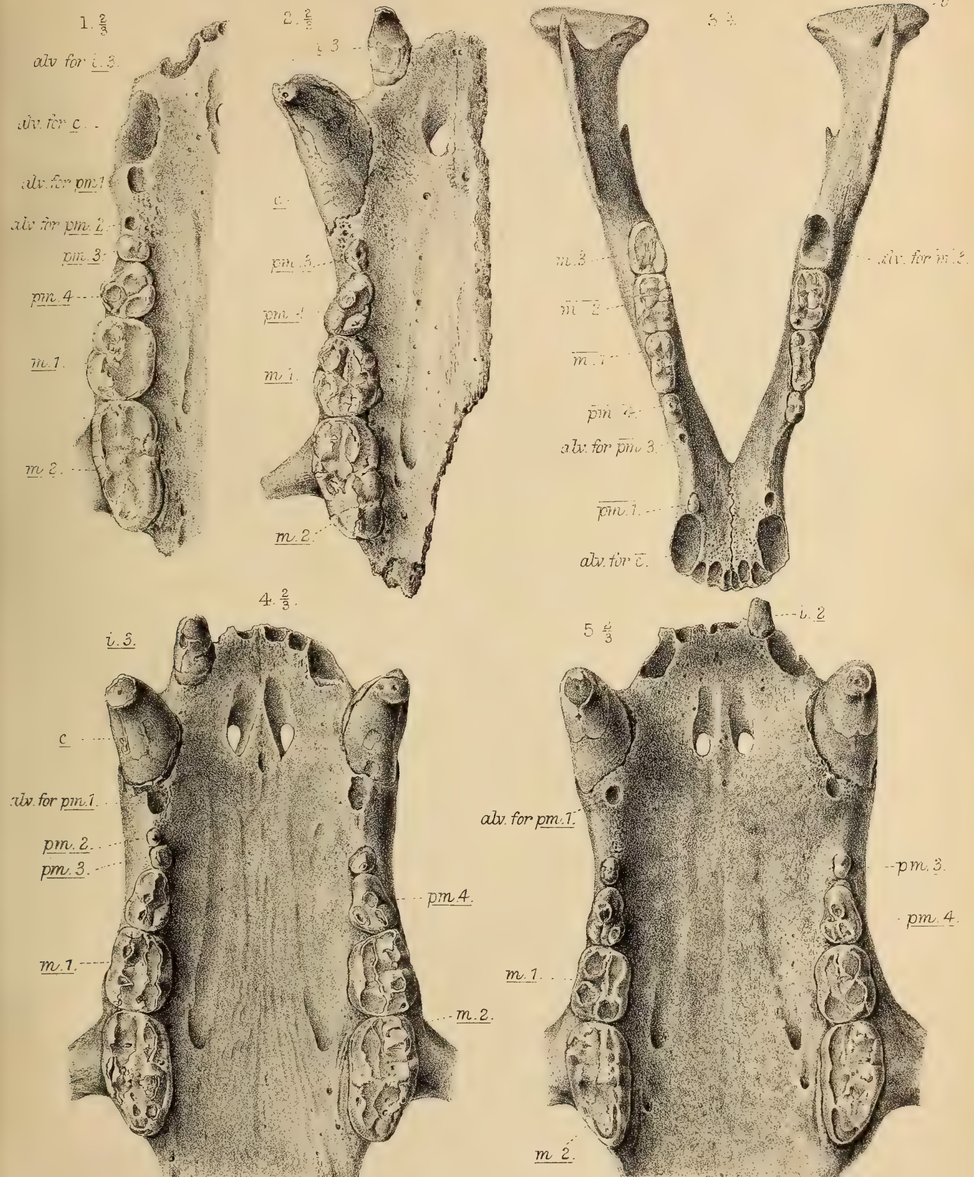
FIG.

1. Part of cranium from Crayford (No. M. 5041). Only the teeth of the right side and the neighbouring portion of the palate are figured. In the British Museum this specimen is labelled *U. spelæus*, but as all the upper premolars are represented, it seems better to attribute it to *U. arctos*.
2. Part of the right maxilla and premaxilla from Manea Fen (No. 40405).
3. Mandible from Burwell Fen.
4. Anterior part of cranium from Manea Fen.
5. Anterior part of cranium from Bourn, Lincolnshire.

The Manea Fen cranium (fig. 4) and the Burwell Fen mandible (fig. 3) are preserved in the Sedgwick Museum, Cambridge. The Bourn cranium (fig. 5) is in the Museum of Practical Geology, Jermyn Street. The other specimens are in the British Museum (Nat. Hist.), South Kensington.

a. Mandibular condyle.

b. Coronoid process.



J. Green del. lith et imp

URSUS ARCTOS.
Mandible & portions of crania.

PLATE VI.

PLEISTOCENE BEARS.

Permanent Dentition.

(Natural size.)

FIG.

1.	Left upper teeth seen from the inner side	*U. arctos*, Torbryan Caves, Torquay (Mus. of Pract. Geol., Jermyn St.).
2.	Left lower teeth seen from the inner side	
3.	Left upper teeth seen from the outer side	
4.	Left lower teeth seen from the outer side	

5. Grinding surface of left $\overline{\text{m. 3}}$ of *U. spelæus*, Kent's Cavern, Torquay (Brit. Mus.).

5 *a*. Grinding surface of left $\overline{\text{m. 3}}$ of *U. arctos*, Torbryan, Torquay (Brit. Mus.).

6 *a*. Left $\overline{\text{pm. 4}}$ *U. spelæus*, mandible No. M. 5995, Cromer Forest Bed (Brit. Mus.).

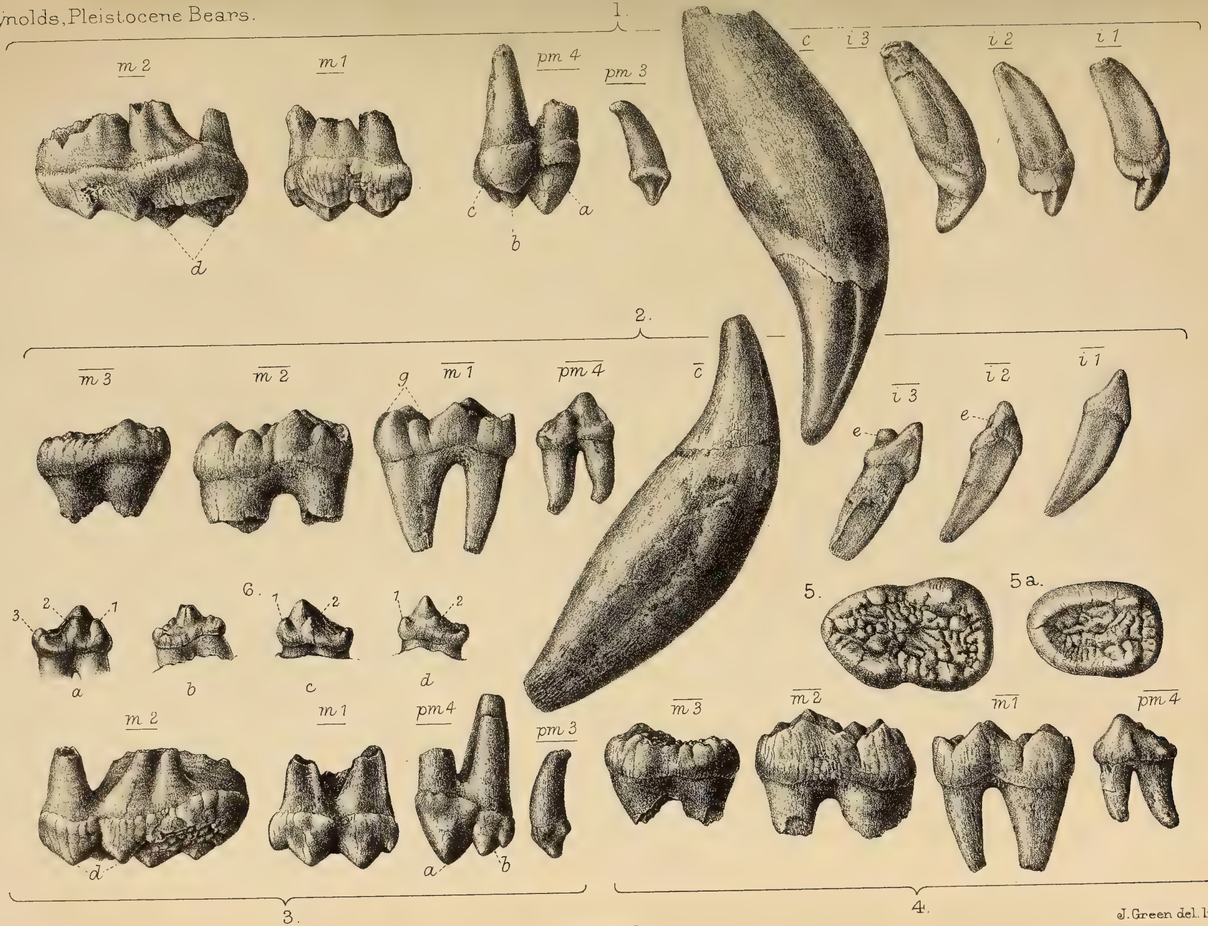
6 *b*. Left $\overline{\text{pm. 4}}$ *U. ferox* (*horribilis*), mandible No. 22029, Grays, Essex (Brit. Mus.).

6 *c*. Right $\overline{\text{pm. 4}}$ *U. spelæus*, mandible from Bacton (Brit. Mus.).

6 *d*. Right $\overline{\text{pm. 4}}$ *U. arctos*, a recent skull, No. 96.4.27.1, from Jesso, Japan (Brit. Mus.). All the teeth in fig. 6 are seen from the inner side.

a. Anterior cone.
b. Posterior cone.
c. Inner cusp or lobe.
d. Anterior external cusp.
e. Outer tubercle.

In fig. 6, 1 = anterior, 2 = middle, 3 = posterior — of the small cusps referred to in the last column of the table on p. 31.



URSUS.
Dentition.

J. Green del. lith. et imp.

PLATE VII.

Pleistocene Bears.

Vertebræ.

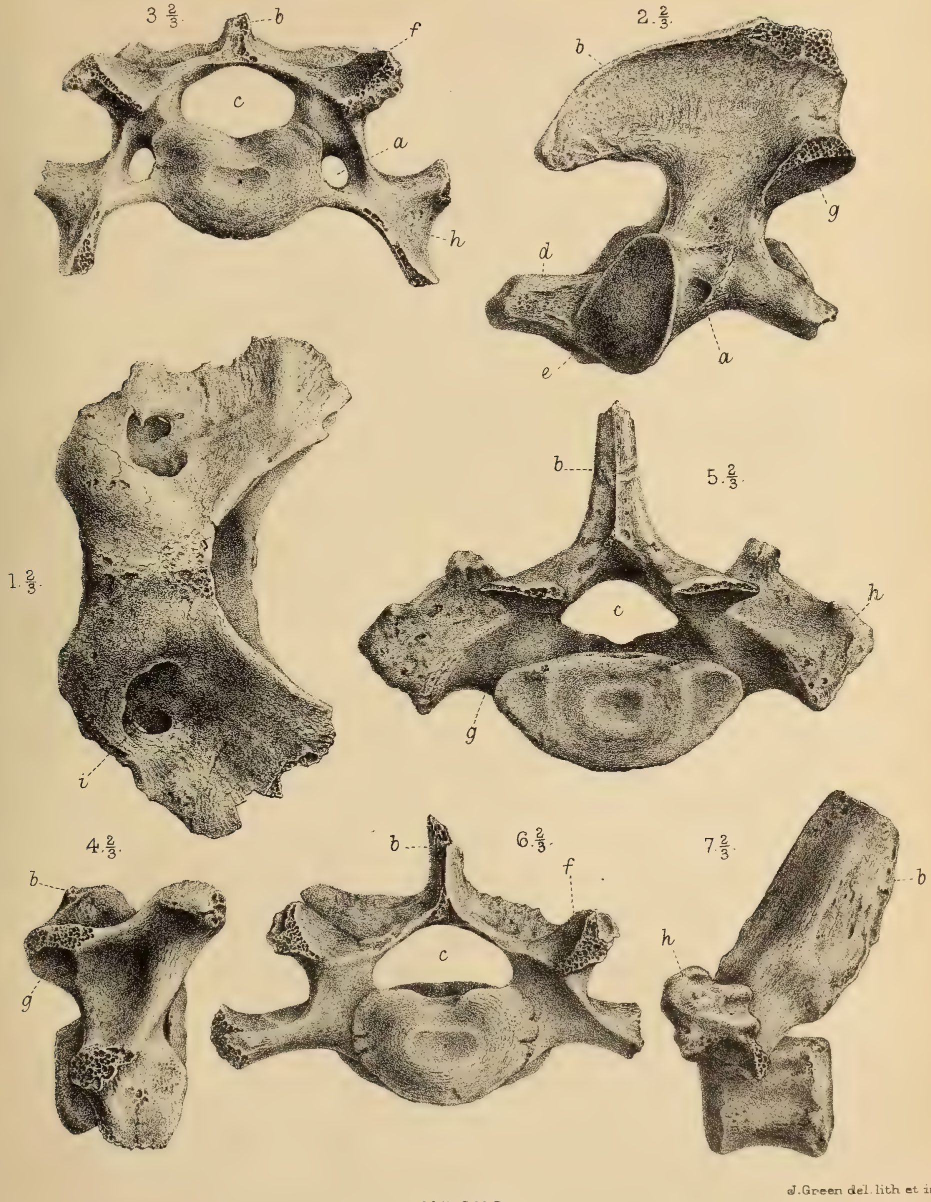
(Two thirds natural size.)

Fig.

1. Atlas, dorsal aspect.
2. Axis, seen from left side.
3. Fourth cervical, front view.
4. Fourth cervical, seen from the right side.
5. Seventh cervical, back view.
6. First thoracic, front view.
7. Second thoracic, seen from the left side.

All the above specimens are from Sandford Hill, Somerset, and are preserved in the Taunton Museum.

a. Vertebrarterial canal.
b. Neural spine.
c. Neural canal.
d. Odontoid process.
e. Anterior articulating surface for atlas.
f. Pre-zygapophysis.
g. Post-zygapophysis.
h. Transverse process.
i. Foramen for exit of spinal nerve.



J.Green del. lith et imp

URSUS.
Vertebræ.

PLATE VIII.

Pleistocene Bears.

(*Vertebræ.*)

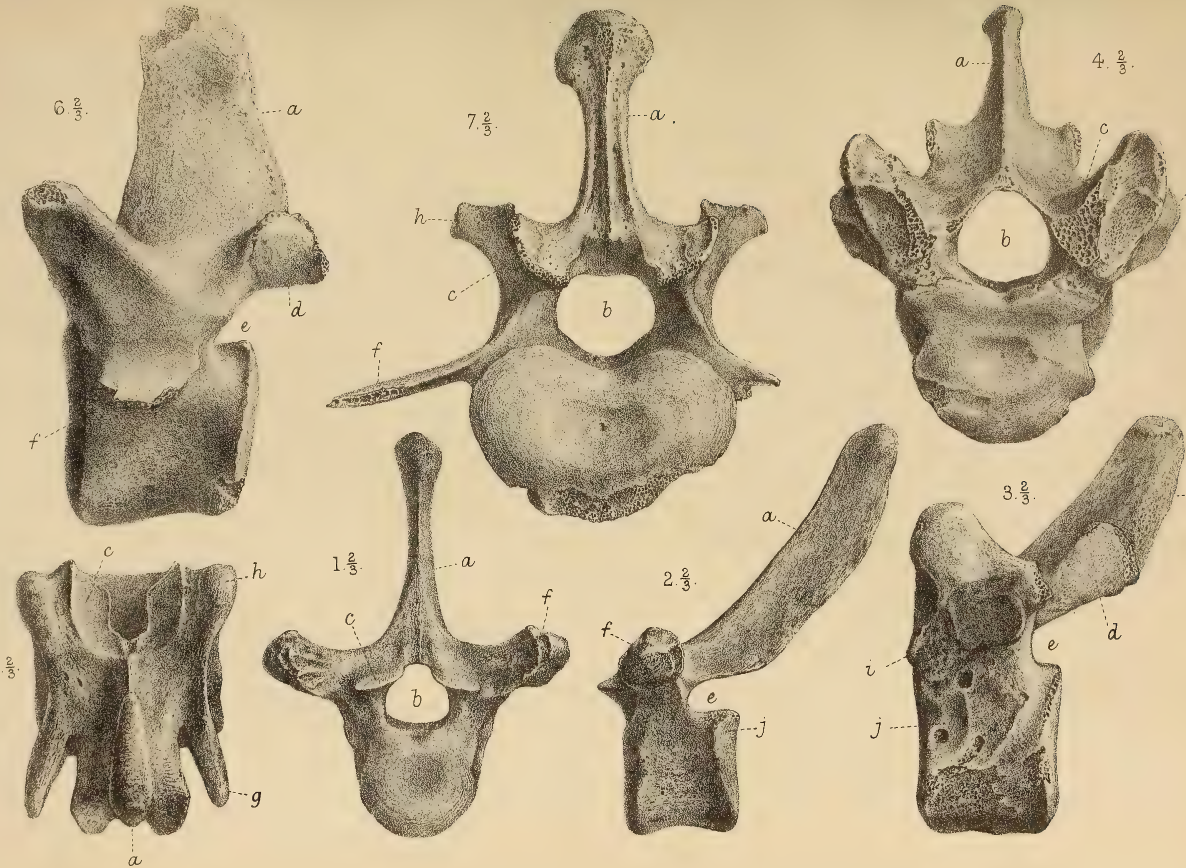
(Two thirds natural size.)

Fig.

1. Third thoracic, front view.
2. Fifth thoracic, left side view.
3. Twelfth thoracic, left side view.
4. Twelfth thoracic, front view.
5. Fourteenth thoracic, dorsal view.
6. Third lumbar, left side view.
7. Third lumbar, front view.

Figs. 1, 2, and 5 are drawn from vertebræ found in the peat at Burwell Fen, and now preserved in the Sedgwick Museum, Cambridge; the others are from Sandford Hill, and are preserved in the Taunton Museum.

a. Neural spine.
b. Neural canal.
c. Pre-zygapophysis.
d. Post-zygapophysis.
e. Notch for exit of spinal nerve.
f. Transverse process.
g. Anapophysis.
h. Metapophysis.
i. Facet for articulation with tubercle of rib.
j. Facet for articulation with head of rib.



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Vertebræ.

Palæontographical Society, 1909.

A MONOGRAPH

OF THE

BRITISH PLEISTOCENE MAMMALIA

VOL. II, PART III.

THE CANIDÆ.

BY

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MONOGRAPH

ON

THE BRITISH MAMMALIA

OF THE

PLEISTOCENE PERIOD.

THE CANIDÆ.

Order—CARNIVORA.

Family—CANIDÆ.

Genus—Canis.

I. HISTORICAL INTRODUCTION.

At the commencement of a previous memoir dealing with the Pleistocene [1] bears reference was made to the difficulty which the study of those animals presented owing to the practical impossibility of coming to a satisfactory conclusion with regard to the mutual relationship of the various species and varieties. That difficulty presents itself in perhaps an even more marked form in the case of the Canidæ.

The earliest reference to the existence of fossil Canidæ is Esper's [2] account (1774) of the finding of bones in the cave at Gailenreuth which he recognised as those of wolf. Rosenmüller [3] (1794), in a pamphlet written in Latin and dealing principally with the fossil bears, stated that bones of dogs and foxes, as well as of wolves, had been found in caves, but considered that the bones of foxes were intro-

[1] The terms "Pleistocene" and "Prehistoric" are used in the following pages in the sense as defined by Dawkins and Sanford, 'Monograph of the British Pleistocene Mammalia,' vol. i, p. 7.

[2] 'Ausführliche Nachricht—Zöolithen Bayreuth.'

[3] 'Quædam de Ossibus fossilibus animalis,' Leipzig, p. 27.

duced by diluvial action, and were not contemporaneous with the associated bear and hyæna bones. The earlier writers were disposed to doubt the identity of the canine bones found in caves with those of living species. Thus Goldfuss, who in 1810 had figured [1] the skull of a wolf from Müggendorf, when describing thirteen years later [2] (1823) a wolf's skull from Gailenreuth, regarded it as specifically distinct from *Canis lupus*.

Cuvier,[3] too (1812 and 1825), was apparently disposed to regard the wolf remains in his possession as specifically distinct from the modern species. He made further comparisons of the skeletal characters of wolves and dogs, and agreed with Daubenton [4] (1758) in recognising the extreme difficulty in distinguishing between the skull of a wolf and that of a dog.

The first author to express himself decisively as to the identity of the fossil remains of the wolf with those of the living species was Schmerling [5] (1833) in his description of bones from the caverns of Liège. M. de Serres, Dubrueil, and Jeanjean [6] (1839), though not expressing themselves very definitely, attributed the canine bones found in the caves of Lunel Viel to the living species.

The question as to the specific identity of the recent and fossil species was, however, fully considered by de Blainville [7] (1844), who, in his 'Ostéographie,' discussed and summarised all the evidence, strongly supporting the view that no distinction could be drawn between the wolves, dogs, and foxes of the caves and those living at the present day.

Owen, too, in his 'British Fossil Mammals and Birds'[8] (1846), in which a full account of the fossil Canidæ was given, agreed that "the wolves which our ancestors extirpated were of the same species as those which . . . left their bones in the limestone caverns . . ."

Since then almost all zoologists who have considered the subject have agreed as to the specific identity of the fossil remains of the wolf with those of the living species, but Pomel (1854) and Bourguignat as lately as 1875 maintained the contrary view, the latter author retaining the name *Canis spelæus* of Goldfuss for the fossil wolves of the caverns.

Meanwhile the bones of wolf and fox had been described from many British caves, such as Kirkdale (Buckland,[9] 1822), where, however, they were very scanty,

[1] 'Die Umgebungen von Müggendorf' (Erlangen).

[2] 'Saügethiere der Vorwelt,' p. 451.

[3] 'Oss. Foss.,' tom. iv, iv, pp. 5—9 (1812), and ibid., ed. 3, tom. iv, pp. 457—467 (1825).

[4] In Buffon's 'Histoire Naturelle,' tom. vii, p. 53.

[5] 'Recherches sur les Ossemens fossiles des Cavernes de Liège,' tom. ii, pp. 22—46.

[6] 'Recherches Oss. humatiles des Cavernes de Lunel Viel,' pp. 72—74.

[7] 'Ostéographie—Carnassiers,' pp. 101—104.

[8] 'British Fossil Mammals and Birds, p. 132.

[9] 'Phil. Trans.,' cxii, p. 182.

Paviland (Buckland,[1] 1824), Oreston (Clift and Whidbey,[2] 1823), Banwell (Rutter,[3] 1829), Yealm Bridge, Devon (Bellamy,[4] 1839). Buckland, in the 'Reliquiæ Diluvianæ'[5] (1824), gives a table showing that these animals had been recognised in various other Pleistocene deposits, both in Britain and on the continent.

The question as to the specific identity of the fossil Canidæ of the caves with those living at the present time being settled, the far more difficult one concerning the mutual relationship of the wolves, jackals, and dogs occupied attention. This question had, as has been already mentioned, been considered by Cuvier and Daubenton. It was fully discussed in 1844 by de Blainville,[6] who went beyond those anatomists in being unable to recognise any osteological distinction between dogs and wolves, and by Pictet[7] (1853), who was the earliest author to suggest as the origin of the domestic dogs, not any known species of *Canis* living or fossil, but an unknown species assumed to have existed in Pleistocene times.

Between 1859 and 1885 appeared a long series of papers dealing with the Pleistocene and Prehistoric Canidæ of Ireland, which were described from the following localities: Dunshaughlin, co. Meath (Wilde,[8] 1859, dog); Shandon, co. Clare (Adams,[9] 1879, wolf and fox); Knockninny, co. Fermanagh (Haughton,[10] 1876, wolf, dog, fox); Ballynamintra, co. Waterford (Adams,[11] 1881, wolf, dog); Knockmore, co. Fermanagh (Ball,[12] 1885, wolf). More recent are the records from Kesh, co. Sligo (Scharff, 1903, wolf, dog, fox), and Edenvale, co. Clare (Scharff, 1906, wolf, dog, fox, Arctic fox).

At Shandon and Kesh it is probable that deposits of both Pleistocene and Prehistoric date occur. At all the other Irish localities in the above list it is probable that the remains belong solely to the Prehistoric period.

Other important records of Pleistocene canine remains are those of Kent's Cavern, Torquay (MacEnery,[13] 1859, wolf, fox), Wookey Hole near Wells (Dawkins,[14] 1862 and 1863, wolf, fox), Creswell Crags, Derbyshire (Busk,[15] 1875, wolf, fox, Arctic fox). The occurrence of the Arctic fox in Britain had not been previously noted. The records from Norwich (Denny,[16] 1859, dog) and from

[1] 'Reliquiæ Diluvianæ,' p. 85.
[2] 'Phil. Trans.,' cxiii, p. 88.
[3] 'Delin. Co. Somerset,' p. 156.
[4] 'Nat. Hist. S. Devon.' Bellamy's account is reproduced by Pengelly in his paper on "The Literature of the Caverns near Yealmpton, S. Devon," 'Trans. Devon. Assoc.,' iv, 1871, p. 92.
[5] 'Reliquiæ Diluvianæ,' facing p. 1.
[6] 'Ostéographie—Carnassiers,' pp. 101—104.
[7] 'Traité de Paléontologie,' tom. i, p. 202.
[8] 'Proc. Roy. Irish Acad.,' vii, p. 193.
[9] 'Trans. Roy. Irish Acad.,' xxvi (Sci.), p. 227.
[10] 'Proc. Roy. Irish Acad.,' (2), ii (Sci.), p. 482.
[11] 'Trans. Roy. Dublin Soc.' (2), i, p. 205.
[12] Ibid. (2), iii, p. 335.
[13] 'Cavern Researches.'
[14] 'Quart. Journ. Geol. Soc.,' xviii, p. 124; and xix, p. 267.
[15] Ibid., xxxi, pp. 684—687.
[16] 'Proc. Yorks. Geol. Polyt. Soc.,' iii, p. 538.

Burrington Combe, Somerset (Dawkins,[1] 1864, wolf, fox), are of Prehistoric, not Pleistocene remains.

More recent are Newton's[2] account (1894) of the fauna of the Ightham fissure near Maidstone, in which the Arctic fox was again met with, and Newton and Arnold Bemrose's[3] account (1905) of the Hoe Grange Cave, Derbyshire, where scanty remains of the wolf and common fox were found.

More comprehensive records are those of Falconer[4] (1868), who showed that bones of both wolf and fox had been recognised in all eight of the Gower caves, and Dawkins[5] (1869), who, in his well-known paper on the 'Distribution of the British Post-Glacial Mammals,' gives a long list of localities for canine bones.

Much additional information with regard to both the Pleistocene and Prehistoric Canidæ is contained in Dawkins and Sanford's introduction to their Memoirs on the British Pleistocene Mammalia (Palæontographical Society, 1866). Harting's 'Extinct British Animals,' published in 1880, though chiefly concerned with the wolf during the historic period, has some account of its occurrence in Britain in Pleistocene and Prehistoric times, and adds some further localities[6] to Dawkins' list. Pennington's 'Notes on the Barrows and Bone Caves of Derbyshire' (1877), though treating the subject in a more or less popular fashion, contains some further information.

During the middle and latter part of the last century, too, the question of the mutual relationship of the Canidæ was not left unconsidered, being discussed by Rütimeyer[7] (1862), Jeitteles[8] (1872 and 1877), and Bourguignat[9] (1875), while more recently the subject has been taken up by Huxley[10] (1880), Woldrich[11] (1881 and 1886), Lydekker[12] (1884), von Pelzeln[13] (1886), Wilckens[14] (1886), Nehring[15] (1888), Boule[16] (1889), Vieira[17] (1894), Gaudry and Boule[18] (1892), Studer[19] (1902)

[1] 'Proc. Somerset. Arch. and Nat. Hist. Soc.,' xii, pp. 161—176.

[2] 'Quart. Journ. Geol. Soc.,' l, pp. 201—203.

[3] Ibid., lxi, pp. 49 and 50.

[4] 'Pal. Mem.,' ii, p. 525.

[5] 'Quart. Journ. Geol. Soc.,' xxv, p. 192.

[6] Op. cit., p. 118.

[7] 'Untersuchung der Tierreste aus Pfahlbauten der Schweiz' (1862).

[8] 'Mittheil. d. anthropol. Gesell. in Wien,' ii, p. 169 (1872), and 'Die Stammväter unserer Hunderassen' (1877).

[9] 'Ann. des Sciences Géol.,' vi, p. 33.

[10] 'Proc. Zool. Soc.,' 1880, pp. 238—288.

[11] 'Mittheil. der anthropol. Gesell. in Wien' (1881), xi, and 'Anz. Akad. Wien' (1886), p. 12.

[12] 'Palæont. Indica,' ser. 10, vol. ii, p. 240.

[13] 'Zool. Jahrbuch,' i, pp. 225—240.

[14] 'Biol. Centralbl.,' v, pp. 719 and 751.

[15] 'Naturwissenschaft. Wochenschrift,' ii.

[16] 'Comptes Rend.,' cviii, p. 201.

[17] 'Ann. Sci. Nat. Porto,' i, p. 109.

[18] 'Mat. pour l'Hist. des Temps quatern.,' fasc. iv, pp. 123—129.

[19] 'Abh. schweiz. pal. Ges.,' xxviii, art. 1 (1902).

and Keller[1] (1903). A very brief summary of their several conclusions is given subsequently when dealing with the mutual relationship of the Pleistocene and Prehistoric Canidæ.

II. DISTRIBUTION IN BRITAIN.

Although this memoir is, strictly speaking, only concerned with the Pleistocene Canidæ, when the range of a species extends into other strata, whether pre- or post-Pleistocene, brief reference must be made to such remains as occur.

The Wolf (*Canis lupus*[2]).

The oldest British formation in which the remains of the wolf have been found is the Red Crag. Owen,[3] in 1856, first noted their occurrence in British Pliocene deposits, describing certain teeth from Woodbridge, which he attributed, with some hesitation, to this species. Newton[4] (1891) described two canine teeth from the Red Crag of Boyton, which he believed to be those of the wolf. Owen also identified a humerus from the Forest Bed, but Newton remarks that it is very doubtful whether there is evidence of the wolf being represented at this horizon. The bone in question is now preserved in the Museum of the Geological Survey at Jermyn Street, London. These scanty records comprise the whole evidence for the occurrence of the wolf in Britain in pre-glacial times.

During Pleistocene times, however, wolves abounded throughout England, their remains having been found in nearly every bone-cave of this period (see list, p. 10) and in many river deposits,[5] etc.

There have been comparatively few records of the wolf from Scotland, this probably being largely due to the lack of caves and deposits suitable for the preservation of the bones. This explanation will not, however, account for the scarcity and generally fragmentary condition of the wolf-bones found in Ireland. Fragmentary bones were recorded by Adams[6] from the Shandon Cave, where they were associated with the Mammoth and were clearly of Pleistocene age, and in

[1] 'Vierteljahrschr. Ges. Zürich,' xlviii.

[2] It has been thought desirable, following Flower and Lydekker ('An Introduction to the Study of Mammals, Living and Extinct,' p. 546), to include wolves, jackals, dogs, and foxes in the old comprehensive genus *Canis*.

[3] 'Quart. Journ. Geol. Soc.,' xii, 1856, p. 227.

[4] 'Vertebrata of the Pliocene Deposits of Britain,' p. 8.

[5] The lengthy account of the wolf in Harting's 'Extinct British Animals' is mainly concerned with its distribution in historic times.

[6] 'Trans. Roy. Irish Acad.,' xxvi (Sci.) (1879), p. 221.

recent years they have been recorded by Scharff[1] from the prehistoric caves of Edenvale, co. Clare, and from those of Kesh, co. Sligo, which yielded remains referable in all probability to both the Pleistocene and Prehistoric periods.

Bones of the wolf have also been found in Prehistoric deposits at Knockninny[2] and Knockmore,[3] co. Fermanagh, and bones somewhat doubtfully referable to the wolf at Ballynamintra,[4] co. Waterford; but with these exceptions no wolf-bones have been recorded from Irish Prehistoric deposits, a somewhat remarkable fact in view of its great abundance in Ireland in historic times.[5]

The Dog (*Canis familiaris*).

Owing to the frequent references to the bones of dogs in various papers dealing with the Irish Mammalian remains some allusion must be made to them here, though it is at least doubtful whether any animal that could be called a dog existed in the British Isles in Pleistocene times.

Owen[6] admits the dog to the number of his British fossil mammals, but does not describe any British specimens. The dog is not included by Dawkins[7] in his table showing the distribution of British post-glacial mammals, and is not mentioned by Lydekker in his 'Catalogue of the Fossil Mammalia in the British Museum.' Woodward and Sherborn[8] admit it among the British fossil vertebrates, but (?) Prehistoric deposits at Norwich and Walthamstow are the only occurrences in Great Britain to which they allude. Skulls attributed as a rule, owing to the length and slender character of the muzzle, to the large extinct Irish wolf-hound, have been repeatedly referred to by writers on Irish mammals. Wilde[9] (1859) described examples from near Dunshaughlin, co. Meath; Haughton[10] (1876) referred to the occurrence of the dog in Knockninny cave near Lough Erne; Adams[11] (1880) and Ball[12] (1885) referred to the skulls described by Wilde, and agreed with him in attributing them to dogs; and Adams[13] (1881) described slender mandibles from

[1] 'Trans. Roy. Irish Acad.,' xxxii, B., pt. 4 (1903), p. 201, and xxxiii, B., pt. 1 (1906), p. 43.

[2] 'Proc. Roy. Irish Acad.' (2), ii (Sci.), 1876, p. 482.

[3] 'Trans. Roy. Dublin Soc.' (2), iii, 1885, p. 335.

[4] Ibid. (2), i, 1881, p. 205.

[5] See Adams, 'Proc. Roy. Irish Acad.' (2), iii, 1878, p. 99; and Scouler, 'Journ. Geol. Soc. Dublin,' i, 1838, p. 225.

[6] 'Brit. Foss. Mammals and Birds,' p. 133.

[7] 'Quart. Journ. Geol. Soc.,' xxv, 1869, p. 192.

[8] 'A Catalogue of British Fossil Vertebrata,' 1890, p. 324.

[9] 'Proc. Roy. Irish Acad.,' vii, 1859, p. 194.

[10] Ibid. (2), ii (Sci.), 1876, p. 482.

[11] 'Sci. Proc. Roy. Dublin Soc.,' ii, 1880, p. 66.

[12] 'Trans. Roy. Dublin Soc.' (2), iii, 1885, p. 340.

[13] Ibid. (2), i, 1881, p 205.

Ballynamintra cave, co. Waterford, which he attributed to the Irish wolf-hound. There can be little doubt that all these are of post-Pleistocene date, and belong to the Prehistoric period.

Numerous bones, clearly of dogs, have been found in peat and other Prehistoric deposits in many parts of Great Britain, especially in the alluvium of the lower part of the Thames valley.

The Fox (*Canis vulpes*).

The occurrence of the fox in the Red Crag is well authenticated, a well-preserved palate from Boyton in Suffolk having been figured and described by Lydekker.[1] He gives measurements showing that its size considerably exceeds that of a full-grown recent specimen, but in spite of this concludes that the specimen is to be referred to the fox—an opinion in which he is supported by Newton.

The evidence for the occurrence of the fox in the Forest Bed is not very good. It is based on part of a humerus which Newton[2] hesitated to refer to the fox. Lydekker, however, thought that the specimen was correctly referred to this species.

From Pleistocene times onwards the distribution of the fox throughout the British Isles has been practically universal. In the cavern deposits its distribution shows a remarkable correspondence with that of the wolf (see Table, p. 10).

The Arctic Fox (*Canis lagopus*).

As yet the remains of the Arctic fox have been recognised at only a very few localities in Britain. The earliest record is that of Busk[3] (1875), who found among the bones from the rock fissures of the Creswell Crags an axis vertebra which he carefully described and figured, referring it to the Arctic fox on account of (1) its small size; (2) the slenderness and abrupt divergence of the transverse processes; (3) the prominence of the median keel on the ventral surface of the centrum; (4) a difference in the form of the anterior articular facets from those in the common fox.

The second record is by Newton,[4] from the Ightham fissure near Maidstone. Newton figured and ascribed to the Arctic fox a femur, a tibia, a humerus, a mandibular ramus, and part of the upper jaw. Many other bones of the Arctic fox from the same locality are in the collections of Dr. F. Corner, of Poplar, and

[1] 'Geol. Mag.,' dec. iii, i, 1884, p. 443.
[2] Ibid., dec. ii, vii, 1880, p. 152.
[3] 'Quart. Journ. Geol. Soc.,' xxxi, 1875, pp. 685—687.
[4] Ibid., l, 1894, p. 202, pl. xii, figs 5—9.

Mr. W. J. Lewis Abbott, of St. Leonard's (see Pls. V and VI, and Text-figs. 1—7). In the same paper by Newton a reference is made to a skull belonging to Dr. H. P. Blackmore, of Salisbury, who obtained it in 1875 from the brick earth of Fisherton, near Salisbury, where it was associated with the following Arctic animals [1]: *Lepus variabilis* (the mountain hare), *Microtus nivalis*, *Myodes torquatus* (the lemming), *Ovibos moschatus* (the musk ox), and *Rangifer tarandus* (the reindeer). The reindeer was also found associated with the Arctic fox at Creswell Crags and Ightham, and Newton [2] is further of opinion that certain vertebræ and other bones from a small cave at Walton near Clevedon are to be attributed to the Arctic fox; here the presence of another arctic animal, the lemming, is indicated. The only record of the occurrence of the Arctic fox in Ireland is contained in Scharff's [3] account of the Newhall cave, Edenvale, co. Clare, where a jaw clearly to be attributed to this species was met with. Here again it was associated with the reindeer and lemming.

Skeletal Differences between the Common and Arctic Foxes.

The common fox is, as a rule, very considerably larger than the Arctic fox, but as small individuals may occur this difference is not always a safe criterion. There are, however, many differences in the skull. The skull of the common fox is the larger, and has the length of the jaws relatively greater in proportion to the size of the cranium, and hence the anterior premolars are more widely spaced than in the Arctic fox. On the other hand, the cranium of the common fox is somewhat narrower in proportion to its length than that of the Arctic fox, especially just behind the post-orbital processes. These tend to be longer in the common fox than in the Arctic fox. Scharff mentions that the length of $\overline{\text{m. } 2}$ is somewhat greater in the common fox than in the Arctic fox, but this difference seems scarcely appreciable in the British Museum specimens.

? Lycaon anglicus, Lyd.

This name is applied by Lydekker [4] to a left mandibular ramus from the Sprit-sail Tor cave, Gower, which was originally described and figured by Falconer [5] under the name of "hyænoid wolf." The specimen was subsequently fully des-

[1] "The Geology of the Country around Salisbury," 'Mem. Geol. Surv. of England and Wales,' 1903, p. 68.

[2] 'Proc. Bristol Nat. Soc.,' 4th ser., i, pt. 3, p. 186, 1907 (issued for 1906).

[3] 'Trans. Roy. Irish Acad.,' xxxiii, B., pt. 1, p. 48.

[4] 'Geol. Mag.,' dec. iii, i, 1884, p. 443.

[5] 'Pal. Mem.,' ii, pl. xxxvi, figs. 1, 2.

cribed by Lydekker[1] in his 'Catalogue of the Fossil Mammalia in the British Museum.' The feature upon which he principally relies in the attribution of this specimen to the genus *Lycaon* is the presence of a "distinct anterior talon" to the fourth premolar. There is no doubt that an anterior cusp is very distinctly present in this specimen (see Pl. V, figs. 7, 8); and in a large series of wolf-skulls in the British Museum no specimen was found showing any comparable development, though in certain cases, *e. g.* the skull of a wolf from Kandahar (168a) and a North American example (165d), slight indications of an anterior cusp occur. But on the other hand $\overline{\text{pm. 2 and 3}}$ of the Spritsail Tor specimen are identical with those of the wolf, being considerably longer in proportion to the height of the crown than are the corresponding teeth in any of the skulls of *Lycaon* examined in the British Museum; $\overline{\text{pm. 4}}$, too, agrees precisely in the characters of its main lobe and posterior cusps with the corresponding tooth of the wolf, and differs considerably from the *Lycaon* type. In view of the known variability in the teeth of Canidæ and of the difficulties of geographical distribution involved in the addition of a southern form like *Lycaon* to the British faunal list, it seems the most satisfactory course, on the whole, to regard the Spritsail Tor specimen as a somewhat abnormal wolf.

TABLE SHOWING DISTRIBUTION OF BRITISH PLEISTOCENE CANIDÆ IN RIVER DEPOSITS, ETC.

	Wolf.	Fox.	Arctic Fox.
Beilbecks, Yorks	×	...	...
Bracklesham, Sussex	×	...	...
Crayford	×	...	...
Dartford	...	×	...
Fisherton, Salisbury	×	×	×
Grays	×	×	...
Ilford	×	...	...
Ipswich	×	×	...
Murston, Sittingbourne	×	...	...
Newbury	×	...	...
Slade Green, near Erith	×	...	...
Tewkesbury	×	...	...
Thame	×	...	...
Weston-s.-mare	...	×	...
Windsor	×	...	...

[1] 'Catalogue of the Fossil Mammalia in the British Museum,' pt. i, p. 122, 1885.

TABLE SHOWING DISTRIBUTION OF BRITISH PLEISTOCENE CANIDÆ IN CAVERNS.

	Wolf.	Fox.	Arctic Fox.
Anstey's Cave, Torquay	...	×	...
Bacon Hole, Gower	×	×	...
Banwell	×	×	...
Bench Cave, Brixham	×	×	...
Bleadon	×	×	...
Bosco's Hole, Gower	×	×	...
Cae Gwyn, Clwyd Vale	×	...	...
Caswell Bay, Gower	...	×	...
Cefn, near St. Asaph	×	...	...
Creswell Crags, Derbyshire	×	×	×
Crow Hole, Gower	×	×	...
Deborah Den, Gower	×	...	...
Ffynnon Beuno, Clwyd Vale	×	×	...
Durdham Down	×	×	...
Hoe Grange, near Longcliff, Derbyshire	×	×	...
Hutton	×	×	...
Ightham Fissure near Maidstone	×	×	×
Kent's Cavern, Torquay	×	×	...
Kirkdale	×	×	...
Langwith Bassett, near Mansfield	×	×	...
Long Hole, Gower	×	×	...
Minchin Hole, Gower	×	×	...
Oreston	×	×	...
Paviland, Gower	×	×	...
Pleasley Vale, Derbyshire	×	...	...
Ravenscliff, Gower	×	×	...
Sandford	×	×	...
Shandon Cave, Dungarvon	×	×	...
Spritsail Tor, Gower	×	×	...
Teesdale	×	...	...
Torbryan, Torquay	×	×	...
Uphill	×	×	...
Walton, near Clevedon	×	×	×
Waterhouses, Staffordshire	×	...	...
Windy Knoll, Castleton	×	×	...
Wookey Hole	×	×	...
Yealm Bridge	×	×	...

III. DESCRIPTION OF THE REMAINS.

The Canidæ[1] comprise the only family of the section Cynoidea, the second of the three into which the Carnivora Vera are divisible. With regard to the dentition they show less specialisation than any other group of living Carnivora, and in other respects approach relatively near to the primitive type. The structure of the auditory bulla and adjacent parts of the skull is intermediate in character between that of the Æluroidea and that of the Arctoidea, as the Cynoidea agree with the Æluroidea in having the auditory bulla inflated and the paroccipital process of the

[1] See Flower and Lydekker, 'Mammals, Living and Extinct,' p. 544, *et seq.*

exoccipital in contact with it, while they agree with the Arctoidea in the almost complete absence of a septum dividing the auditory bulla, in the large size of the glenoid foramen, and in the presence of an alisphenoid canal. In the living forms there is no entepicondylar foramen. The upper molars have a triangular crown, and the blade of the upper carnassial consists of two lobes.

A. The Skull (Plates I—IV).

The cranium is moderately elongated, the jaws long, tapering, and somewhat compressed. The zygomatic processes of the frontal and malar are short, so that the orbit communicates widely with the temporal fossa. The pterygoid has a well-developed hamular process. The auditory meatus forms a short but fairly prominent bony tube.

The following are characters upon which most stress has been laid in attempting to discriminate between the skulls of wolves, dogs and foxes:

(1) The relative proportions of the jaws and cranium;

(2) The extent to which the temporal ridges, always widely separate in young animals, approach and coalesce into a sagittal crest in the adult;

(3) The greater or less backward extension of the nasals;

(4) The character of the post-orbital process of the frontal;

(5) The union of the nasal processes of the frontals with the ascending processes of the premaxillæ, or the separation of these processes from one another by the meeting of the maxillæ and nasals;

(6) The length of $\underline{\text{pm. 4}}$ as compared with that of $\underline{\text{m. 1 and 2}}$ taken together;

(7) The orbito-frontal angle or the obliquity of the opening of the orbit to the brow.

B. Dentition (Plate V).

(1) *Distinctive Features of the Teeth in the Genus Canis.*—The typical dental formula is i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{4}$, m. $\frac{2}{3}$, as in *Ursus*, but in aberrant forms (*Cyon*) the molars are $\frac{2}{2}$, and in a fossil form, *Canis* (*Lycorus*) *nemesianus*, the premolars are $\frac{4}{3}$. Further, in *Canis cancrivorus* the missing last upper molar is occasionally present. The formula embracing these variations is i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{3-4}$, m. $\frac{2-3}{2-3}$.

The contrast in size between the canine and incisor teeth is not so great as in either cats or bears. The upper carnassial tooth, $\underline{\text{pm. 4}}$, differs from that in bears, and resembles that in cats and hyænas in possessing an antero-internally placed inner tubercle supported by a distinct root.

In accordance with the method adopted in previous memoirs it has been

(1) TABLE OF COMPARATIVE MEASUREMENTS OF CANINE SKULLS.

	C. lupus, recent, Yesso, No. 86.11.18.1. (Brit. Mus.).	*C. lupus*, Pleistocene, Kent's Cave, Torquay (Torquay Mus.).	*C. lupus*, Pleistocene, Banwell Cave, No. 44640 (Brit. Mus.).	*C. lupus*, Pleistocene, Hutton Cave, No. 44739a (Brit. Mus.).	*C. sp.*, Prehistoric, peat, Denver, Norfolk (Sedgwick Mus.).	*C. familiaris*, Prehistoric, turbary, Walthamstow, No. 41439 (Brit. Mus.).	*C. familiaris*, Prehistoric, Bawdsey bog, Suffolk, No. 27508 (Brit. Mus.).	*C. vulpes*, recent, Villa-marique, No. 95.9.4.7 (Brit. Mus.).	*C. vulpes*, Prehistoric, peat, Newbury, No. 44777 (Brit. Mus.).	*C. vulpes*, Pleistocene, Ightham, near Maidstone (Lewis Abbott Coll.).	*C. lagopus*, recent, Kam-skatcha, No. 88.2.20.8 (Brit. Mus.).	*C. lagopus*, Pleistocene, Ightham, near Maidstone (Lewis Abbott Coll.).
1. Length from intercondylar notch to anterior end of skull	23·6	22·0*	21·3*	20·9*	21·65	17·1	16·8	14·4	14·5	12·35*	12·2*	10·1*
2 Extreme width across zygomatic arches	15·05	...	...	12·5	13·15	10·65	11·55	8·4	9·0	...	7·25	7·2
3. Vertical height from suture between basi-occipital and basi-sphenoid to top of sagittal crest	7·3	7·55	7·35	6·7	6·6	6·45	5·9	4·1	4·9	4 6	3·9	3·45
4. Width at lachrymal foramen	5·8	5·8	4·85	...	5·45	4·75	4·4	3·5	3·55	3·05	3·2	2·6
5. Width between ends of post-orbital processes of frontal	6·75	6·35	4·8	5·6	7·15	4·95	5·8	4·0	4·6	3·55	3·5	2 95
6. Width below foramen lacerum anterius	1·15	1·18	...	1·1	1·2	1·25	1·5	·9	·95	·85	·85	·65
7. Transverse measurement across occipital condyles	4·55	4·85	4·5	4·2	4·6	3·9	3·9	2·7	3·1	2·6	2·5	2·2
8. Transverse measurement across external auditory meatus	7·7	...	6·7	7·2	7·4	6·0	6·3	4·25	4·7	4·4	4·2	3·7
9. Transverse diameter of foramen magnum	2·3	2·05	...	...	1·95	2·0	1·8	1 6	1·65	1·5	1·5	1·3
10. Length of palate	13·2	12·85	...	...	...	9·8	9·65	8·1	...	6·8	6·7	5·6
11. Orbito-frontal angle	40†	...	42†	45†	53†	48†	47†	...	...	...	...	...
12. Maximum length of mandibular ramus measured to end of condyle	20·55	...	...	17·4	18·1	12·3	...	11·7	9·8*†	8·15*†	9·55	...
13. Height from angle to top of coronoid process	8·05	...	...	...	7·25	4·2	...	4·0	3·5	3·2	3·7	...

* Figured. † It is uncertain whether these mandibles belong to the crania.

Note.—All measurements are given in centimetres.

thought best when describing the teeth not to use terms involving assumptions of homology and requiring long explanatory prefixes. The terms "cusp" and "tubercle" are regarded as synonyms for small elevations of the surface of a tooth. The term "cone" is used as denoting a rather larger elevation, and the terms "talon" or "heel" for posteriorly-placed segments of a tooth.

(2) *Permanent Dentition of the Upper Jaw in Canis lupus* (Pl. V).—In drawing up the following description, the skulls and teeth of a number of wolves, recent and fossil, now preserved in the British Museum have been examined, but the principal part of the description is based on a skull of a male wolf from Pekin, No. 90.7.8.2 in the British Museum collection.

I. 1 and 2 are very similar teeth, differing only in the slightly larger size of i. 2. The principal cone is somewhat recurved and there are small laterally-placed accessory cusps. The cingulum is rather strongly marked. In some cases the lateral accessory cusps are scarcely noticeable, but the cingulum is raised into slight cusps posteriorly. The root is about three times as long as the crown and is much laterally compressed.

I. 3 is a rather larger and more caniniform tooth than i. 1 and 2 and shows some variability, the postero-internal face being sometimes marked by a cingulum, sometimes raised into a pair of laterally-placed cusps. The root is about twice as long as the crown and is triangular in cross-section, not laterally compressed as in i. 1 and 2.

C. The canine has the form usual in the Carnivora. Its crown constitutes about two thirds of its length.

Pm. 1 is a small, single-rooted tooth with a fairly well-marked cingulum surrounding the principal cone. Very slight accessory cusps may be developed on the cingulum posteriorly and antero-internally.

Pm. 2 is a larger and more elongated two-rooted tooth with a conical crown triangular in outline. A posteriorly-placed cusp may be present or absent.

Pm. 3 closely resembles pm. 2, differing only in its larger size and in the greater prominence of the posterior cusp, which may be double.

Pm. 4, the upper carnassial, is a large three-rooted tooth with a powerful trenchant blade divided into an anterior more conical portion and a posterior portion with a chisel-like edge. Placed anteriorly is a low inner tubercle supported by a distinct root.

M. 1. This is a large tooth, somewhat wider than long. The outer portion of the crown is formed by two prominent cones of which the anterior is the larger; the inner portion of the tooth is much depressed, but the inner edge is raised into a more or less prominent ridge and two low cusps lie between this and the outer portion of the tooth. Two roots support the outer portion, and a third and stouter root the inner portion.

M. 2 is a considerably smaller tooth than m. 1 but is constituted on the same plan, having two relatively prominent cones or cusps on the outer part of the tooth, and a depressed inner area bearing several slight cusps. Two roots support the outer portion of the tooth, a third and larger root the inner portion.

(3) *Permanent Dentition of the Lower Jaw of Canis lupus* (Pl. V).—I. 1, 2 and 3 are all very similar teeth, differing only by their progressive increase in size, and in the fact that while i. 1 and 2 have the root strongly laterally compressed i. 3 has it more or less triangular in section. Each tooth has a somewhat chisel-shaped edge with a small accessory cusp placed externally to the main cone.

C. This tooth is of the usual type and differs from c. only in the fact that the inner border tends to be rather more sharply curved.

Pm. 1, which is sometimes wanting, is a small single-rooted tooth with a simple conical blade, bearing, as a rule, a very slight cusp posteriorly placed.

Pm. 2, 3, 4 are very similar two-rooted teeth each with a triangular blade, which in pm. 3 and 4 may be slightly recurved. There is a slight cusp posteriorly placed in pm. 2, and this becomes larger in pm. 3 and 4. The cingulum is well marked on the inner surface of the teeth, and in pm. 3, and more often in pm. 4, may give rise to a second posteriorly-placed cusp. In some cases each of these teeth bears a slight cusp anteriorly placed.

M. 1. This is a large tooth supported by two stout roots. The anterior two thirds is formed by the powerful bilobed blade, the posterior lobe being slightly the larger and having a small cusp placed postero-internally. The last third of the tooth forms a depressed talon or heel and bears two cusps placed side by side, the outer one being somewhat the larger.

M. 2 is a rather small, somewhat oblong tooth supported by two roots. The anterior part of the crown bears a pair of cusps placed side by side, while a third cusp lies postero-externally. In some cases there are indications of a fourth cusp placed postero-internally.

M. 3 is a very small one-rooted tooth with a nearly oval crown bearing one or more slight cusps.

(4) *Milk or Deciduous Dentition* (Pl. V).[1]—The formula for this is d.i. $\frac{3}{3}$, d.c. $\frac{1}{1}$, d.m. $\frac{3}{3} = 28$.

The first permanent premolar has no milk predecessor.

(A) *Milk Dentition of the Upper Jaw.*—D.i. 1, 2 and 3. These are all small and extremely simple teeth with short crowns and long, somewhat tapering roots.

D.c. is a reduced representative of the permanent tooth and requires no special description.

[1] The description is drawn up from a made-up set of milk-teeth of *Canis ? lupus* from Torbryan, Torquay, now in the British Museum.

D.m. 1 is a good deal like pm. 2, the blade having a principal cone and often a slight posteriorly-placed accessory cusp. The two teeth differ, however, in the fact that d.m. 1 has the roots strongly divergent.

D.m. 2, the milk carnassial, is the largest of the deciduous teeth. The major portion of the crown is formed by a powerful bilobed blade, of which the anterior lobe is conical, the posterior more depressed and chisel-like. In front of the blade are two low cusps. There is further a prominent inner cusp anteriorly placed. This is supported by a special root, and two other strong roots support the outer part of the tooth.

D.m. 3 is a very irregular tooth. The outer edge, which bears certain ill-defined cusps, is raised anteriorly and supported by a small root, while posteriorly it is depressed and supported by a strong triangular, divergent root. There is an inner cusp supported by a third root.

(B) *Milk Dentition of the Lower Jaw.*—D.i. 1, 2 and 3. These are even slighter and simpler teeth than those of the upper jaw, and have very long, tapering roots.

D.c. This is practically identical in character with that of the upper jaw.

D.m. 1.—Except for its smaller size and the more divergent character of the roots, this is identical with pm. 2.

D.m. 2 very closely resembles pm. 3, but the accessory cusp anterior to the principal cone is better developed than in that tooth.

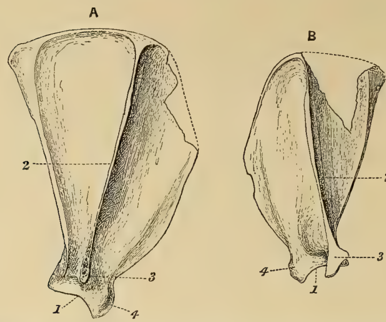
D.m. 3, the milk carnassial, is a large tooth supported by two strong divergent roots. Four fifths of the crown is formed by a bilobed trenchant blade, and behind this is a considerable cusp.

C. The Vertebral Column (Plate VI).

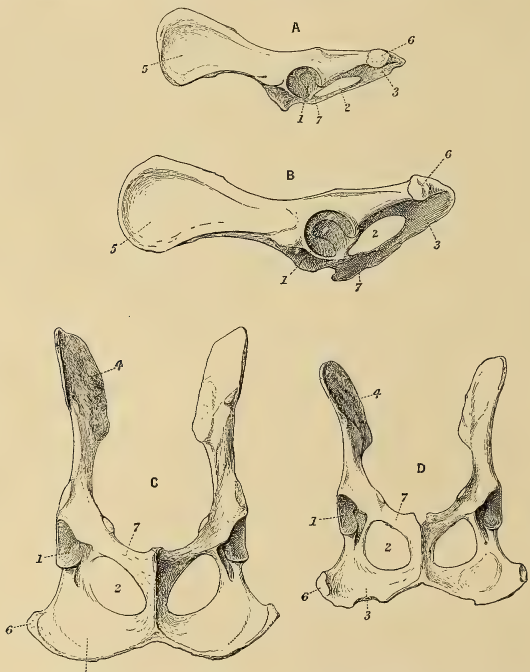
Little or nothing can be mentioned as specially characteristic of the vertebral column in the Canidæ in comparison with that in other Carnivora, but the variable number of the caudal vertebræ may be alluded to, the number ranging from seventeen to twenty-two. There are thirteen thoracic and seven lumbar vertebræ. Only three vertebræ are fused together in the sacral region, while in bears the number may be as many as five.

D. The Limb Girdles.

The Shoulder Girdle.—The scapula (Text-fig. 1) scarcely calls for special comment, though it may be mentioned that the coracoid process is very slightly developed. The British fossil specimens are almost always in a very fragmentary condition. The clavicle is in a much reduced state, though better developed than in bears.



Text-fig. 1.—A. Right scapula of a common fox (*Canis vulpes*) seen from the outer side. B. Left scapula of an Arctic fox (*Canis lagopus*) seen from the outer side. Both from Ightham (Lewis Abbott Coll.). ⅔ natural size. 1, glenoid cavity; 2, spine; 3, acromion; 4, coracoid process.



Text-fig. 2.—A. Pelvic girdle of an Arctic fox (*Canis lagopus*) seen from the left side. B. Pelvic girdle of a common fox (*Canis vulpes*) seen from the left side. C. Pelvic girdle of a common fox (*Canis vulpes*) seen from below. D. Pelvic girdle of an Arctic fox (*Canis lagopus*) seen from below. The Arctic fox is from the Pleistocene of Ightham near Maidstone (Lewis Abbott Coll.), the common fox from the Prehistoric alluvium of the Thames Valley, Walthamstow (Brit. Mus.). ⅔ natural size. 1, acetabulum; 2, obturator foramen; 3, ischium; 4, sacral surface of ilium; 5, gluteal surface of ilium; 6, ischial tuberosity; 7, pubis.

(2) Tables of Comparative Measurements of the Limb Girdles.

Table of measurements of the scapula.	*C. vulpes*, Pleistocene, Ightham, near Maidstone. (Lewis Abbott Coll.)	*C. lagopus*, Pleistocene, Ightham, near Maidstone. (Lewis Abbott Coll.)
1. Maximum length	8·25*	6·45*
2. Maximum width	—	3·25
3. Minimum width at the neck	1·7	1·3
4. Width at proximal end measured to end of coronoid process	1·9	1·45
5. Height from top of acromion to inner edge of glenoid cavity	—	1·8
Table of measurements of the pelvic girdle.		
1. Maximum length	9·3	7·0
2. Length from acetabulum to supra-iliac border of ilium	5·5	4·0
3. Dorso-ventral measurement of ilium at widest point	3·15	2·1
4. Antero-posterior diameter of acetabulum ...	1·45	1·1
5. Length from acetabulum to posterior border of ischium	—	2·35
6. Maximum diameter of obturator foramen ...	2·15	1·6
7. Measurement along ischium from symphysis to end of ischial spine	3·8	3·1

* Figured.

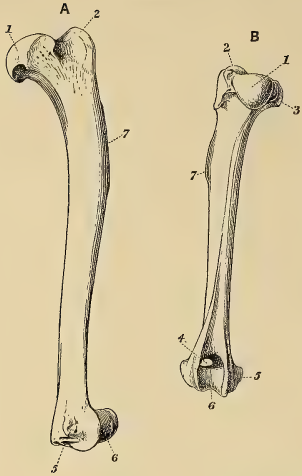
(2) *The Pelvic Girdle.*—This (Text-fig. 2) does not present any specially characteristic features.

E. The Limbs.

These are of moderate length, and agree with those of the Felidæ and differ from those of the Ursidæ in being strongly digitigrade. All the digits are terminated by non-retractile claws.

(1) *The Anterior Limb.*—The humerus (Text-fig. 3) is rather short. There is no entepicondylar foramen, but a supra-trochlear foramen is always present. The metacarpals are longer and more curved than in *Felis*. Five digits are present, but the pollex is much shorter than the others and does not reach the ground.

Text-fig. 3.



Text-fig. 4.

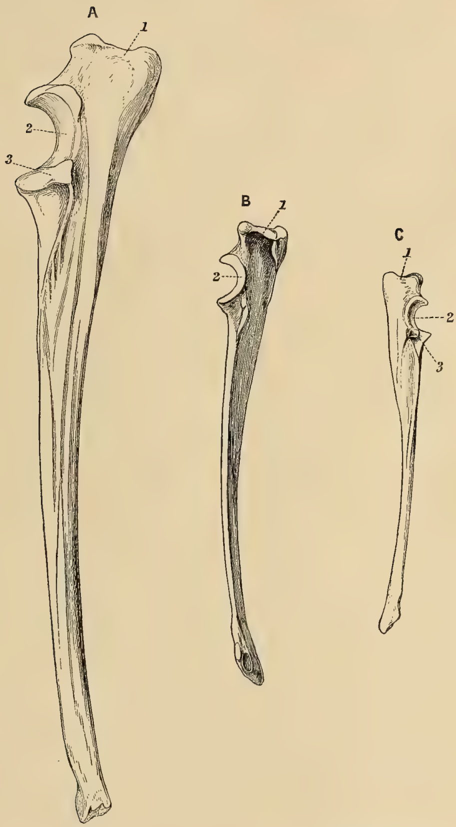
Text-fig. 3.—a. Left humerus of a common fox (*Canis vulpes*) seen from the inner side. b. Left humerus of an Arctic fox (*Canis lagopus*) seen from behind. Both from Ightham (Corner Coll.). ⅔ natural size. 1, head; 2, greater tuberosity; 3, lesser tuberosity; 4, supra-trochlear foramen; 5, internal condyle; 6, trochlea; 7, deltoid ridge.

Text-fig. 4.—a. Right radius of a common fox (*Canis vulpes*) seen from front. b. Left radius of an Arctic fox (*Canis lagopus*) seen from behind. Both from Ightham (Brit. Mus., No. M.7232, and Corner Coll.). ⅔ natural size. 1, surface for articulation with ulna; 2, surface for articulation with carpus.

(3) Table of Comparative Measurements of Bones of Anterior Limb.

Humerus.	*C. lupus* (left). Pleistocene. Banwell. No. 44640 (Brit. Mus.).	*C. vulpes* (left). Pleistocene. Ightham, near Maidstone. (Corner Coll.)	*C. lagopus* (left). Pleistocene. Ightham, near Maidstone. (Corner Coll.)
1. Maximum length	19·75	12·3*	9·4*
2. Diameter of proximal end passing across centre of articulating surface and greater tuberosity	...	2·6	1·9
3. Antero-posterior diameter of shaft at middle of deltoid ridge	2·5	1·15	1·0
4. Transverse diameter at same point	1·75	0·8	0·7
5. Maximum transverse diameter at distal end	4·4	2·1	1·7

* Figured.



TEXT-FIG. 5.—A. Left ulna of a wolf (*Canis lupus*), incomplete at distal end, seen from the left side. From Kent's Cavern, Torquay (Brit. Mus., No. M.830). B. Right ulna of a common fox (*Canis vulpes*) seen from the left side. From Ightham (Brit. Mus., No. M.7232). C. Right ulna of an Arctic fox (*Canis lagopus*) seen from the right side. From Ightham (Lewis Abbott Coll.). $\frac{2}{3}$ natural size. 1, olecranon; 2, surface for articulation with the trochlea; 3, surface for articulation with the radius.

(3) Table of Comparative Measurements of Bones of Anterior Limb—*continued.*

Radius.	*C. lupus* (left). Pleistocene. Ightham, near Maidstone. (Corner Coll.)	*C. vulpes* (right). Pleistocene. Ightham, near Maidstone. No. M.7232 (Brit. Mus.).	*C. lagopus* (left). Pleistocene. Ightham, near Maidstone. (Corner Coll.)
1. Maximum length	18·15	11·05*	8·7*
2. Shorter, *i. e.* right to left, diameter at humeral articulation	1·4	0·75	0·6
3. Longer, *i. e.* antero-posterior, diameter at humeral articulation	2·4	1·15	0·95
4. Shorter, *i. e.* right to left, diameter at carpal articulation	1·6	0·75	0·6
5. Longer, *i. e.* antero-posterior, diameter at carpal articulation	3·05	1·45	1·2
Ulna.	*C. lupus* (left). Pleistocene. Kent's Cavern, Torquay. No. M.830 (Brit. Mus.).	*C. vulpes* (right). Pleistocene. Ightham, near Maidstone. No. M.7232 (Brit. Mus.).	*C. lagopus* (right). Pleistocene. Ightham, near Maidstone. (Lewis Abbott Coll.)
1. Maximum length	...	12·9*	10·05*
2. Antero-posterior or vertical measurement at sigmoid notch	1·9*	1·0	0·7
3. Maximum transverse measurement of olecranon	1·55	0·7	0·5

(2) *The Posterior Limb.*—The tibia (Text-fig. 7) has the crest somewhat sharply truncated. The second to fifth digits are well developed, but the hallux is absent, or vestigial and suspended in the skin without bony connection with the rest of the pes.

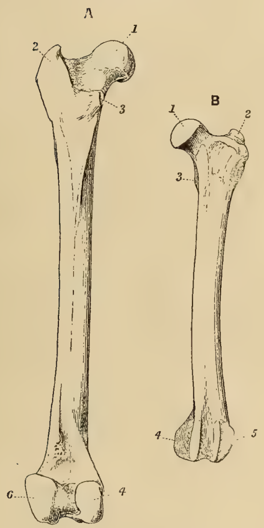
(4) Table of Comparative Measurements of Bones of Posterior Limb.

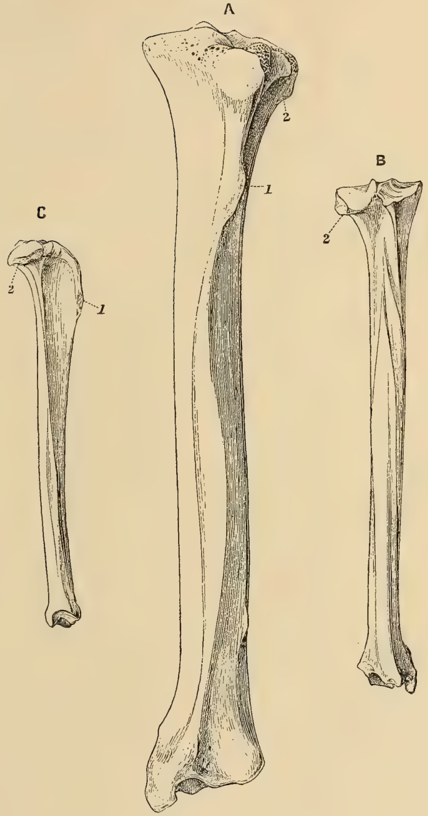
Femur.	*C. lupus* (right). Pleistocene. Ightham, near Maidstone. (Corner Coll.)		*C. vulpes* (left). Pleistocene. Ightham, near Maidstone. (Corner Coll.)	*C. lagopus* (left) Pleistocene. Ightham, near Maidstone. (Corner Coll.)
1. Maximum length	21·4		13·9*	9·9*
2. Transverse or right to left diameter at condyles	4·0		2·15	1·75
3. Antero-posterior diameter of head	2·4		1·3	1·0
4. Vertical or antero-posterior diameter of shaft at middle	1·75		0·85	0·7
5. Transverse diameter at proximal end measured across head and great trochanter	5·0		2·8	2·25

* Figured.

TEXT-FIG. 7.

TEXT-FIG. 6.





TEXT-FIG. 6.—A. Left femur of a common fox (*Canis vulpes*) seen from behind. B. Left femur of an Arctic fox (*Canis lagopus*) seen from front. Both from Ightham (Corner Coll.). $\frac{2}{3}$ natural size. 1, head; 2, great trochanter; 3, lesser trochanter; 4, internal condyle; 5, external condyle.

TEXT-FIG. 7.—A. Left tibia of a wolf (*Canis lupus*) seen from front. From Torbryan Cavern, Torquay (Brit. Mus.). B. Left tibia of a common fox (*Canis vulpes*) seen from behind. From Ightham (Brit. Mus., No. M.7232). C. Right tibia of an Arctic fox (*Canis lagopus*) seen from the right side. From Ightham (Lewis Abbott Coll.). $\frac{2}{3}$ natural size. 1, cnemial crest; 2, facet for articulation with fibula.

(4) Table of Comparative Measurements of Bones of Posterior Limb—*continued.*

Tibia.	*C. lupus* (left). Pleistocene. Torbryan, Torquay. No. M.4563 (Brit. Mus.).	*C. lupus* (left). Pleistocene. Ightham, near Maidstone. (Corner Coll.)	*C. vulpes* (left). Pleistocene. Ightham, near Maidstone. No. M.7232 (Brit. Mus.).	*C. lagopus* (right). Pleistocene. Ightham, near Maidstone. (Corner Coll.)
1. Maximum length	21·45*	21·7	14·3*	10·75
2. Transverse or right to left diameter at proximal end	4·4	4·4	2·45	1·85
3. Vertical or antero-posterior diameter at proximal end measured to top of crest	3·4	4·3	1·7	1·7
4. Transverse diameter at distal end	3·05	3·0	1·6	1·25
5. Vertical or antero-posterior diameter at distal end	2·3	2·05	1·1	0·85

* Figured.

IV. MUTUAL RELATIONS OF THE PLEISTOCENE AND POST-PLEISTOCENE CANIDÆ.

This most difficult subject has puzzled zoologists from the time of Buffon and Daubenton to the present day. It cannot be entirely overlooked in such a memoir as the present, but no attempt will be made to deal exhaustively with it.

Two questions are involved, which, though distinct, have the most intimate bearing upon one another.

The first of these is, whether any valid and reliable distinction can be found between the dogs, on the one hand, and the wolves and jackals on the other. The second is, whether the origin of the domestic dogs is to be sought wholly or partially in the existing wild Canidæ—wolf, jackal, or certain kinds of wild dog, or whether it may be found in one or more fossil species known or as yet undiscovered. The former of these questions may be first considered. A large number of points have been referred to by zoologists in their attempts to find valid osteological distinctions between dog and wolf. To each point in the following list the names of certain authors who allude to it are appended; but it is not implied that in every case the points are accepted as valid distinguishing characters by the authors who allude to them.

(1) Wolves have the triangular part of the cranium between the orbits a little narrower and flatter than in dogs (Cuvier, Denny).

(2) The sagittal crest is longer and more elevated in wolves than in dogs (Cuvier, Denny, Vieira).

(3) The teeth, especially the canines, are longer in wolves than in dogs (Cuvier, Denny).

(4) The length of the upper carnassial pm. 4 is superior or at least equal to that of the molars m. 1 and 2 in wolves, while in dogs the length of pm. 4 is less than, or at most equal to, that of the m. 1 and 2 (Gaudry and Boule).

(5) The plane of the eye-socket is more obliquely inclined to the brow, *i. e.* the orbito-frontal angle is less in wolves than in dogs (Studer) (see Text-fig. 8).

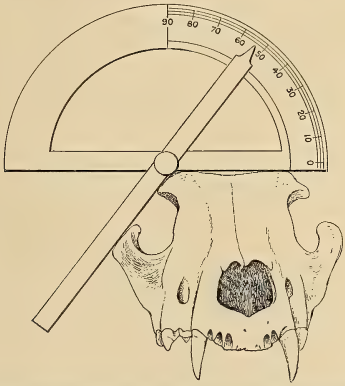
(6) The brow is more swollen at the base of the muzzle in dogs (de Blainville).

(7) The zygomatic arch is less curved and shorter in the wolf (Vieira).

(8) The coronoid process reaches above the zygomatic arch in the dog but not in the wolf (Vieira).

(9) The caudal vertebræ are more variable in the dog (de Blainville).

Denny[1] also refers to the following points: (*a*) The intermaxillaries (? nasal



Text-fig. 8.—Anterior view of the skull of a dog, and instrument for measuring the orbito-frontal angle.

processes of the premaxillæ) and nasals are longer and narrower in dogs than in wolves; (*b*) the nasal cavity is wider in wolves; (*c*) the orbital projections (probably the post-orbital processes of the frontals) are more acute in dogs; (*d*) the jaws are wider; and (*e*) the tympanics are larger in wolves.

The above is a considerable list, but the great majority of the points amount to very little and are quite inconstant and unreliable.

Probably the most important character is No. 5, for which we are indebted to Studer.[2] The angle to which he alludes can be better realised by the preceding diagram (Text-fig. 8) than by description. He regards as belonging to wolves, skulls in which the angle between the plane of the orbit and that of the brow measures 40–45°, and as belonging to dogs, skulls in which the angle is greater

[1] 'Proc. Yorks. Geol. Polyt. Soc.,' iii, 1857 (1859), p. 538.

[2] 'Abh. schweiz. pal. Ges.,' xxviii, p. 13.

than 45°. The effect of this greater obliquity of the plane of the orbit in the wolf is to produce the "oblique leering eye which gives the wolf a false expression as compared with the noble, trustful expression of a dog, whose eye, with rounder opening, is more directed forwards." He remarks that if we look at a wolf's or jackal's skull from above, more of the orbit is visible than in a dog's skull.

The reliability of this distinction, which is accepted by Scharff[1] and used in discriminating the canine skulls from the Edenvale caves, has been to some extent tested by examination of skulls at the British Museum and at Bristol with the following results :

Number of specimens.	Species.	From	Maximum angle.	Minimum angle.	Average angle.
(*a*) 8	Wolf (recent)	Brit. Mus.	45°	40°	42°
(*b*) 5	Dog (prehistoric)	,, ,,	53°	46°	$49\frac{3}{5}$°
(*c*) 27	Dog (recent)	,, ,,	62°	45°	$50\frac{1}{2}$°
(*d*) 9	,, ,,	Bristol Univ.	54°	48°	$51\frac{2}{3}$°

Belonging to each of the first three groups there were, however, certain exceptional skulls which are not included in the above table. Thus two additional wolf skulls belonging to group (*a*) gave angles of 47° and 48° respectively, two dog skulls in group (*b*) had angles of 42°, three skulls in group (*c*) had angles below 45°.

The angle is not very easy to measure even with a clinometer such as is shown in the figure, and it was found that when the same skull was measured on different occasions slightly varying results were sometimes obtained.

The measurement was in each case taken over the ends of the post-orbital processes of the frontal and jugal.

Though it can hardly be claimed that the results of the measurement of the fifty-six skulls referred to in the above table afford a complete test of the reliability of the orbito-frontal angle as a distinguishing character between dogs and wolves, they certainly confirm Studer's contention that the angle tends to be decidedly less in the wolf than in the dog, and that it affords a useful distinction of practical value. The occurrence, however, of dog skulls with an angle of less than 45°, and of wolf skulls with an angle of over 45°, shows that the distinction is not absolute, and cannot be relied on in all cases.

The second point, that of the origin of the domestic dogs, is the subject of a most voluminous literature. It is beyond the scope of the present memoir and no attempt can be made to discuss it. The different opinions which have been maintained are, however, briefly the following: Daubenton and Cuvier were

[1] 'Trans. Roy. Irish Acad.,' xxxiii, B., pt. 1, p. 203.

disposed to derive the domestic dogs from the wolf; Nehring, partly from the wolf and partly from the jackal; Gueldenstädt, and G. St. Hilaire, from the jackal; de Blainville, Pictet, Boule (1889), Gaudry and Boule (1892), Bourguignat and Woldrich, from one or more extinct types of dog, neither wolves nor jackals; Studer, partly from wolves, partly from extinct types of dog; finally, von Pelzeln has recourse to all the above-mentioned sources—wolves, jackals and extinct types of dogs, and in addition derives certain races from the existing wild dogs, *Canis sinensis* and *Canis pallipes*. Jeitteles also has recourse to several living species, including the jackal and *Canis pallipes*.

V. CONCLUSIONS.

These may be very briefly stated and contain no element of novelty. In Pliocene times the wolf (*Canis lupus*) and common fox (*Canis vulpes*) were already inhabitants of Britain. In Pleistocene times they abounded and the Arctic fox (*Canis lagopus*) was sparingly represented; but no animals which can be distinguished as dogs have been recognised in Britain in Pleistocene deposits. In Prehistoric times, however, true dogs abounded. Doubt is expressed with regard to the desirability of recognising the occurrence of the genus *Lycaon* in England.

My sincere thanks are tendered to Mr. W. J. Lewis Abbott and Dr. F. Corner for kindly placing their large collections of canine bones from the Ightham fissure at my disposal for examination and figuring. I am much indebted to Mr. H. Bolton, Prof. T. McK. Hughes, Mr. A. Somervail and Dr. A. Smith Woodward for the loan of specimens preserved respectively in the Bristol, Sedgwick, Torquay and British Museums. I further wish to thank Dr. A. Smith Woodward, Dr. C. W. Andrews, Mr. R. Lydekker and Dr. R. F. Scharff for help and information, and Mr. J. Green for the care he has taken with the illustrations.

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PLATE I.

PLEISTOCENE CANIDÆ.

Cranium.

Wolf (*Canis lupus*).

(Two thirds natural size.)

FIG.

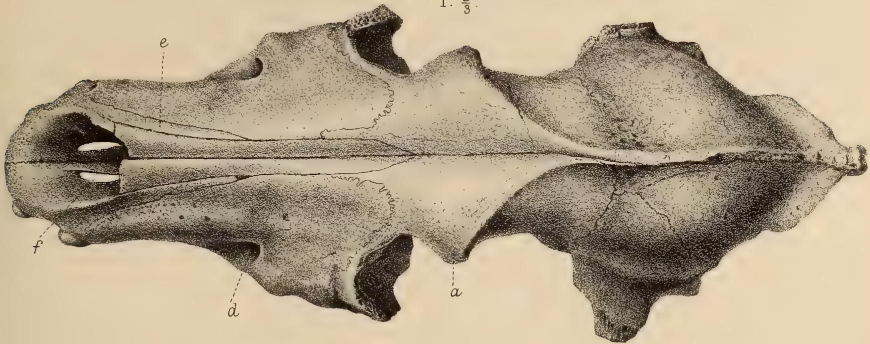
1. Dorsal
2. Lateral
3. Ventral

} view of a cranium from Kent's Cavern, Torquay.

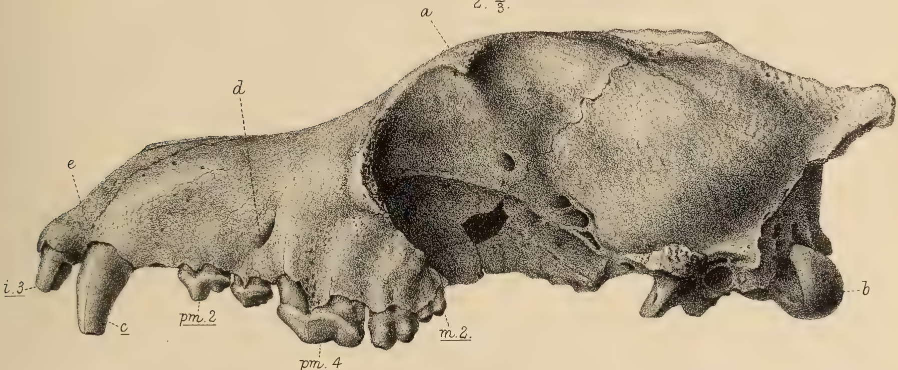
This specimen, which was figured by MacEnery ('Cavern Researches,' Frontispiece) and by Owen ('British Fossil Mammals and Birds,' p. 123), is preserved in the Torquay Museum. Since these authors figured the skull, the mandible has been lost and the cranium has been somewhat damaged.

a. Post-orbital process of frontal.
b. Occipital condyle.
c. Canine tooth.
d. Infra-orbital foramen.
e. Premaxilla.
f. Anterior palatine foramen.

1. $\frac{2}{3}$.



2. $\frac{2}{3}$.



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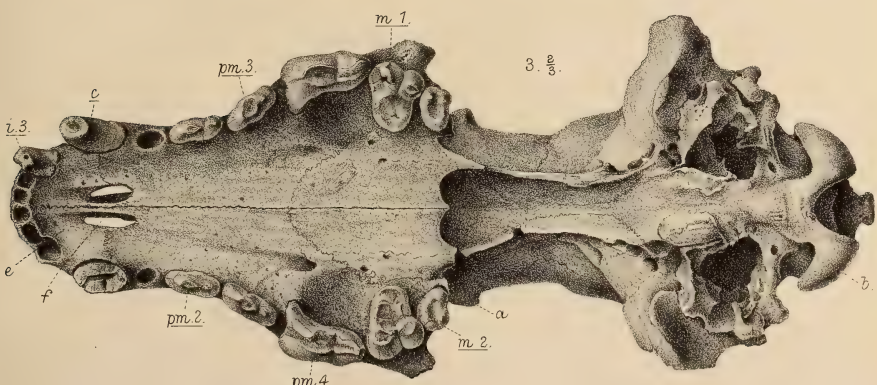


J. Green del. lith. et imp.

WOLF, CANIS LUPUS.
Cranium.

PLATE II.

Pleistocene Canidæ.

Cranium and Mandible.

Wolf (*Canis lupus*).

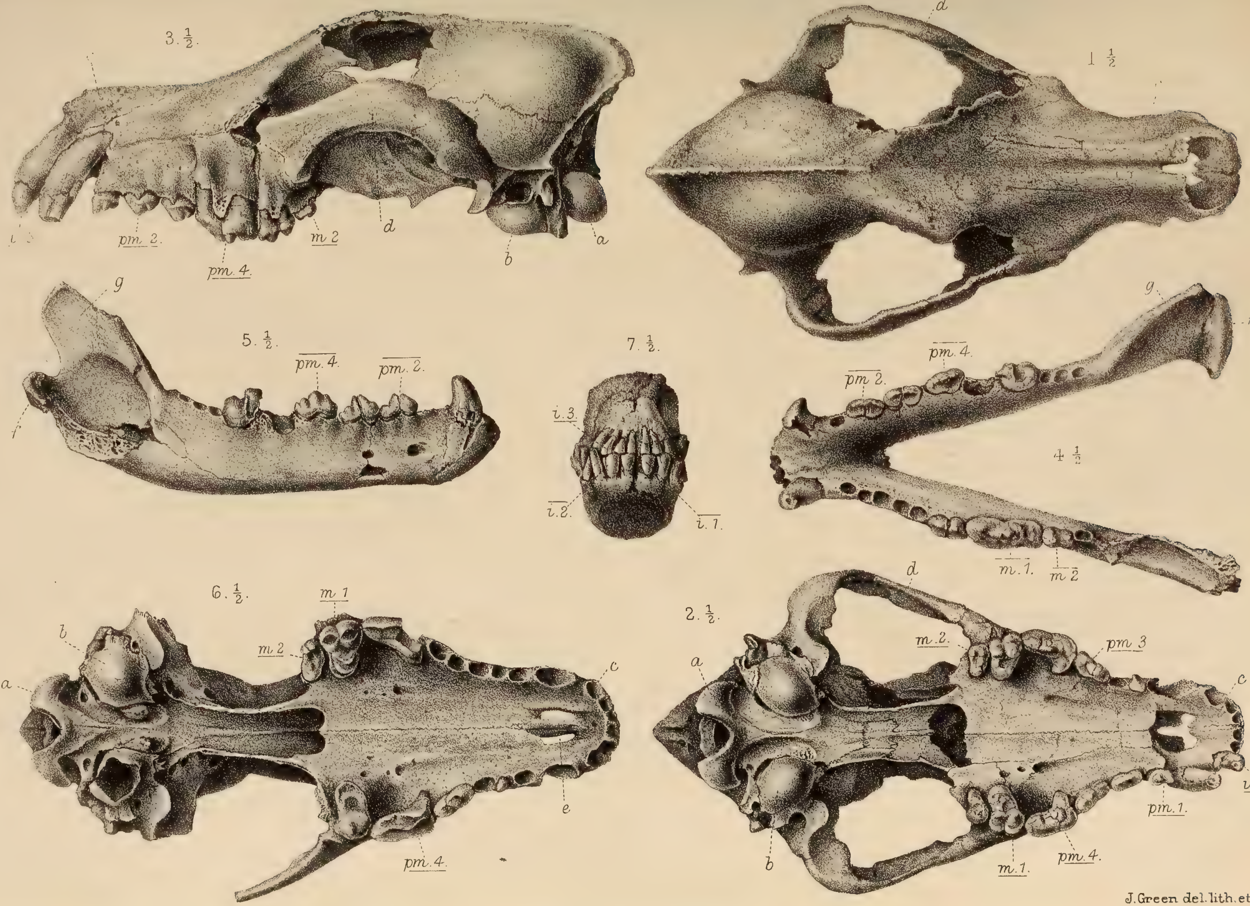
(One half natural size.)

Fig.

1. Dorsal } view of a cranium from Hutton Cave, Somerset.
2. Ventral } view of a cranium from Hutton Cave, Somerset.
3. Lateral } view of a cranium from Hutton Cave, Somerset.
4. Palatal } view of the corresponding mandible.
5. Lateral } view of the corresponding mandible.
6. Ventral view of a cranium from Banwell Cave, Somerset.
7. Anterior view of the jaws from Oreston Cave, Plymouth.

All the above are preserved in the British Museum.

a. Occipital condyle.
b. Auditory bulla.
c. Premaxilla.
d. Jugal.
e. Anterior palatine foramen.
f. Mandibular condyle.
g. Coronoid process.



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WOLF, CANIS LUPUS.
Cranium & mandible.

PLATE III.

PLEISTOCENE CANIDÆ.

Cranium and Mandible.

Common Fox (*Canis vulpes*).

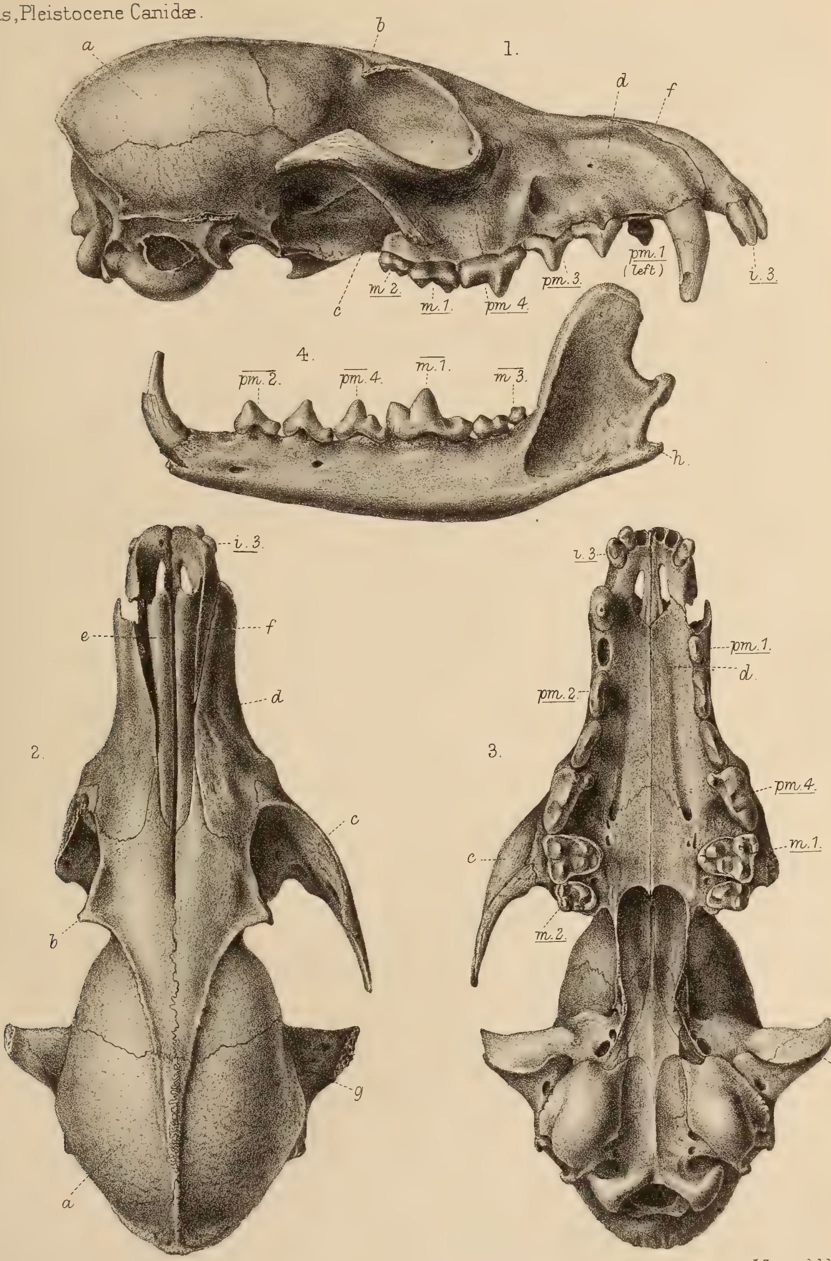
(Natural size.)

FIG.

1. Lateral } view of cranium.
2. Dorsal } view of cranium.
3. Ventral } view of cranium.
4. Left mandibular ramus seen from the outer side.

These specimens are from the Pleistocene of the Ightham fissure, near Maidstone, and are preserved in the collection of Mr. W. J. Lewis Abbott, F.G.S., of St. Leonard's-on-Sea.

a. Parietal.
b. Post-orbital process of frontal.
c. Jugal.
d. Maxilla.
e. Nasal.
f. Nasal process of premaxilla.
g. Zygomatic process of squamosal.
h. Angle of mandible.



J. Green del. lith, et imp

COMMON FOX, CANIS VULPES.
Cranium & mandible.

PLATE IV.

PLEISTOCENE CANIDÆ.

Cranium and Mandible.

Arctic Fox (*Canis lagopus*).

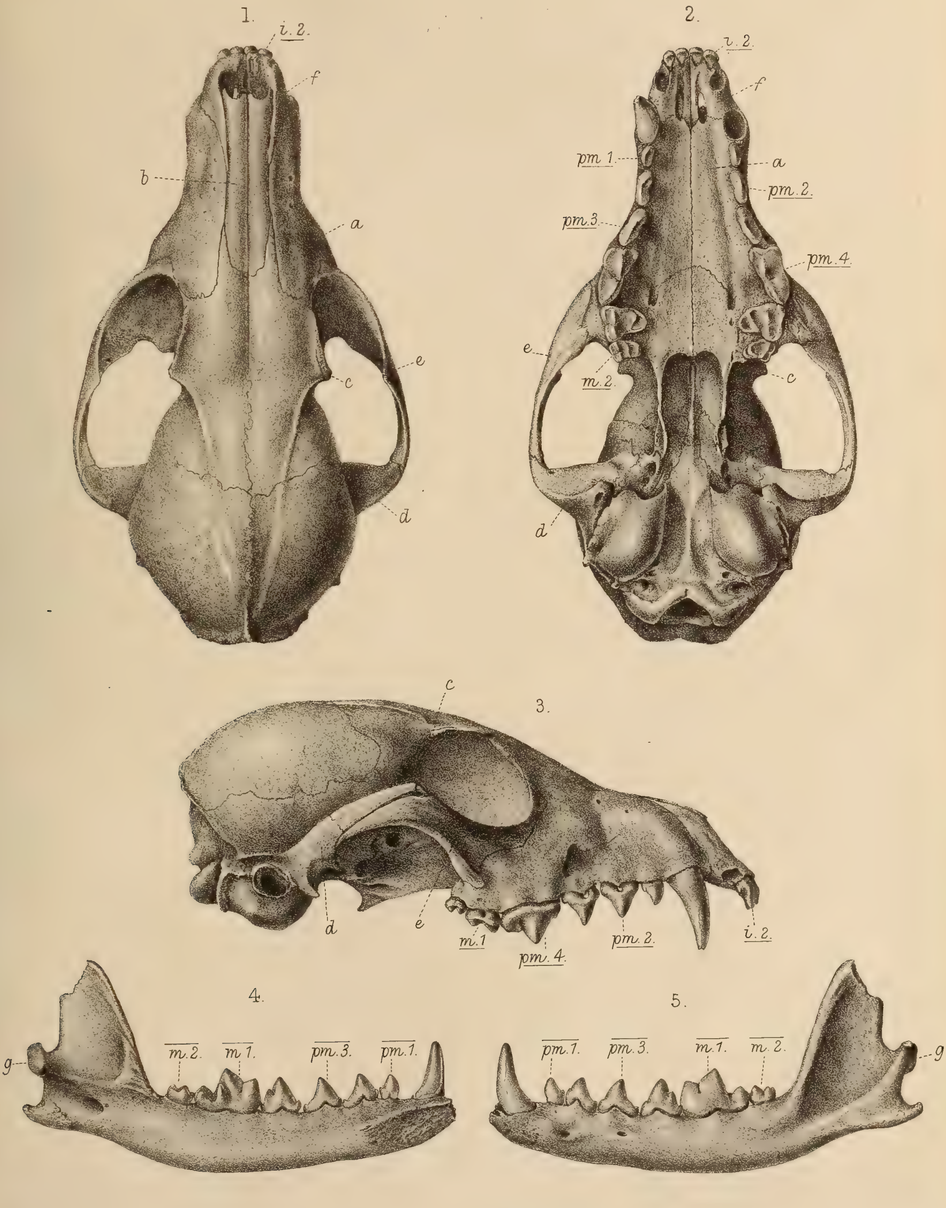
(Natural size.)

FIG.

1. Dorsal
2. Ventral } view of cranium.
3. Lateral
4. Left mandibular ramus seen from the inner side.
5. The same seen from the outer side.

These specimens are from the Pleistocene of the Ightham fissure, near Maidstone, and are preserved in the collection of Mr. W. J. Lewis Abbott, F.G.S., of St. Leonard's-on-Sea.

a. Maxilla.
b. Nasal.
c. Post-orbital process of frontal.
d. Zygomatic process of squamosal.
e. Jugal.
f. Premaxilla.
g. Condyle of mandible.



J. Green del. lith. et imp.

ARCTIC FOX, CANIS LAGOPUS.
Cranium & mandible.

PLATE V.

PLEISTOCENE CANIDÆ.

Dentition.

(Natural size.)

FIG.

1. Right upper permanent dentition of *Canis lupus*.
2. Right lower permanent dentition of *Canis lupus*.
3. Right upper deciduous dentition of *Canis* sp.
4. Right lower deciduous dentition of *Canis* sp.

The above teeth, which are all from the Pleistocene of the Torbryan Cave, Torquay, are in each case seen from the inner side. $\overline{\text{D.i.3.}}$ and $\overline{\text{d.c.}}$ were not represented in the series figured and are shown merely in outline. Preserved in the British Museum.

5. Right } mandibular ramus of a young Arctic Fox (*Canis lagopus*).
6. Left }

These specimens, both seen from the outer side, are from the Pleistocene of the Ightham fissure, near Maidstone, and are preserved in the collection of Mr. W. J. Lewis Abbott, F.G.S., of St. Leonard's-on-Sea.

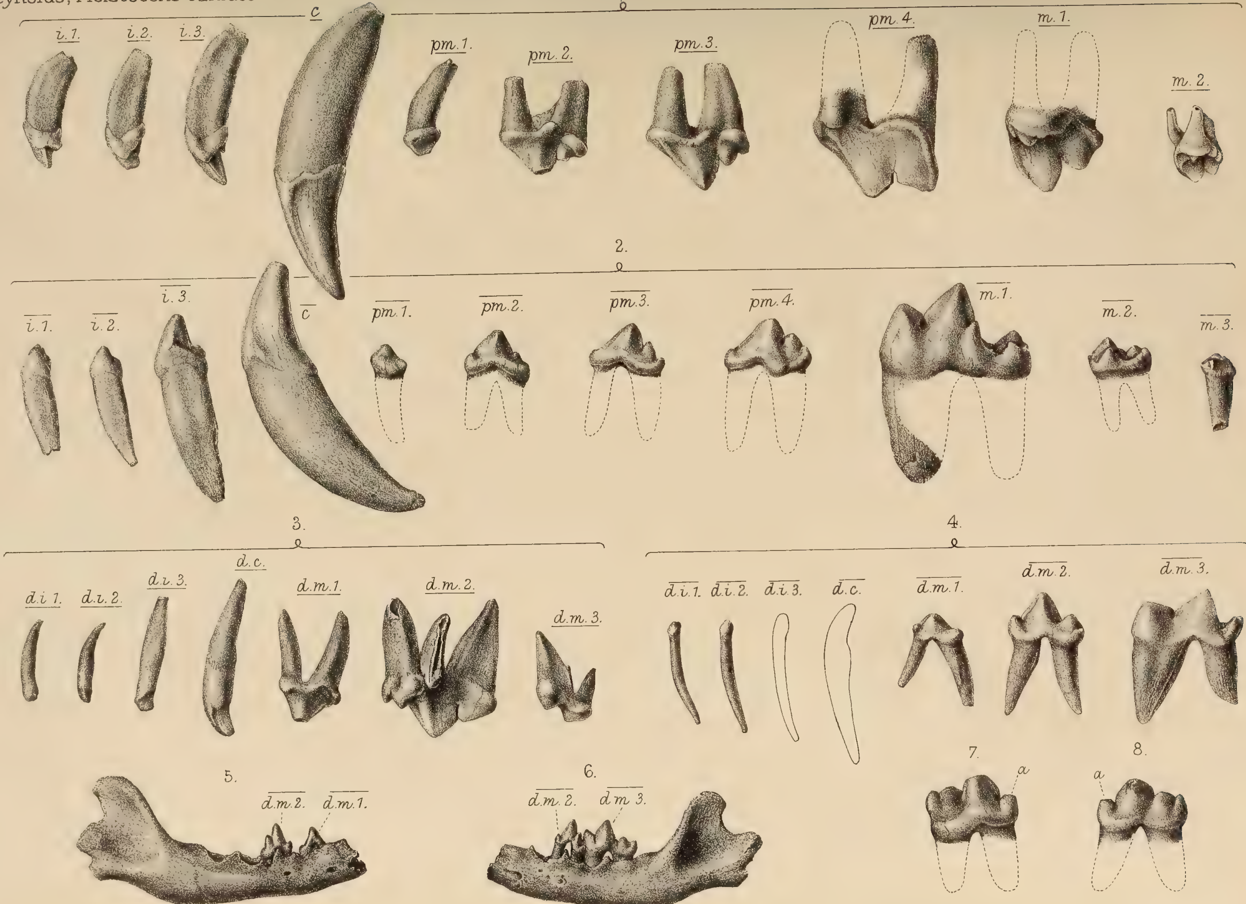
7. and 8. Fourth lower premolar of the specimen from Spritsail Tor, Gower, described as *Lycaon anglicus*. This specimen is preserved in the British Museum.

7. Outer aspect. 8. Inner aspect.

a. Anterior cusp.

In all the above specimens the roots when shown in outline are not visible, being hidden by the bone of the jaw.

Reynolds, Pleistocene Canidæ.



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Dentition.

PLATE VI.

Pleistocene Canidæ.

Vertebræ.

(Natural size.)

Fig.

1. Atlas, Wolf (*Canis lupus*), Oreston, ventral view.

2. 3. 4. 2, Axis; 3, fifth cervical; and 4, first thoracic; Wolf (*Canis lupus*), Durdham Down, all seen from the left side.

5. Sacrum, Wolf (*Canis lupus*), Oreston, ventral view.

All the above are preserved in the Bristol Museum.

6. Atlas, posterior view
7. Axis, seen from left side
8. Third cervical, posterior view
9. Fourth cervical, posterior view
10. Fifth cervical, seen from left side

} Common Fox (*Canis vulpes*).

The above are from the Pleistocene of the Ightham fissure, near Maidstone, and are preserved in the collection of Dr. F. Corner, F.G.S., of Poplar.

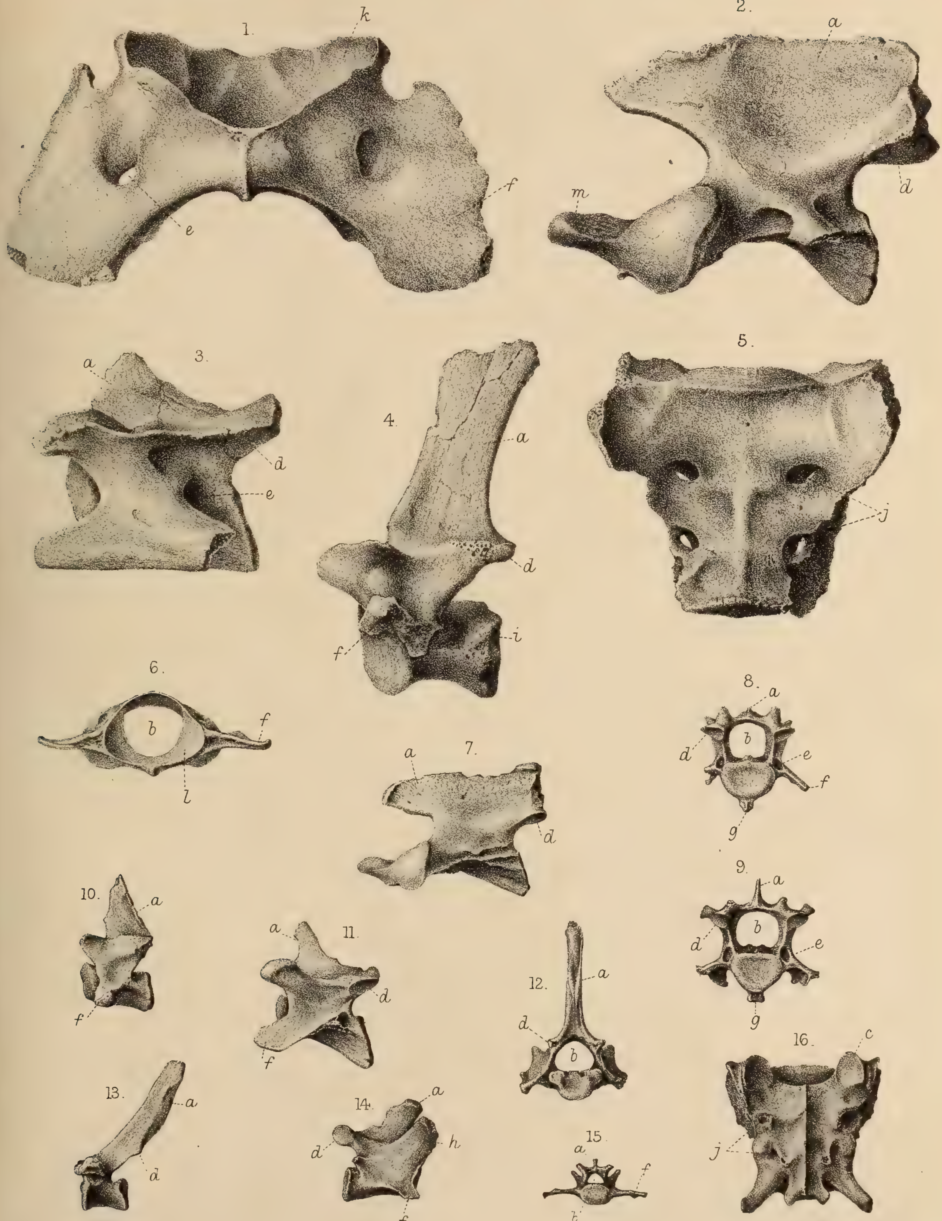
11. Seventh cervical, seen from left side
12. First thoracic, posterior view
13. Seventh thoracic, seen from left side
14. First lumbar, seen from right side
15. First free caudal, posterior view

} Arctic Fox (*Canis lagopus*).

The above are also from the Ightham fissure, and are preserved in the collection of Mr. W. J. Lewis Abbott, F.G.S.

16. Sacrum, Common Fox (*Canis vulpes*), Durdham Down, dorsal view, Bristol Museum.

a. Neural spine.
b. Neural canal.
c. Pre-zygapophysis.
d. Post-zygapophysis.
e. Vertebrarterial canal.
f. Transverse process.
g. Hypapophysis.
h. Metapophysis.
i. Surface for articulation with head of rib.
j. Nerve foramina.
k. Surface for articulation with condyle of cranium.
l. Posterior articular surface.
m. Odontoid process of axis.



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Vertebræ.

Palæontographical Society, 1911.

A MONOGRAPH

OF THE

BRITISH PLEISTOCENE MAMMALIA

VOL. II, PART IV.

THE MUSTELIDÆ.

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MONOGRAPH

ON

THE BRITISH MAMMALIA

OF THE

PLEISTOCENE PERIOD

THE MUSTELIDÆ.

Order—CARNIVORA.

Family—MUSTELIDÆ.

I. INTRODUCTION.

The Pleistocene Mustelidæ,[1] which form the subject of the present memoir, are an easier group to deal with than either the Ursidæ or Canidæ, not showing the variability and inconstancy of character which render it so difficult to come to a satisfactory conclusion about the mutual relationship of the members of the above groups. Including, as the group does, the glutton, badger, and otter, in addition to the Mustelinæ (marten, polecat, stoat, weasel, etc.), it is somewhat too extensive and diverse to be conveniently treated from the historical aspect as a single entity. In the following paragraphs only the literature of a more general character will be referred to, each species being subsequently considered separately.

As was the case with the bears and hyænas, the remains from the great Continental caves attracted attention at an earlier date than those of Britain, Goldfuss[2] recording bones of the glutton from the caves of Gailenreuth in 1818

[1] As in a previous memoir dealing with the Pleistocene Canidæ, the classification and nomenclature adopted are those of Flower and Lydekker, 'An Introduction to the Study of Mammalia, Living and Extinct' (1891). The generic name *Mustela* is employed in a wider sense than is now usual, most zoologists adopting Nilsson's name *Putorius* for the polecat, stoat and weasel.

[2] 'Nova Acta Acad. Caes. Leop.,' ix, 1818, p. 313, and 'Säugethiere der Vorwelt,' p. 468.

and Sundvig in 1823, and Schmerling[1] those of the badger, marten, and polecat, from the caves of Liège in 1833. Marcel de Serres, Dubrueil and Jeanjean[2] figured an otter's mandible from Lunel Viel in 1839, while Croizet and Jobert[3] recorded the same species from the Puy-de-Dôme deposits in 1828. The remains of the smaller Mustelidæ were naturally not as a rule recognised at so early a date as those of the larger species, but Buckland,[4] as early as 1822, figured musteline teeth from Kirkdale, which he attributed to the weasel, and Goldfuss[5] figured a mandible from Gailenreuth, which he attributed to a *Viverra*. Schmerling,[6] however, pointed out that the latter bone was musteline.

The records to the date of writing were summarised by H. v. Meyer[7] (1832), F. Holl[8] (1829—1831), de Blainville[9] (1844), and Giebel[10] (1847), while Owen, in 1842,[11] and subsequently in 1846,[12] gave a full account of the available information regarding British occurrences. Gervais[13] (1859) dealt fully with all French records.

Five species of Mustelidæ were recorded by Falconer[14] (1868) from the various caves of Gower, and other records were given by Dawkins[15] (1869) in his paper on the "Distribution of British Post-glacial Mammals."

Very little has been written concerning Musteline remains from Ireland, though Adams,[16] in 1881, recorded the marten and badger from Ballynamintra, co. Waterford, and Scharff the badger, otter and stoat from the caves of co. Clare,[17] and the stoat from Kesh,[18] co. Sligo.

The most important records of quite recent date in England are those of the Ightham[19] fissure, in which, in addition to *Mustela robusta*, the polecat, weasel and badger were met with.

During comparatively recent times a number of important papers dealing with the Pleistocene Mustelidæ have been published on the Continent. E. Cornalia, in his 'Mammifères fossiles de Lombardie'[20] (1858—1871), described remains of the badger, marten, and polecat, some of the polecat skulls being very large. This

[1] 'Recherches Oss. foss. Cavernes de Liège,' I, pp. 158—166; II, pp. 5—15.

[2] 'Recherches Oss. humatiles Cavernes de Lunel Viel,' p. 70, pl. ii, figs. 14 and 15.

[3] 'Recherches Oss. foss. Dept. Puy-de-Dôme,' p. 89.

[4] 'Phil. Trans.,' cxii, p. 182, pl. xx.

[5] 'Die Umgebungen von Muggendorf,' p. 282, pl. v, fig. 3.

[6] 'Recherches Oss. foss. Cavernes de Liège,' ii, p. 5.

[7] 'Palæologica,' p. 47.

[8] 'Handbuch der Petrefactenkunde,' p. 36.

[9] 'Ostéographie,' fasc. 4.

[10] 'Fauna der Vorwelt,' i, pp. 55—64.

[11] "Brit. Foss. Mammals," 'Rep. Brit. Assoc.' (Manchester, 1842), pp. 70—72.

[12] 'Brit. Foss. Mamm. and Birds,' pp. 109—122.

[13] 'Zoologie et Paléontologie Françaises,' pp. 243—253.

[14] 'Pal. Mem.,' p. 525.

[15] 'Quart. Journ. Geol. Soc.,' xxv, p. 192.

[16] 'Trans. Roy. Dublin Soc.,' (2) i, p. 205.

[17] 'Trans. Roy. Irish Acad.,' xxxiii, B, pt. i, pp. 40—43.

[18] Ibid., xxxii, B, pt. 4, p. 205.

[19] 'Quart. Journ. Geol. Soc.,' l, p. 200, and lv, p. 425.

[20] 'Pal. Lomb.,' ed. Stoppani, ser. 2.

paper was followed in 1879 by Liebe's[1] account of the caves at Vypustek, in Moravia, where glutton, marten, stoat, and polecat were met with. In Woldrich's[2] three beautifully illustrated papers (1880, 1882, 1884), on the fauna of Zuzlawitz, near Winterberg, in the Böhmerwald, remains of polecat, stoat and weasel are figured, and in particular some very large skulls, which are attributed to the polecat, closely resemble the form afterwards described by Newton as *Mustela robusta*. Lastly, in 1886 appeared an important paper by Winterfeld,[3] giving a general account of the Quaternary Musteline remains of Germany.

II. GENERAL ACCOUNT OF THE VARIOUS BRITISH MUSTELIDÆ.

Mustela martes, THE PINE MARTEN.

Two British species of marten, the pine marten (*Mustela martes*, Linn., or *abietum*, Fleming) and the beech marten (*Mustela foina*, Erxl.), have commonly been recognised as members of the British fauna. Alston,[4] however, shows good reason for believing that *Mustela martes* is identical with *Mustela sylvatica* of Nilsson, and that *Mustela foina* is not really an inhabitant of the British Isles. He mentions among others the following points of difference between the skulls of *M. martes* and *M. foina*, though many of them appear to be inconstant or inappreciable.

M. martes.	*M. foina.*
1. The breadth of the skull across the zygomatic arches is rather more than half the length.	1. The breadth of the skull across the zygomatic arches is much more than half the length.
2. The arches are highest posteriorly, whence they slope rather suddenly downwards and forwards.	2. The arches are regularly curved, and broadest and highest in the middle.
3. The sides of the muzzle are nearly parallel.	3. The sides of the muzzle are converging.
4. The anterior narial opening is oval.	4. The anterior narial opening is heart-shaped.
5. The palate is comparatively narrow.	5. The palate is comparatively broad.
6. The upper premolars are placed regularly in the line of the series; the fourth has the inner cusp large and placed nearly at right angles to the axis of the tooth.	6. The upper premolars are crowded, and often placed diagonally, their anterior extremities being directed inwards; the inner cusp is small and placed somewhat diagonally.
7. $\overline{\text{m. 1}}$ has a slightly developed inner tubercle.	7. $\overline{\text{m. 1}}$ has a well-developed inner tubercle.

The marten was not mentioned by Owen in his 'British Fossil Mammals and

[1] 'Sitzb. k. Akad. Wiss. Wien,' lxxix, pt. i, p. 472.

[2] Ibid., lxxxii, pt. i, p. 32; lxxxiv, pt. 1, p. 194; and lxxxviii, pt. i, p. 993.

[3] 'Ueber quartäre Mustelidenreste Deutschlands,' Berlin.

[4] 'Proc. Zool. Soc.,' 1879, pp. 468—474, and 'Zoologist,' iii, 1879, pp. 441—448.

Birds,' and was not included by Dawkins in his list[1] of preglacial mammals, but part of a right mandibular ramus found in the Upper Freshwater Bed at West Runton was described by Newton.[2]

Records of the remains of the marten in British Pleistocene deposits are scanty. Dawkins and Sanford[3] mentioned a skull and lower jaw imbedded in breccia in the Williams collection from Bleadon. Falconer[4] detected marten remains which he attributed with hesitation to *Mustela foina* in three of the Gower caves, viz. Long Hole, Ravenscliff, and Spritsail Tor. Adams[5] recorded it from Ballynamintra, co. Waterford.

Scharff[6] mentioned that while abundant remains of martens were found in the Newhall and Barntick caves, co. Clare, these were all in the upper strata, and hence, it may be concluded, were probably not Pleistocene. A (probably) Prehistoric skull from Edenvale, co. Clare, and a mandibular ramus from the Langwith cave are figured on Pl. II, figs. 4, 5, of the present memoir. Cuvier[7] and Krüger[8] have alluded to the occurrence of bones of marten at Gailenreuth.

Mustela robusta, THE GIANT POLECAT.

This name was applied by Newton[9] to the remains of a large Musteline found in England, as yet only in the Ightham fissure. In the first instance only a left humerus, a right ulna and certain bones of the extremities were found, and as a result of a careful comparison with the corresponding bones of the marten and polecat, Newton arrived at the conclusion that they were distinct. A further series of limb-bones with part of a skull and mandible was described and figured by the same author[10] in 1899, and their affinities to the polecat rather than to the marten were pointed out.

Though the Ightham specimens were the first remains of the giant polecat which had been found in Britain, such had long been known on the Continent. Cornalia[11] (1870) had figured large fossil skulls of polecat from Lombardy. Woldrich[12] (1881—1883), others from Zuzlawitz, near Winterberg, in Bohemia,

[1] 'Quart. Journ. Geol. Soc.,' xxv (1869), p. 210.

[2] 'Mem. Geol. Surv.,' "Vert. of Forest Bed," p. 25.

[3] "British Pleistocene Mammalia: Felidæ," 'Pal. Soc.' (1866), p. xxii.

[4] 'Pal. Mem.,' ii, 1868, p. 525.

[5] 'Trans. Roy. Dublin Soc.,' (2), i, 1881, p. 208.

[6] 'Trans. Roy. Irish Acad.,' xxxiii (1906), B, pt. 1, p. 41.

[7] 'Oss. Foss.,' ed. 2 (1823), iv, p. 467.

[8] 'Geschichte der Urwelt,' ii, p. 851.

[9] 'Quart. Journ. Geol. Soc.,' l (1894), p. 200.

[10] Ibid., lv (1899), p. 425.

[11] "Mon. Mamm. foss. de Lombardie," 'Pal. Lomb.,' ii (1870), p. 33, pl. xi.

[12] 'Sitzb. k. Akad. Wiss. Wien,' lxxxii, pt. 1 (1880), pl. ii, figs. 24—26, and ibid. lxxxviii, pt. 1 (1883), pl. ii, figs. 1, 2.

while Hensel[1] (1881) gave full figures and measurements of large recent skulls. Boule and Chauvet[2] (1899) alluded to the occurrence of the remains of a large polecat among an Arctic fauna described by them from the Charente.

All these authors agree in referring the large skulls to the recent species of polecat, *Mustela putorius*.

Newton was the first to propose a distinctive name for this large form. He, however, thought it possible that the Ightham form might be the same as that to which Meyer[3] gave the name *Mustela antiqua*. The latter author's use of the name is, however, unaccompanied by any description, and he does not indicate that he intended to apply it to large forms of the polecat.

The splendidly preserved cranium figured in the present memoir (Pl. I, figs. 7—9) was obtained by Mr. W. J. Lewis Abbott from the Ightham fissure in 1907. A comparison of this skull with skulls of *Mustela martes* in the British Museum and Bristol University collection shows that there are a number of obvious points of difference. *Mustela robusta* differs from *Mustela martes* in (1) the width and shortness of the palate; (2) the shortness antero-posteriorly of $\overline{\text{m. 1}}$; (3) the absence of $\underline{\text{pm. 1}}$; (4) the less inflated character of the auditory bulla; and (5) the somewhat more flattened character of the cranial roof. The skull is clearly that of a polecat, the only appreciable difference from *Mustela putorius* being in point of size.

Mustela putorius, THE POLECAT.

The records of the occurrence of the polecat in British Pleistocene deposits are very scanty. Owen[4] figured a skull from Berry Head, and mentioned that an almost entire skull had been found in a raised beach near Plymouth. Falconer[5] recorded it from Bacon Hole, Long Hole, and Spritsail Tor, Gower, and Newton[6] from the Ightham fissure. The British Museum contains a considerable number of bones from the Brixham cave, and a few have been obtained by the Rev. E. H. Mullins at Langwith.

Of the continental records the following may be alluded to: Cuvier described[7] some musteline bones which de Blainville[8] referred to the polecat. Schmerling[9] figured a good cranium and mandible from Liège. Krüger[10] referred to polecat

[1] "Craniologische Studien," 'Nova Acta Acad. Caes. Leop.,' xlii (1881), pl. vi, figs. 1, 2.

[2] 'Comptes Rendus,' cxxviii (1899), p. 1188.

[3] 'Palæologica,' 1832, pp. 54, 130.

[4] 'Brit. Foss. Mamm. and Birds,' p. 112.

[5] 'Pal. Mem.,' ii, p. 525.

[6] 'Quart. Journ. Geol. Soc.,' lv (1899), p. 425.

[7] 'Ann. Mus.,' xx, p. 437, and subsequently 'Oss. Foss.,' ed. 2 (1823), p. 467.

[8] 'Ostéographie—Mustela,' p. 57.

[9] 'Recherches Oss. Foss. Cavernes de Liège,' ii, pl. i.

[10] 'Geschichte der Urwelt,' p. 851.

remains from Gailenreuth. The descriptions of the bones of polecats by Cornalia (1870), Woldrich (1880 and 1883), Hensel (1881), Boule and Chauvet (1899), have been sufficiently dealt with under the head of *Mustela robusta*, and need not be repeated here.

Mustela erminea, THE STOAT OR ERMINE.

The fact of the stoat being a member of the British Pleistocene cave-fauna was established by Owen,[1] who figured a skull from Berry Head, near Brixham. The teeth and larger of the jaws figured by Buckland[2] from the Kirkdale cave as weasel, were shown by Owen[1] to be those of the stoat. It was obtained by McEnery[3] from Kent's Hole, Torquay, and by Falconer[4] from Bacon Hole, Gower, while Scharff recorded it from the Kesh[5] caves, co. Sligo, and the Newhall and Edenvale[6] caves, co. Clare.

Early continental records of the occurrence of *Mustela erminea* are, to say the least, very scanty. Neither Cuvier, de Blainville, nor Schmerling refer to it. Liebe[7] (1879) records it from Vypustek, Woldrich[8] (1882, 1884, 1888) from Zuzlawitz, Winterfeld[9] (1886) from O. Ruzsin, in Hungary.

Mustela vulgaris, THE WEASEL.

Though it cannot be doubted that the remains of the weasel have occurred in many British Pleistocene deposits, the records are very scanty. Buckland[10] recorded it from the Kirkdale cave, but, as Owen[11] pointed out, the teeth and jaws figured by him are in the main too large for the weasel, and should be attributed to the stoat. The smallest mandible figured ('Rel. Div.,' pl. xxiii, fig. 12) may belong to the weasel. McEnery[12] figured a skull from Kent's cave, which he attributed to the weasel, and de Blainville[13] assented as to the correctness of this determination; Owen,[14] however, attributed McEnery's specimen to the stoat, and in this was

[1] 'Brit. Foss. Mammals and Birds' (1846), p. 116 et. seq.

[2] 'Reliq. Diluv.' (1824), pl. vi, figs. 28, 29, and pl. xxiii, figs. 11, 13.

[3] 'Cavern Researches' (1859), pl. E, fig. 17.

[4] 'Pal. Mem.' (1868), p. 525.

[5] 'Trans. Roy. Irish Acad.,' xxxii, B, pt. 4, p. 205.

[6] Ibid., xxxiii, B, pt. 1, p. 40.

[7] 'Sitzb. k. Akad. Wiss. Wien,' lxxix, pt. 1, p. 477.

[8] Ibid., lxxxii, pt. 1, p. 35; lxxxiv, pt. 1, p. 199; and lxxxviii, pt. 1, p. 997.

[9] 'Ueber quartäre Mustelidenreste Deutschlands' (1886), p. 25.

[10] 'Reliq. Diluv.,' table facing p. 1 and description of pls. vi and xxiii (1824).

[11] 'Brit. Foss. Mamm. and Birds' (1846), p. 117.

[12] 'Cavern Researches' (1859), pl. E, fig. 17.

[13] 'Ostéographie—Carnassiers, Mustela,' p. 59.

[14] 'Brit. Foss. Mamm. and Birds' (1846), p. 117.

followed by Woodward and Sherborn.[1] Owen gives no special account of the weasel in his 'British Fossil Mammals and Birds,' and it is not included by Dawkins in his list of British post-glacial Mammalia. Passing to the continental records: Schmerling[2] figured a musteline cranium and mandible which he did not venture to name, but which agreed in point of size with the weasel. Woldrich,[3] in each of his three papers on the 'Diluvial Fauna of Zuzlawitz,' described bones of the weasel, referring very small specimens to a new species under the name of *Fœtorius minutus*.

Newton[4] recorded skulls and limb-bones from the Ightham fissure both of the common weasel and of a smaller variety, which he, following Woldrich,[5] referred to under the specific name of *minuta*. It is represented in the Manchester Museum by an imperfect mandible from Creswell Crags, and by other remains from Dog Holes, Warton Crag, Lancashire.

Gulo luscus, THE GLUTTON.

The earliest recognition of the glutton as a member of the Pleistocene fauna is due to Goldfuss[6] who in 1818 gave a good figure of an almost perfect skull from Gailenreuth, seeking to make of it a new species under the name of *Gulo spelæus*. At a later date he obtained a specimen from Sundwig to which he referred in his 'Säugethiere der Vorwelt,' 1823 (p. 481). Soemmering also procured a very well-preserved skull from Gailenreuth, which he submitted to Cuvier, who gave a reduced figure of it.[7] Schmerling[8] obtained only teeth, a femur and part of a pelvis from the caverns of Liège.

The remains of the glutton found in Britain are rare and fragmentary. They are first met with in the Forest Bed, part of a left mandibular ramus having been described by Newton[9] from Mundesley. It has been recorded from a considerable number of Pleistocene caves. The earliest record is that of Bellamy[10] from Yealm Bridge, Devon, confirmed by Pengelly[11] in 1871.

1 'Catal. Brit. Foss. Vertebrata' (1890), p. 368.

2 'Recherches Oss. Foss. Cavernes de Liège,' ii, pl. i, figs. 4—6.

3 'Sitzb. k. Akad. Wiss. Wien,' lxxxviii (1884), pt. i, p. 1000.

4 'Quart. Journ. Geol. Soc.,' lv (1899), p. 425.

5 Ibid., l (1894), p. 201.

6 'Nova Acta Acad. Caes. Leop.,' ix (1818), p. 311, pl. viii. The mandibular ramus attributed by Goldfuss to a *Viverra* and figured by him ('Die Umgebungen von Muggendorf,' v, 1810, 3) is assigned by Schmerling to a marten or polecat ('Cavernes de Liège,' ii, p. 5) and by de Blainville ('Ostéographie—Carnassiers, Mustela,' p. 53) to the glutton.

7 'Oss. Foss.,' ed. 2, 1825, pl. xxxi, figs. 23—25.

8 'Recherches Oss. Foss. Cavernes de Liège,' i, p. 167.

9 'Geol. Mag.' [2] vii, 1880, p. 424, pl. xv, and "Vert. Forest Bed" ('Mem. Geol. Surv.,' 1882), p. 17, pl. vi.

10 'Nat. Hist. S. Devon.,' pp. 89, 94, 102.

11 'Trans. Devon. Assoc.,' iv, 1871, pp. 98, 102.

Dawkins and Sanford[1] (1866) include it in their list of Pleistocene mammals on the evidence of the crowns of three canine teeth obtained from the caves of Bleadon and Banwell, Somerset, and from one of the Gower caves (see Text-fig. 1, C, D, and E, for the Somerset specimens). It is not, however, mentioned by Falconer[2] in his list of the Gower cave-fauna, and Woodward and Sherborn[3] do not include Gower as one of the localities where its remains have been met with. Dawkins[4] in 1871 described a left mandibular ramus from the Plas Heaton cave, Cefn, near S. Asaph, this fine specimen, which is shown in Text-fig. 1, A, being now preserved in the Grosvenor Museum, Chester. Finally, in 1875 Busk[5] added Creswell Crags to the list of localities, though the determination was based only on two fragments of pelvis (see Text-fig. 2).

A comparatively recent continental record of the occurrence of the glutton is by Liebe[6] (1879) from Vypustek in Moravia. Winterfeld[7] (1886) discussed its distribution, and gave some German records of its occurrence in loess and other deposits.

Meles taxus, THE BADGER.

The remains of the badger were discovered in Pleistocene caves at an early date, and have been recorded from a very large number, though, perhaps, not from so many as the habits of the animal would lead one to expect.

The earliest records of the badger from Pleistocene deposits are by Schmerling[8] (1833), who gave good figures of the skull and limb-bones from the caves of Liège, and by Münster[9] (1836), who described it from the neighbourhood of Baireuth.

Both these authors regarded their species as distinct from the modern species, Schmerling referring to his as *Meles antediluvianus* and Münster to his as *Meles antiquus*.

M. de Serres, Dubrueil and Jeanjean[10] in 1839 figured a skull and other bones from Lunel Viel, and affirmed the identity of the badger of the caves with the recent species, a point concerning which subsequent writers have been unanimous.

1 "British Pleistocene Mammalia" ('Pal. Soc.,' 1866), pt. 1, p. 21.

2 'Pal. Mem.,' ii, 1868, p. 525.

3 'Catal. Brit. Foss. Vertebrata,' 1890, p. 350.

4 'Quart. Journ. Geol. Soc.,' xxvii, 1871, p. 406.

5 Ibid., xxxi, 1875, p. 687.

6 'Sitzb. k. Akad. Wiss. Wien.,' lxxix, 1879, pt. 1, p. 476.

7 'Ueber quartäre Mustelidenreste Deutschlands,' 1886, p. 40.

8 'Recherches Oss. foss. Cavernes de Liège,' i, 1833, p. 158.

9 'Verzeichniss der Versteinerungen . . . zu Baireuth,' 1836, p. 87.

10 'Recherches Oss. humatiles Cavernes de Lunel Viel,' 1839, pl. i.

Nordmann[1] in 1847 recorded it from Odessa, and McEnery, as reported by de Blainville[2] (1844) from Kent's Cave, Torquay. Owen[3] (1846) figured

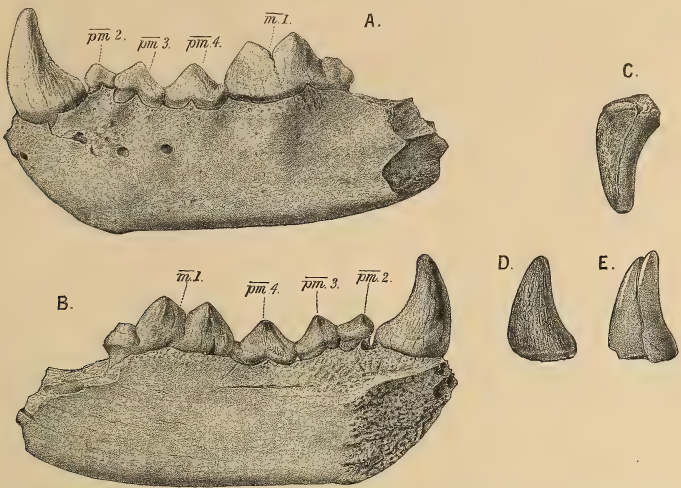

Fig. 1.—Glutton (*Gulo luscus*). A. Left mandibular ramus seen from the outer side. B. The same seen from the inner side. From the Pleistocene of the Plas Heaton Cave, Cefn, near St. Asaph (Grosvenor Museum, Chester). C. Crown of left upper canine. From the Pleistocene of the Bleadon Cave, Somerset (Taunton Museum). D. and E. Crowns of left lower canines. From the Pleistocene of Banwell Cave, Somerset (Taunton Museum). All three teeth seen from the outer side. Nat. size.

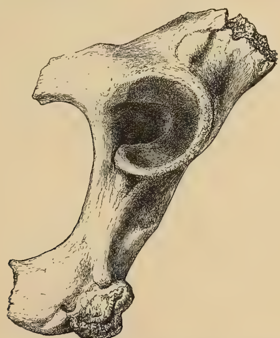

Fig. 2.—Glutton (*Gulo luscus*). Busk's figure of a fragmentary innominate bone from the Pleistocene of Creswell Crags. Reproduced by permission of the Council of the Geological Society. Nat. size.

[1] 'Découv. Gîtes riches en Oss. foss. Odessa,' p. 4.

[2] 'Ostéographie,' fasc. 4.

[3] 'Brit. Foss. Mamm. and Birds,' p. 109.

McEnery's specimen—a well-preserved mandible, now in the British Museum. He also recorded the badger from Berry Head.

H. von Meyer[1] (1859) described remains of the badger from the neighbourhood of Weimar, giving a number of references to French and other records.

Dawkins and Sanford[2] (1866) recorded it from Banwell and Wookey Hole, and Falconer[3] (1868) from a number of the Gower caves. Other records are from the caves or fissures of Durdham Down,[4] Uphill,[5] Ightham,[6] Cefn[7] (near St. Asaph), and Hoe Grange.[8]

Pleistocene deposits other than caves have yielded bones of the badger at Newbury, Berkshire, and Grovehurst, Kent, though the age of the latter deposit is somewhat doubtful.

Adams[9] records it from Ballynamintra, co Waterford, and Scharff[10] from the Edenvale, Newhall and Barntick caves, co. Clare.

The remains of the badger were remarkably abundant in the Langwith cave, near Mansfield, and included the remarkably elongated skull figured in Pl. V.

Lutra vulgaris, THE OTTER.

Owen[11] referred to a mandible of this animal as having been found in the Norwich Crag at Southwold, and to a humerus found in the same beds at Aldborough, but Newton[12] was unable to see the specimens and verify the record. He, however, recorded[13] it from the Forest Bed of East Runton. He further believed that an otter occurred in Britain in Red Crag times, referring[14] to de Blainville's species *Lutra dubia*, a specimen from the Red Crag of Foxhall, near Woodbridge, which differed from *Lutra vulgaris* in having the carnassial tooth longer from before backwards, and narrower than in the recent species, while

1 'Palæontographica,' vii, 1859, pp. 41—45.
2 "British Pleistocene Mammalia" ('Pal. Soc.,' 1866), pt. 1, p. xxii.
3 'Pal. Mem.,' ii, p. 525.
4 'Proc. Bristol Nat. Soc.,' N.S., v, 1885—88, p. 44.
5 Ibid., N.S., ix, 1898—1900, p. 159.
6 'Quart. Journ. Geol. Soc.,' lv, 1899, p. 428.
7 'Geol. Mag.' [3] iii, 1886, p. 571.
8 'Quart. Journ. Geol. Soc.,' lxi, 1905, p. 50.
9 'Trans. Roy. Dublin Soc.' [2] i, 1881, p. 208.
10 'Trans. Roy. Irish Acad.,' xxxiii, B., pt. 1, p. 42.
11 'Brit. Foss. Mamm. and Birds,' p. 119.
12 'Geol. Mag.' [3] iv, 1887, p. 145.
13 'Quart. Journ. Geol. Soc.,' xlvi, 1890, p. 444.
14 "Vert. Pliocene Deposits" ('Mem. Geol. Surv.,') p. 12.

the inner tubercle is also smaller. The specimen further differs from *Lutra vulgaris* in that each of the premolars has the posterior root much longer in proportion than the anterior. In the same memoir (p. 13) Newton described a new

1. Table showing the Distribution of Mustelidæ in the Pleistocene Deposits of the British Isles.

	Marten (*Mustela martes*).	Giant polecat (*Mustela robusta*).	Polecat (*Mustela putorius*).	Stoat (*Mustela erminea*).	Weasel (*Mustela vulgaris*).	Glutton (*Gulo luscus*).	Badger (*Meles taxus*).	Otter (*Lutra vulgaris*).
Pliocene deposits	+	...	...	...	...	+	+	...
Pleistocene	Caves	and	Fissures.					
Bacon Hole, Gower	...	...	+	+	...	...	+	.
Ballynamintra, co. Waterford	+	...	...	...	...	...	+	...
Banwell	...	...	...	...	...	+	+	+
Barntick, co. Clare	+	.	...	...	...	...	+	...
Bench	...	...	...	...	...	...	+	.
Berry Head	...	...	+	+	...	...	+	..
Bleadon	+	...	...	...	...	+	...	+
Brixham	...	...	+	+	+?	...	...	..
Cefn, near St. Asaph	...	...	...	...	...	+	+	.
Creswell Crags	...	...	...	...	+	+	...	...
Dog Holes, Warton Crag	...	...	...	...	+	...	+	...
Durdham Down	.	.		...	..	...	+	+
Edenvale, co. Clare	...	...	...	+	...	...	+	..
Grays Thurrock, Essex	...	...	...	...	...	...	...	+
Happaway, Torquay	+?	...	+	...	...	...	+	..
Hoe Grange, near Matlock	...	...	...	...	...	...	+	..
Ightham	...	+	+	...	+	...	+	...
Ipswich	...	...	...	...	...	...	...	+
Kent's Cave, Torquay	...	...	...	+	+	...	+	+
Kesh, co. Sligo	...	...	...	+	...	...	...	..
Kirkdale	...	...	...	+?	+?	...	...	...
Langwith Bassett, near Mansfield	+	...	+	...	+	...	+	+
Long Hole, Gower	+	...	+	...	...	...	+	+
Newhall, co. Clare	+	...	...	+	...	...	+	+
Oreston	...	...	...	+?	.	.	...	...
Plymouth (raised beach)	.	..	+	.	...	...	...	...
Ravenscliff, Gower	+	...	...	...	...	...	+	...
Shandon	...	...	...	...	...	...	+	...
Spritsail Tor, Gower	+	...	+	...	...	...	+	...
Teesdale	...	...	...	...	...	...	...	+
Uphill	...	...	.	...	..	..	+	...
Wookey	..	..	.	...	.	...	+	...
Yealm Bridge, Devon	..		..	..	..	+	..	...

Note.—Some of the records from co. Clare are probably Prehistoric rather than Pleistocene.

species (*Lutra reevesi*), founding it on a right lower carnassial tooth which had not cut the jaw, from the Norwich Crag of Bramerton.

As is natural from the habits of the animal, the remains of the otter are scanty in caves, but more abundant in river-gravels and similar deposits. Marcel de Serres, Dubrueil and Jeanjean[1] described and figured a lower jaw from Lunel Viel, which they referred to a new species, and Croizet and Jobert[2] described bones from the Puy-de-Dôme district.

The only Post-Pliocene specimens referred to by Owen in his 'British Fossil Mammals and Birds' are from the peat and its associated marls of Cambridgeshire, and belong to the Prehistoric rather than to the Pleistocene fauna. Dawkins and Sanford[3] (1866) stated that the only Pleistocene remains of the otter with which they were acquainted were from Kent's Hole, Torquay, and Banwell Cave, and from the brick-earth of Gray's Thurrock, Essex. In Dawkins' paper[4] on the "Distribution of the British Post-glacial Mammals" (1869) the additional cave-localities of Durdham Down and Long Hole, Gower, were given, with Ipswich, as a river deposit. The otter occurs rarely in the Langwith Cave.

Scharff[5] recorded the otter from the Newhall Cave, co. Clare, this being the first notice of its occurrence in Ireland in Pleistocene strata.

III. DESCRIPTION OF THE SKELETON.

The Mustelidæ form a large and somewhat heterogeneous group of Carnivores, and are grouped with the Ursidæ and Procyonidæ in the section Arctoidea.

The cranial part of the skull tends to be considerably elongated and somewhat sharply marked off from the facial portion. The glenoid cavity is relatively far forward. The Mustelidæ agree with the Felidæ and Hyænidæ, and differ from the great majority of the Ursidæ, Viverridæ, and Canidæ, in having no alisphenoid canal. The auditory bulla is not as a rule much inflated. The palate is generally considerably produced behind the last molars. The hamular process of the pterygoid is prominent. The infra-orbital foramen is generally very large, and the orbit communicates widely with the temporal fossa. The post-glenoid process tends to curve over the mandibular condyle, and sometimes holds the mandible attached to the cranium.

The dental formula in the great majority of cases is i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{3-4}{3-4}$, m. $\frac{1}{2}$. In

[1] 'Reçherches Oss. humatiles Cavernes de Lunel Viel,' p. 70, pl. ii, figs. 14, 15.

[2] 'Oss. foss. Dept. Puy-de-Dôme,' p. 89.

[3] 'British Pleistocene Mammalia" ('Pal. Soc.,' 1866), pt. 1, p. xxii.

[4] 'Quart. Journ. Geol. Soc.,' xxv, 1869, p. 198.

[5] 'Trans. Roy. Irish Acad.,' xxxiii, B. pt. 1, p. 41.

rare cases the molars may number $\frac{1}{1}$ or $\frac{2}{2}$. The upper carnassial, pm. 4, differs from that in Ursidæ and resembles that in Felidæ, Hyænidæ, and Canidæ, in possessing a more or less antero-internally placed inner tubercle supported by a distinct root.

A. The Skull.

Mustela.—The cranial portion of the skull is not so sharply marked off from the facial as in *Meles* and *Lutra*. The sagittal and superciliary crests are less developed than in *Meles*; the occipital crest on the other hand is commonly very strong. The post-orbital processes of the frontal and jugal are fairly prominent, and sometimes approach one another, especially in *Mustela erminea*. The foramen magnum is of relatively large size. The auditory bulla is considerably inflated. The infra-orbital foramen is smaller in proportion to the size of the cranium than in *Lutra* and *Meles*, and the post-glenoid process is not sufficiently recurved to hold the mandible attached to the cranium.

Gulo.—The cranial portion of the skull is more strongly marked off from the facial than in *Mustela*, but less so than in *Lutra*. There is a greater development of ridges, especially of the sagittal crest, than in any other British member of the Mustelidæ, except *Meles*. The jaws are very powerful. The foramen magnum is of relatively smaller size than in *Mustela*, and the auditory bulla, though variable, is less inflated. The paroccipital process of the exoccipital is prominent, while the post-orbital process of the jugal is very slightly developed. The post-glenoid process is much incurved, and holds the mandible firmly attached to the cranium.

Meles.—The skull of the common badger bears a very close resemblance to that of the glutton in general form, development of ridges, strength of jaws, and relative size of the foramen magnum. Also in the development of the paroccipital process of the exoccipital and of the post-glenoid process, which attaches the mandible to the cranium perhaps even more firmly than in *Gulo*. The superciliary ridges are somewhat stronger than in *Gulo*, and the zygomatic arch is rather stouter.

Lutra.—The skull of the otter is of a peculiar character, broad and depressed, with the cranial portion, which is much expanded posteriorly, sharply marked off from the facial portion by a strong constriction behind the orbits. The sagittal and superciliary ridges are but slightly developed. The infra-orbital foramen is very large, and the post-glenoid process is not so much recurved as in *Meles*. The ventral surface of the cranial portion of the skull is notably broad and flattened, and the auditory bulla is very little inflated. The mandible is small and weak in comparison with that of *Meles*.

(1) TABLE OF COMPARATIVE MEASUREMENTS OF MUSTELINE SKULLS.

	Mustela martes, ? Prehistoric, Newhall Caves, Co. Clare (Nat. Mus., Dublin).	*Mustela foina* ♂, recent, S. Germany, No 1299B, (Brit. Mus.).	*Mustela robusta*, Pleistocene, Ightham, near Maidstone (Lewis Abbott Coll.).	*Mustela putorius* ♂, recent, Boncath, Cardiganshire, No. 0.10.9.1. (Brit. Mus.).	*Mustela putorius*, ? Prehistoric, Ightham near Maidstone (Corner Coll.).	*Mustela erminea*, Pleistocene, Berry Head, (Brit. Mus.).	*Mustela vulgaris*, Pleistocene, Ightham, near Maidstone (Lewis Abbott Coll.).	*Mustela vulgaris* var. *minuta*, Pleistocene, Ightham, near Maidstone (Corner Coll.).	*Gulo luscus* ♂, recent, Egersund, Norway, No. 10.11.26.1. (Brit. Mus.).	*Meles taxus*, Pleistocene, Grovehurst, Sittingbourne, No. M.1884 (Brit. Mus.).	*Meles taxus*, Pleistocene, Langwith, near Mansfield (Mullins Coll.).	*Meles taxus* var., Pleistocene, Langwith, near Mansfield (Mullins Coll.).	*Lutra vulgaris*, Prehistoric, Burwell Fen (Sedgwick Mus.).
1. Length from intercondylar notch to anterior end of skull	8·15	7·7	7·05	6·2	5·5	4·3	3·3	2·95	13·1	12·6	11 85	13 2	11·1
2. Extreme width across zygomatic arches...	5·8	5·2	4·5	4·1	3·65	...	...	1·45	10·2	8 45	7·6	8·2	7·7
3. Height from suture between basi-occipital and basi-sphenoid to top of sagittal crest..	3·0	2·7	2·3	2·05	2·0	1·45	1·1	1·0	5·3	4·6	4·25	4·15	3·6
4. Width at lachrymal foramen	2·2	2·1	2·0	1·75	1·55	1·2	·75	·7	4·1	3·45	3·3	3·4	2 65
5. Width between ends of post-orbital processes of frontal...........................	3·0	2·7	2·15	2·1	2·1	1·35	·85	·8	4·65	3·7	3·55	3·5	2·25
6. Minimum width of cranium behind post-orbital processes	2·0	1·8	1·7	1·6	1·5	1·05	·75	·75	3·4	2·4	2·15	2·4	1·3
7. Width immediately behind zygomatic process of squamosal	3·75	3·8	3·3	2·95	2·8	2·05	1·55	1·3	8·1	5·8	5·1	5·3	5·8
8. Length of face from point midway between post-orbital processes of frontal to narial opening...........................	2·2	2·3	2·1	1·8	1·45	1·3	·95	·95	3 65	4·55	4·25	4·65	2·35
9. Length of palate measured to alveolus of i. 1	4·3	4·0	3·35	3·0	2·7	1·9	1·3	1·1	7·3	7·4	6·85	7·85	5 05
10. Transverse diameter of foramen magnum	1·3	1·2	1·15	·85	·9	·65	·5	·45	1·65	1·7	1·5	1·5	1·5
11. Length of mandibular ramus measured to end of condyle	...	5·4	4·55	4·05	...	2·6	1·8	1·5	10·25	9·25	...	...	7·5

B. THE DENTITION.

MUSTELA.—Dental formula—i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{3}{3}$–$\frac{4}{4}$, m. $\frac{1}{2}$.

Permanent Dentition of the Upper Jaw.—I. 1 and 2 are very small, one-rooted, simple teeth, i. 3 is a larger and caniniform tooth. The canine is a relatively very large tooth with a long slightly recurved crown. Pm. 1 is a very small one-rooted tooth which, while present in *Mustela martes* and other representatives of the genus *Martes* of Nilsson, is absent in *M. putorius*, *M. robusta*, *M. erminea* and *M. vulgaris*, representatives of the genus *Putorius* of Nilsson. Pm. 2 and 3 are simple conical teeth with two roots and a rather well-marked cingulum. Pm. 4, the carnassial, is a large tooth with a prominent blade consisting of a larger anterior and a smaller posterior lobe. The cingulum is well developed, and there is a prominent inner tubercle near the anterior border of the tooth. M. 1, which is as large a tooth as pm. 4, is short, but very wide, with a raised outer portion bearing several small, ill-defined cusps, and a depressed and more flattened inner portion terminated by a raised semicircular inner border.

Permanent Dentition of the Lower Jaw.—I. 1, 2 and 3 are all very small teeth, their crowns being only from a quarter to a third as long as that of the canine, which is somewhat sharply recurved. Pm. 1 is a small, simple, one-rooted tooth, and like pm. 1, is absent in *Putorius*. Pm. 2, 3 and 4 are all very similar teeth with two roots and conical crowns. In pm. 3, and still more in pm. 4, there are indications of a slight additional cusp on the posterior edge of the main cusp. M. 1 is a large tooth with a bilobed trenchant blade and a depressed posterior portion or talon only half the length of the blade. M. 2 is a small one-rooted tooth with a rounded crown.

GULO.—Dental formula—i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{4}$, m. $\frac{1}{2}$.

Permanent Dentition of the Upper Jaw.—I. 1 and 2 are relatively powerful teeth, rather sharply curved downwards, with edges of a somewhat chisel-shaped character and indications of slight lateral cusps. I. 3 is a large caniniform tooth with a strongly marked cingulum, which passes obliquely along the inner face of the tooth, ending in a slight cusp not far from the point. C. is of the usual character, and powerful, but not specially large. Pm. 1 is a simple, conical, one-rooted tooth. Pm. 2 is two-rooted, and has the apex of the crown placed far forward. Pm. 3 is a very powerful two-rooted tooth with a rather low conical crown. Pm. 4, the carnassial, is a large tooth with a prominent bilobed blade supported by two roots, the anterior lobe being the larger. The inner tubercle, which is supported by a third root, is small and depressed, but very sharply marked off from the rest of the tooth. There is a fairly prominent cingulum which is raised into a slight cusp at the anterior end of the tooth. M. 1 is a rather large tooth transversely placed. A depression divides it into an outer portion supported by two roots and raised into three ill-defined cusps, and an inner somewhat larger portion with a low cusp and a raised inner border.

Permanent Dentition of the Lower Jaw.—I. 1, 2 and 3 are relatively powerful teeth not differing greatly in size, though i. 3 has the crown somewhat expanded; i. 2 arises from the jaw at a point behind i. 1 and i. 3. C. is a powerful tooth with a somewhat prominent cingulum, which often gives off a ridge running along the inner face of the tooth to the apex. Pm. 1 is a small one-rooted tooth with a circular crown. Pm. 2, 3 and 4 are powerful two-rooted teeth increasing progressively in size. The crown is conical, and the apex, central in pm. 4, is further forward in pm. 3 and still further forward in pm. 2. M. 1 is a powerful tooth with a large blade, consisting of two equal-sized trenchant lobes and a small depressed talon. M. 2 is a small tooth with an oval crown not raised into any prominent cusps.

Meles.—Dental formula—i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{4}$, m. $\frac{1}{2}$.

Permanent Dentition of the Upper Jaw.—I. 1 and i. 2 are simple teeth with somewhat chisel-shaped blades, i. 3 is more caniniform. The contrast in size between i. 3 and c. is not so great as in *Lutra*. Pm. 1 is a very small tooth which almost always falls out at an early period. As a rule its alveolus is completely closed in old animals. Pm. 2 and 3 are simple, conical, two-rooted teeth. Pm. 4, the carnassial, has a prominent blade with a large conical anterior lobe and an ill-defined and often scarcely recognisable posterior lobe. The inner tubercle is large and depressed and not so much anteriorly placed as in *Mustela*, or so sharply marked off as in *Gulo*. M. 1 is a very large tooth with a broad surface covered by a series of small tubercles, which rise to form two rather prominent cusps at the antero-external border. This tooth has three roots.

Permanent Dentition of the Lower Jaw.—The lower incisors are simple teeth of the same character as those in the upper jaw. The canine has a thickened base to the crown, which is somewhat sharply recurved. Pm. 1 is very small, and early falls out; pm. 2, 3, and 4, are simple conical two-rooted teeth. M. 1 is a long and relatively very large tooth. The anterior half has a rather ill-defined bilobed blade, with a cusp placed internal to the posterior lobe. The posterior half has a somewhat depressed middle portion surrounded by a series of low cusps. M. 2 is a small one-rooted tooth, bearing several slight elevations on the crown.

Lutra.—Dental formula—i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{3}$, m. $\frac{1}{2}$.

Permanent Dentition of the Upper Jaw.—I. 1 and i. 2 are small cylindrical teeth; i. 3 is somewhat larger and more caniniform, but the canine, which is a rather long and slender tooth, contrasts strongly in point of size with the incisors. Pm. 1 is a very small simple tooth, and often falls out early. Pm. 2 and 3 are simple conical two-rooted teeth. Pm. 4, the upper carnassial, has a trenchant blade, with one very prominent principal lobe and a somewhat smaller posterior lobe. The inner tubercle is large and depressed, with a sharp raised edge. M. 1 is a large, somewhat irregular tooth, broader than long, with two cusps on the outer edge, divided by a depression from two on the inner border.

Permanent Dentition of the Lower Jaw.—I. 1 is very small; i. 2 and 3 are slightly larger, but are very simple one-rooted teeth. The canine, as in the upper jaw, is greatly larger than the incisors. Pm. 2, 3 and 4 are simple, conical, two-rooted teeth, the cone in pm. 2 being obliquely truncated in front. M. 1, the carnassial, is a relatively large tooth, somewhat variable in character. The posterior half, or talon, is depressed; the anterior half bears two trenchant lobes, with a large tubercle internal to the posterior lobe. The cingulum is prominent in m. 1 and all the lower premolars. M. 2 is a rather small square tooth, with a flattened crown and a single root.

c. The Vertebral Column.

The numbers of the vertebræ are as follows:

	Cervical.	Thoracic.	Lumbar.	Sacral.	Caudal.
Mustela	7	14	6	3	18—33
Gulo	7	15	5	3	14 or 15
Meles	7	15	5	3	18
Lutra	7	14—15	5—6	3	25—26

There is little in the vertebral column of the Mustelidæ which demands special comment, but allusion may be made to the following points:

(1) The length of the tail in *Lutra*.

(2) The relatively large size of the atlas vertebra in *Lutra* and *Mustela*.

(3) The length of the spines of the anterior thoracic vertebræ of *Gulo*.

(4) The elongated character and shortness of the neural spines of the lumbar and posterior thoracic vertebræ of *Mustela*.

(5) The expanded character of the transverse processes of the lumbar vertebræ of *Lutra*.

d. The Limb Girdles.

The Pectoral Girdle.—The scapula shows a considerable amount of variation in shape and in the character of the acromion, which is always strongly developed, while the coracoid process is scarcely defined. In *Mustela*, *Gulo*, and *Lutra* there is a very large pre-scapular fossa and the coracoid border is gently curved. The supra-scapular border in *Gulo* and *Lutra* forms an angle not much less than a right angle with the spine. In *Mustela* the supra-scapular border is very short, and the

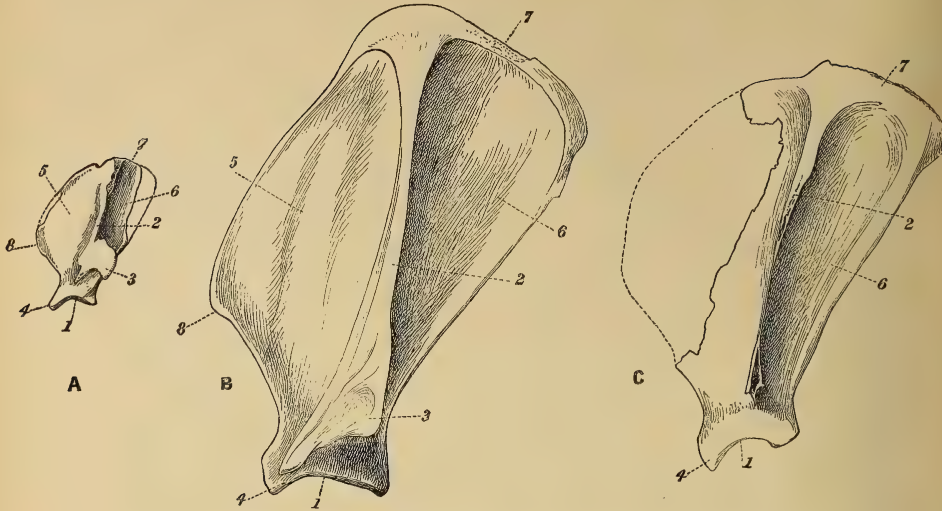

FIG. 3.—The left scapula seen from the outer side. A Polecat (*Mustela putorius*), from the Pleistocene of Ightham (Corner Coll.). B Badger (*Meles taxus*), from the Pleistocene of the Langwith Cave (Mullins Coll.). C Otter (*Lutra vulgaris*), from the Prehistoric peat of Burwell fen (Sedgwick Mus.). Natural size. 1, glenoid cavity; 2, spine; 3, acromion; 4, coracoid process; 5, pre-scapular fossa; 6, post-scapular fossa; 7, supra-scapular border; 8, coracoid border.

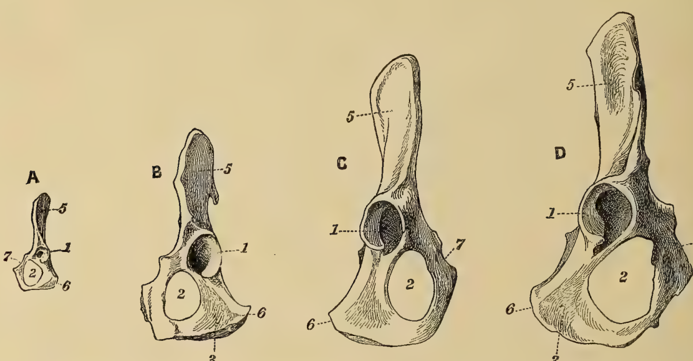

FIG. 4.—A Left innominate bone of a weasel (*Mustela vulgaris*). B left innominate bone of a stoat (*Mustela erminea*). Both from the Pleistocene of Ightham near Maidstone and preserved in Dr. F. Corner's collection. C right innominate bone of a giant polecat (*Mustela robusta*) from the Pleistocene of Ightham (Lewis Abbott Coll.). D right innominate bone of a marten (*Mustela martes*) from the ? Prehistoric deposit of the Edenvale Cave, co. Clare (National Mus., Dublin). Natural size. All bones seen from the ventro-external aspect. 1, acetabulum; 2, obturator foramen; 3, ischium; 4, sacral surface of ilium: 5, iliac surface of ilium; 6, tuberosity of ischium; 7, pubis.

post-scapular fossa is only about half as wide as the pre-scapular fossa at its widest. The scapula in *Meles* differs considerably in shape from those of the other members of the group, especially as regards the post-scapular fossa, which is about equal in size to the pre-scapular. The supra-scapular border forms an angle of about 60° with the spine, and the coracoid border is sharply angular. The development of the spine is greatest in *Meles* and *Lutra*, less in *Gulo*, and slight in

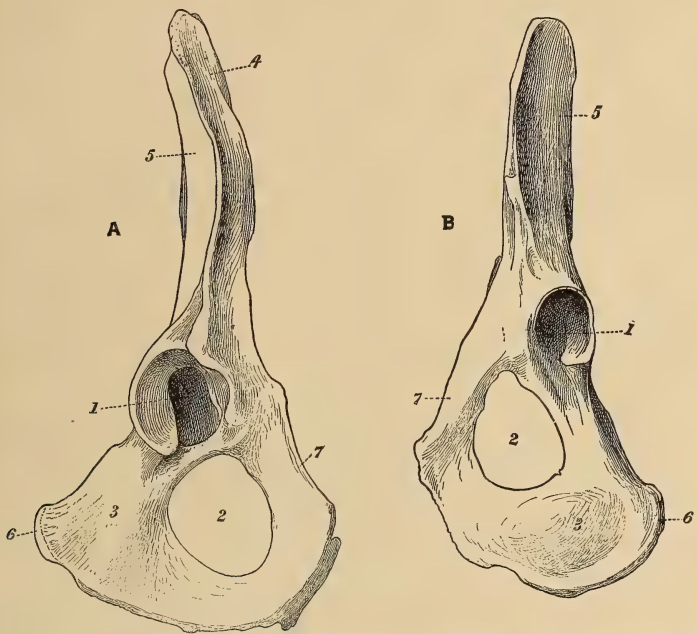

Fig. 5.—A right innominate bone of a badger (*Meles taxus*), from the Pleistocene of the Langwith Cave (Corner Coll.). B left innominate bone of an otter (*Lutra vulgaris*), from the Prehistoric peat of Roach Fen (Sedgwick Mus.). Both bones seen from the ventro-external aspect. Natural size. Lettering as in Fig 4.

Mustela. The acromion is prominent and sharply recurved in all four genera, but less in *Gulo* than in the others.

The Pelvic Girdle.—In *Mustela* and *Lutra* the pelvis is relatively weak and the ilium is little expanded. In *Gulo*, and still more in *Meles*, the ilium is considerably expanded. In *Gulo* the junction between the supra-iliac and acetabular borders of the ilium is gently rounded, while in *Meles*, it forms a prominent projection. The ischial tuberosity is more prominent in *Meles* than in *Gulo*.

(2) Tables of Comparative Measurements of the Limb Girdles.

	Meles taxus, Pleistocene, Langwith (Mullins Coll.).	*Lutra vulgaris*, Prehistoric, Burwell fen (Sedgwick Mus.).
Scapula.		
1. Length from coracoid process to end of spine	9·45	7·7
2. Length measured along glenoid border	7·55	6·0
3. Maximum diameter of neck	2·0	1·8

	Mustela martes, ? Prehistoric, Newhall, Co. Clare (Nat. Mus. Dublin).	*Mustela robusta*, Pleistocene, Ightham, nr. Maidstone (Lewis Abbott Coll.).	*Mustela putorius*, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Mustela vulgaris*, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Meles taxus*, Pleistocene, Langwith (Corner Coll.).	*Lutra vulgaris*, Prehistoric, Reach fen, Cambs. (Sedgwick Mus. Camb.).
Pelvic Girdle.						
1. Maximum length	6·1	5·35	3·9	1·8	11·0	10·4
2. Length from acetabulum to supra-iliac border of ilium	3·2	2·8	2·2	1·1	6·05	4·8
3. Dorso-ventral measurement of ilium at widest point	1·2	1·1	·9	·35	2·8	1·95
4. Antero-posterior diameter of acetabulum	·95	·8	·65	·25	1·7	1·3
5. Length from acetabulum to posterior border of ischium	2·05	1·8	1·35	·5	3·0	4·3
6. Maximum diameter of obturator foramen	1·7	1·35	1·0	·5	2·2	2·3

e. The Limbs.

These show a progressive decrease in relative length from *Gulo,* in which they are longest, through *Meles*, *Lutra*, and the larger members of the genus *Mustela* to *Mustela erminea* and *vulgaris*, in which they are very short. The limbs are sub-plantigrade in *Gulo*, *Meles* and *Lutra*, digitigrade in *Mustela*. The claws are strong (except sometimes in *Lutra*), and in *Mustela* are semi-retractile.

Anterior Limb.—The humerus in *Meles* and *Lutra* is a very powerful bone with strong deltoid and supinator ridges. An ent-epicondylar foramen is present in *Meles*, *Gulo* and *Mustela*, and may or may not be present in *Lutra*. In *Meles* the radius and ulna are also very short powerful bones, the lower end of the ulna bearing a prominent ridge on its inner side. The metacarpals tend to be shorter than the metatarsals, especially in *Lutra*.

Posterior Limb.—In *Mustela* this is considerably longer than the anterior, but the difference is less marked in the other genera. In *Meles* and *Lutra* the femur does not show such conspicuous ridges for the attachment of muscles as does the humerus of these animals. The fibula is slender, and stands somewhat widely away from the tibia except at the extremities. The metatarsals and digits are of greater relative length in *Gulo* than in *Meles*.

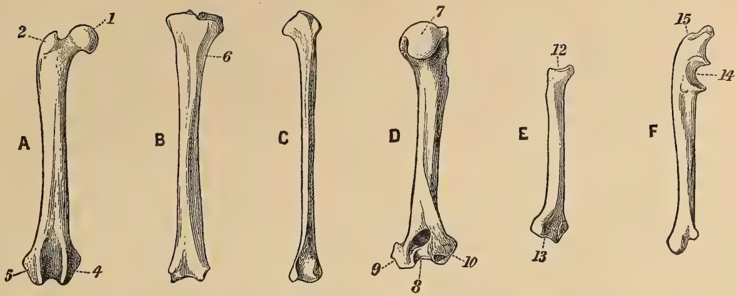

FIG. 6.—Limb bones of a polecat (*Mustela putorius*). A right femur; B left tibia; C right fibula (anterior view); D right humerus; E right radius (antero-external view); F right ulna (inner aspect). All from the Pleistocene of the Brixham Cave and preserved in the British Museum. In Text-figs. 6 to 10 the anterior aspect of the femur and tibia is shown, the posterior aspect of the humerus. Lettering of Text-figs. 6 to 10. 1, head of femur; 2, great trochanter; 3, third trochanter; 4, internal condyle of femur; 5, external condyle of femur; 6, cnemial crest; 7, head of humerus; 8, trochlea; 9, internal condyle of humerus; 10, external condyle of humerus; 11, ent-epicondylar foramen; 12, humeral articulating surface of radius; 13, carpal articulating surface of radius; 14, sigmoid notch; 15, olecranon. All figures of the natural size.

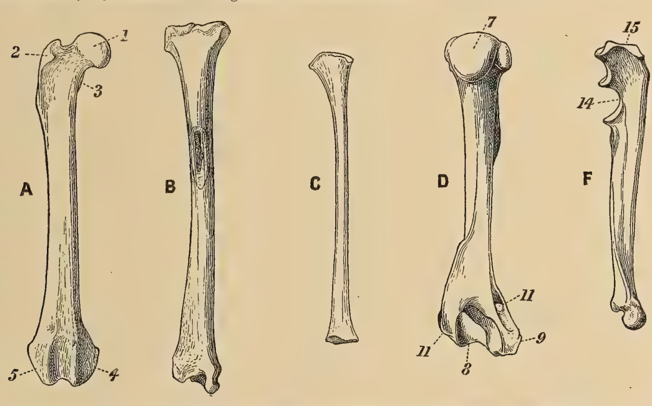

FIG. 7.—Limb bones of a giant polecat (*Mustela robusta*). A right femur; B right tibia; C right fibula (posterior aspect); D left humerus; F right ulna (inner aspect). All from the Pleistocene of the Ightham Fissure. The femur, tibia and humerus are preserved in the collection of Dr. F. Corner, the fibula and ulna in that of Mr. W. J. Lewis Abbott.

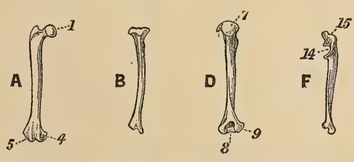

FIG. 8.—Limb bones of a weasel (*Mustela vulgaris*). A right femur; B right tibia; D left humerus; F left ulna (outer aspect). All from the Pleistocene of the Ightham fissure. The femur, humerus and ulna are preserved in the collection of Dr. F. Corner, the tibia in that of Mr. W. J. Lewis Abbott.

(3) TABLES OF COMPARATIVE MEASUREMENTS OF THE BONES OF THE ANTERIOR LIMB.

	Mustela robusta, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Mustela putorius*, Pleistocene, Brixham, No. 48919 (Brit. Mus.).	*Mustela vulgaris*, var. *minuta*, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Meles taxus*, Pleistocene, Happaway, No. M. 5811 (Brit. Mus.).	*Lutra vulgaris*, Prehistoric, Burwell Fen, Camb. (Sedgwick Mus., Camb.).
HUMERUS.					
1. Length	5·7	4·2	2·0	11·5	9·4
2. Maximum diameter at distal end	1·5	1·05	·4	3·3	3·15

	Mustela putorius, Pleistocene, Brixham, No. 48920 (Brit. Mus.).	*Meles taxus*, Pleistocene, Happaway (Brit. Mus.).	*Lutra vulgaris*, Prehistoric Burwell Fen, Camb. (Sedgwick Mus., Cambs.).
RADIUS.			
1. Length	3·0	9·1	6·4
2. Longer diameter at carpal articulations	·6	1·9	1·35

	Mustela robusta, Pleistocene, Ightham, nr. Maidstone (Lewis Abbott Coll.).	*Mustela putorius*, Pleistocene, Brixham, No. 48897 (Brit. Mus.).	*Mustela vulgaris*, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Meles taxus*, Pleistocene, Happaway, No. M. 5808 (Brit. Mus.).	*Lutra vulgaris*, Prehistoric, Burwell Fen (Sedgwick Mus.).
ULNA.					
Length	5·05	3·95	1·7	10·05	8·75

(4) TABLES OF COMPARATIVE MEASUREMENTS OF BONES OF POSTERIOR LIMB.

	Mustela robusta, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Mustela putorius*, Pleistocene, Brixham, No. 48921 (Brit. Mus.).	*Mustela vulgaris*, var. *minuta*, Pleistocene, Ightham, nr. Maidstone (Corner Coll.)	*Meles taxus*, Pleistocene, Happaway, No. M. 5808 (Brit. Mus.).	*Lutra vulgaris*, Prehistoric, Burwell Fen (Sedgwick Mus.).
FEMUR.					
1. Length	6·4	4·7	2·05	12·3	9·45
2. Longer (right to left) diameter at condyles	1·3	1·0	·4	2·7	2·35

Table of Comparative Measurements—*continued.*

	Mustela robusta, Pleistocene, Ightham, nr. Maidstone (Corner Coll.).	*Mustela putorius*, Pleistocene, Brixham, No. 48922 (Brit. Mus.).	*Mustela vulgaris* Pleistocene, Ightham, nr. Maidstone (Lewis Abbott Coll.).	*Meles taxus*, Pleistocene, Happaway, No. M. 4933 (Brit. Mus.).	*Lutra vulgaris*, Prehistoric, Burwell Fen (Sedgwick Mus.).
Tibia.					
1. Length	6·7	4·75	1·85	10·95	10·4
2. Right to left diameter at proximal end	1·25	·95	·35	2·9	2·25

	Mustela robusta, Pleistocene, Ightham, nr. Maidstone (Lewis Abbott Coll.).	*Mustela putorius*, Pleistocene, Brixham (Brit. Mus.).	*Lutra vulgaris*, Prehistoric, Burwell Fen (Sedgwick Mus.).
Fibula.			
Length	5·2	4·65	9·4

IV. CONCLUSIONS.

The present memoir has afforded little scope for critical treatment and is almost purely descriptive in character. No novel conclusions have been reached. Of the eight species of Mustelidæ described, only the marten, glutton and badger appear in British Pliocene deposits, and only *Mustela robusta* and the glutton are no longer found in Britain. No Musteline remains are recorded from Scottish Pleistocene deposits, and only the marten, stoat, badger, and otter from those of Ireland.

Sincere thanks are tendered to Mr. W. J. Lewis Abbott, Dr. F. Corner, and the Rev. E. H. Mullins for kindly placing their large collections of Musteline bones from Ightham and Langwith at my disposal for examination and figuring. I am further indebted to Mr. H. St. George Gray, Mr. A. Newstead, Professor T. McKenny Hughes, Dr. R. F. Scharff and Dr. A. Smith Woodward for the loan of specimens preserved respectively in the Taunton Museum, Sedgwick Museum (Cambridge), Grosvenor Museum (Chester), the National Museum of Ireland and the British Museum. I further wish to thank Dr. C. W. Andrews, Mr. Oldfield Thomas and Mr. H. Woods for help and information, and Mr. J. Green for the care he has taken with the illustrations.

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PLATE I.

Pleistocene Mustelidæ.

Cranium and Mandible.

Polecat (*Mustela putorius*), and Giant Polecat (*Mustela robusta*).

(Natural size.)

Mustela putorius.

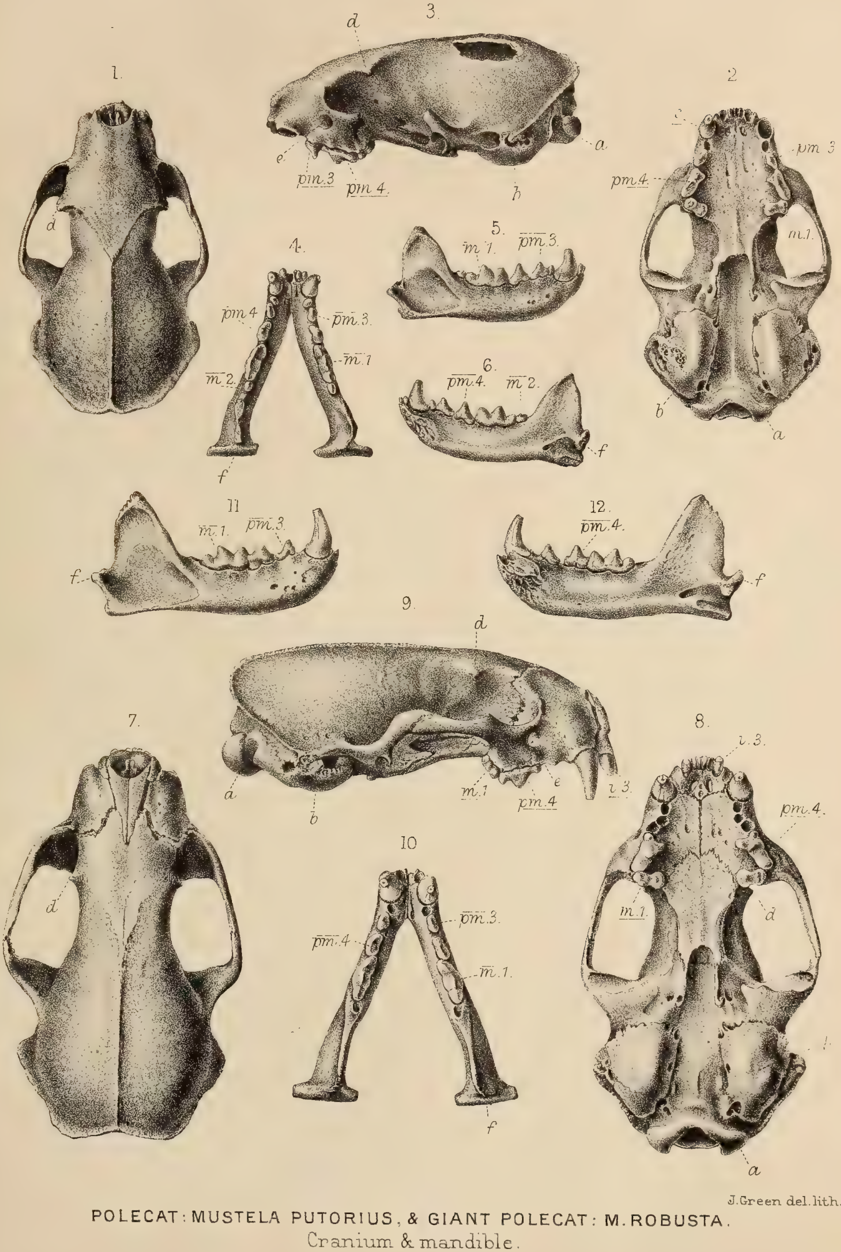
Fig.

1. Dorsal } view of a ? Prehistoric cranium from Ightham, near Maidstone
2. Ventral } (Corner Coll.).
3. Lateral view of a cranium from Brixham (Brit. Mus.).
4. Palatal view of the corresponding mandible (Brit. Mus.).
5. Outer } aspect of the same mandible.
6. Inner }

Mustela robusta.

7. Dorsal } view of a cranium from Ightham, near Maidstone (Lewis Abbott
8. Ventral } Coll.).
9. Lateral }
10. Palatal view of the corresponding mandible (Lewis Abbott Coll.).
11. Outer } aspect of the same mandible.
12. Inner }

a. Occipital condyle }
b. Auditory bulla }
d. Post-orbital process of frontal } Plates I to VI.
e. Infra-orbital foramen }
f. Mandibular condyle }



POLECAT: MUSTELA PUTORIUS, & GIANT POLECAT: M. ROBUSTA.
Cranium & mandible.

PLATE II.

Pleistocene Mustelidæ.

Cranium and Mandible.

Marten (*Mustela martes*), Stoat (*Mustela erminea*), and Weasel (*Mustela vulgaris*).

(All except fig. 12 *a* natural size.)

Mustela martes.

Fig.

1. Dorsal, 2. Ventral, 3. Lateral view of a ? Prehistoric cranium from the Edenvale Cave, co. Clare (National Mus., Dublin).

4. Inner, 5. Outer view of a left mandibular ramus from the Pleistocene of the Langwith Cave, near Mansfield (Mullins Coll.).

Mustela erminea.

6. Dorsal, 7. Lateral view of a cranium from the Pleistocene of Berry Head (Brit. Mus.).

8. Outer aspect of the right ramus of the corresponding mandible (Brit. Mus.).

9. Ventral view of an imperfect cranium from the Pleistocene of Kent's Hole, Torquay (Brit. Mus.).

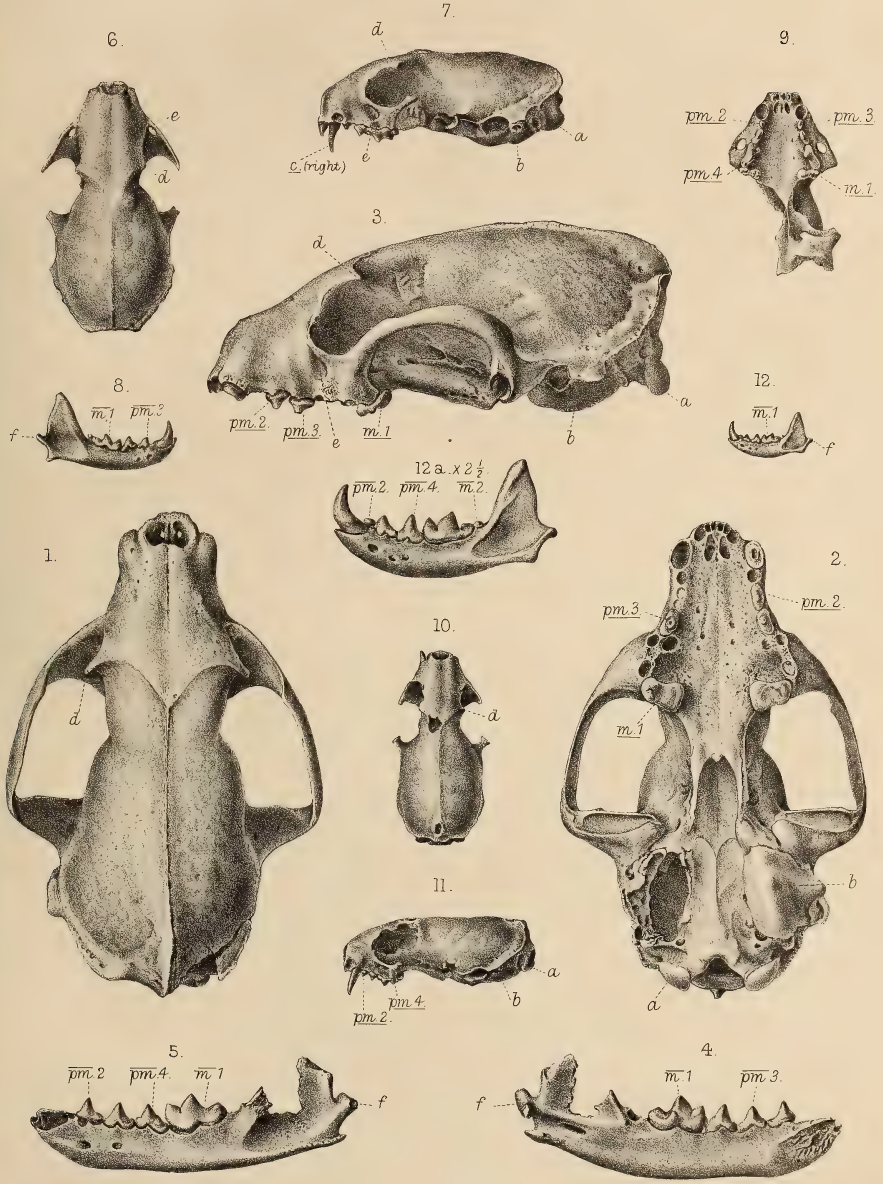
Mustela vulgaris.

10. Dorsal, 11. Lateral view of a cranium from the Pleistocene of the Ightham Fissure, near Maidstone (Lewis Abbott Coll.).

12. Left mandibular ramus seen from the outer side, from the Pleistocene of the Brixham Cave (Brit. Mus.).

12 *a*. The same two and a half times natural size.

Lettering as in Plate I.



J.Green del. lith. et imp.

MARTEN: MUSTELA MARTES, STOAT: M. ERMINEA, & WEASEL: M. VULGARIS.
Cranium & mandible.

PLATE III.

PLEISTOCENE MUSTELIDÆ.

Cranium and Mandible.

Weasel (*Mustela vulgaris*, var. *minuta*), and Badger (*Meles taxus*).

(Natural size except figs. 2 *a* and 4 *a*.)

Mustela vulgaris (var. *minuta*).

FIG.

1. Dorsal, 2. Ventral, 3. Lateral view of a cranium from the Pleistocene of Ightham, near Maidstone (Corner Coll.).

2 *a*. Anterior part of fig. 2 two and a half times natural size.

4. Associated right mandibular ramus seen from the inner side (Corner Coll.).

4 *a*. The same nearly three times natural size.

Meles taxus.

5. Left mandibular ramus of a young individual seen from the inner side.

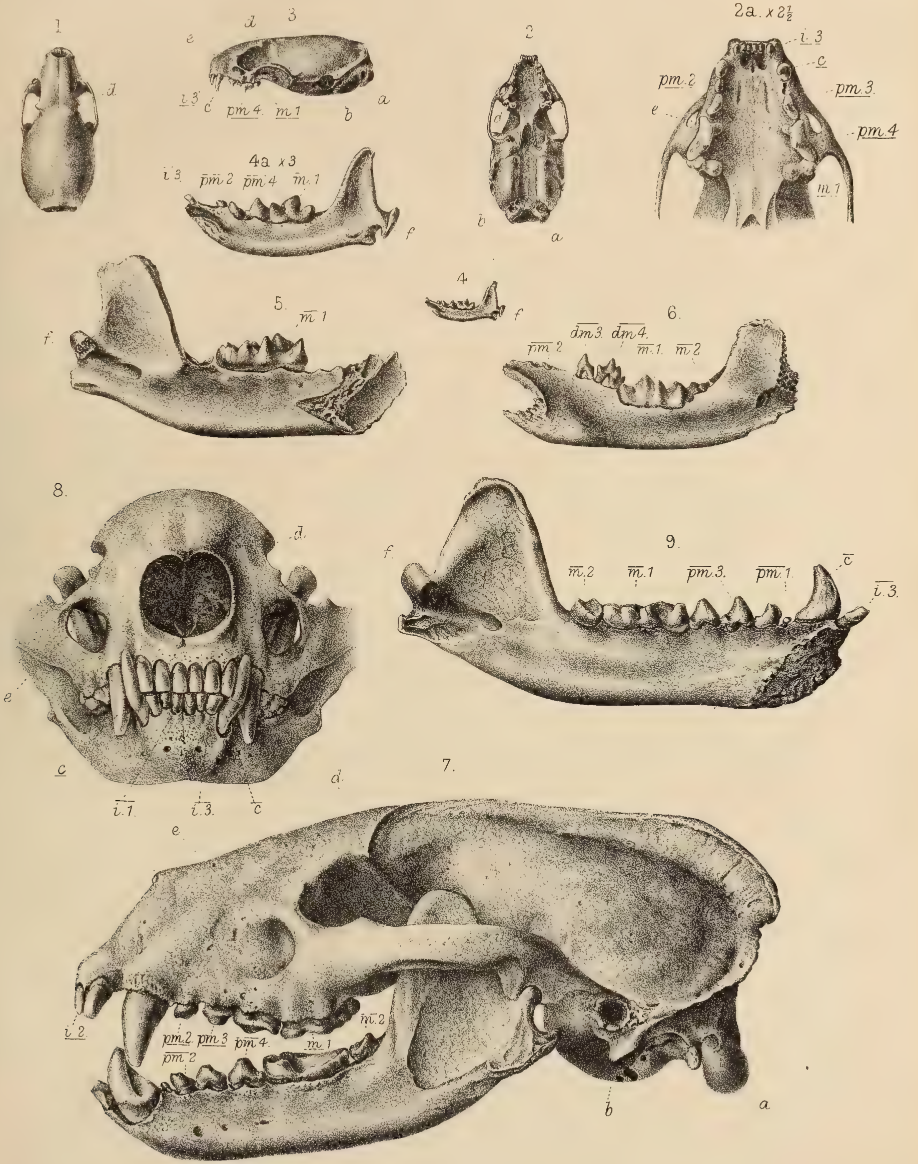
6. Left mandibular ramus of a young individual seen from the outer side.

Both the above specimens are from the Pleistocene of the Happaway Cave; 5 is preserved in Dr. F. Corner's Collection; 6 in the British Museum.

7. Left side view, 8. Anterior view of a cranium and mandible from the Langwith Cave, Mansfield (Mullins Coll.).

9. Inner view of a left mandibular ramus from the same locality (Corner Coll.).

Lettering as in Plate I.



J.Green del.lith.et imp.

WEASEL: MUSTELA VULGARIS (VAR. MINUTA), & BADGER: MELES TAXUS.
Cranium & mandible.

PLATE IV.

PLEISTOCENE MUSTELIDÆ.

Cranium.

Badger (*Meles taxus*).

(Natural size.)

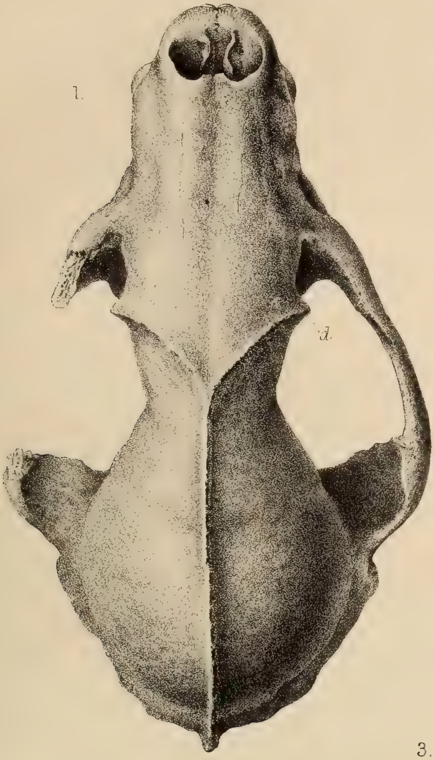
FIG.

1. Dorsal
2. Ventral
3. Lateral

view of a cranium from the Pleistocene of Grovehurst, Sittingbourne (Brit. Mus.).

Lettering as in Plate I.

1.



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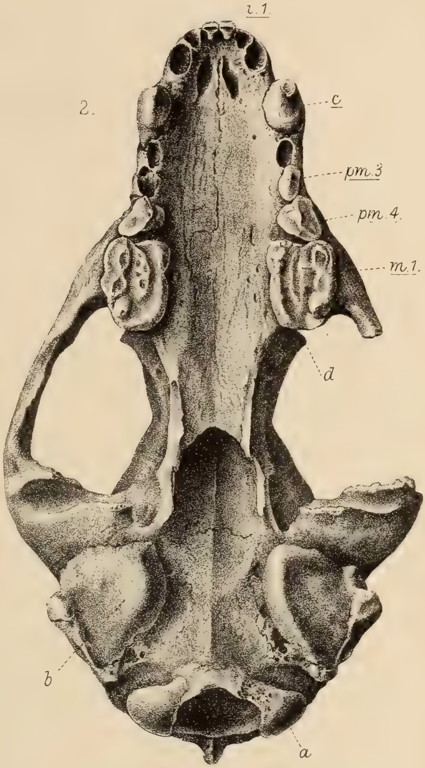

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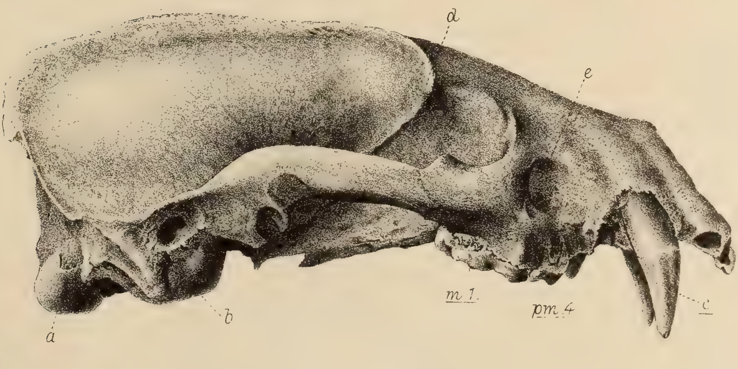


J. Green del. lith. et imp.

BADGER: MELES TAXUS.

Cranium.

PLATE V.

Pleistocene Mustelidæ.

Cranium.

Badger (*Meles taxus*), var.

(Natural size.)

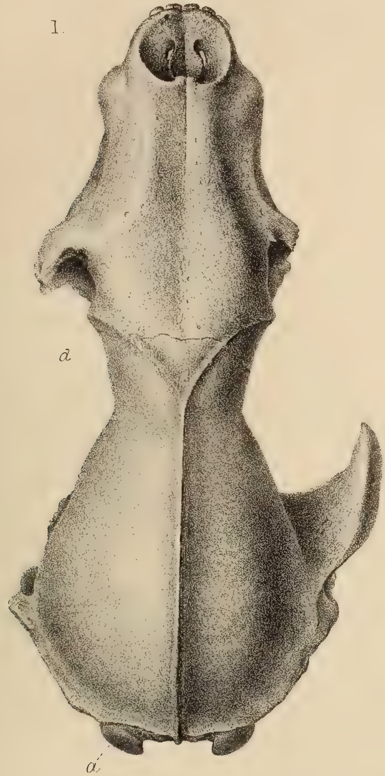
Fig.

1. Dorsal
2. Ventral
3. Lateral

view of a remarkably elongated cranium from the Pleistocene of the Langwith Cave, near Mansfield (Corner Coll.).

Lettering as in Plate I.

1.



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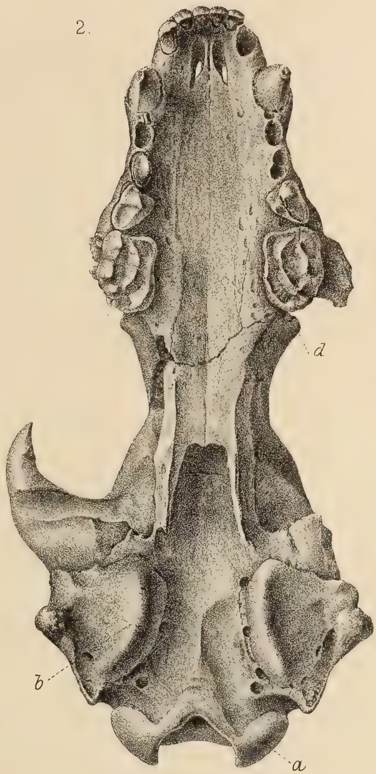

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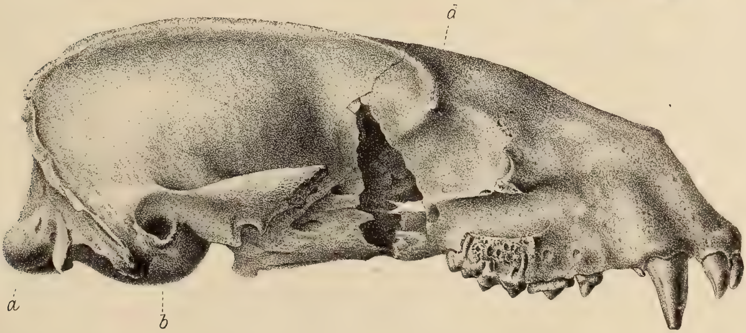


J. Green del. lith. et imp.

BADGER: MELES TAXUS. (VAR.)

Cranium.

PLATE VI.

PLEISTOCENE MUSTELIDÆ.

Cranium and Mandible.

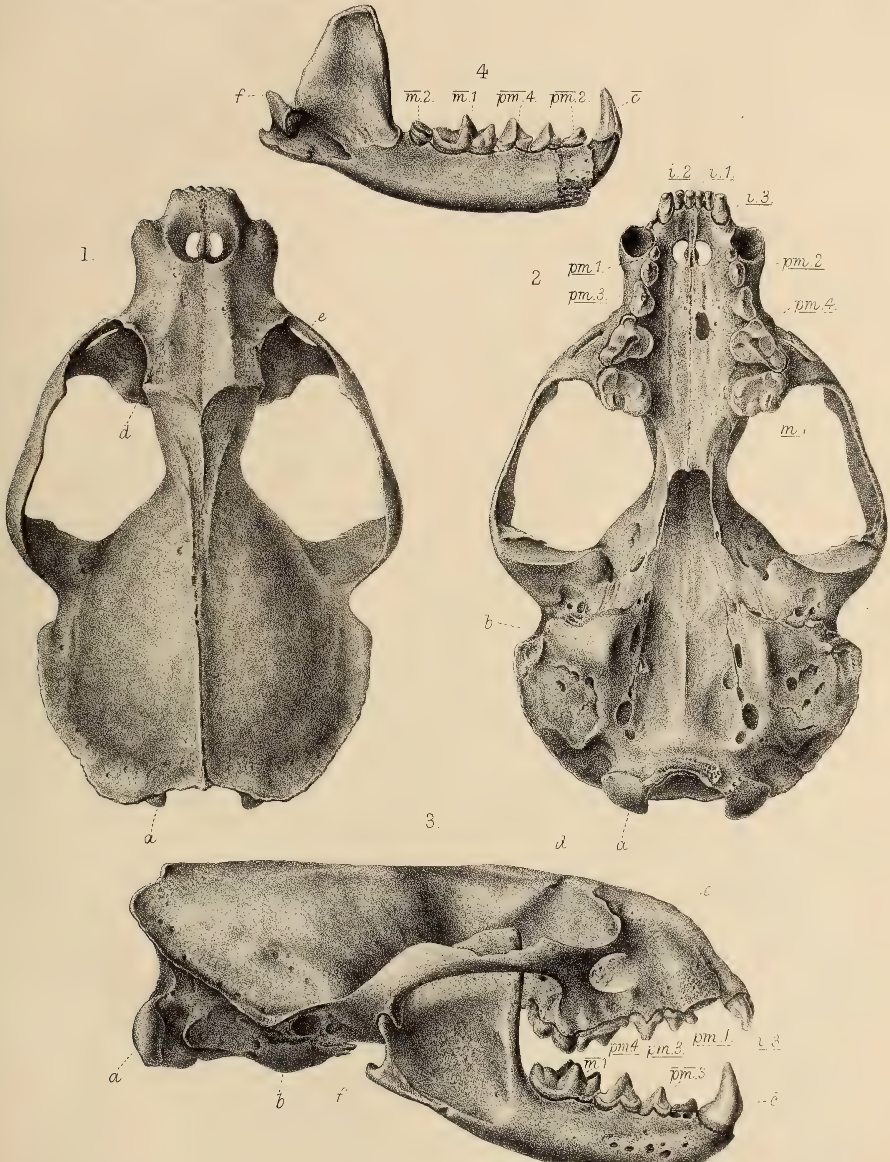
Otter (*Lutra vulgaris*).

(Natural size.)

FIG.

1. Dorsal } view of a cranium from the Prehistoric peat of Burwell Fen
2. Ventral } (Sedgwick Mus., Cambridge).
3. The same cranium with the associated mandible seen from the right side.
4. Inner view of the left ramus of the above mandible.

Lettering as in Plate I.



J. Green del. lith. et imp.

OTTER: LUTRA VULGARIS.
Cranium & mandible

PLATE VII.

Pleistocene Mustelidæ.

Vertebræ.

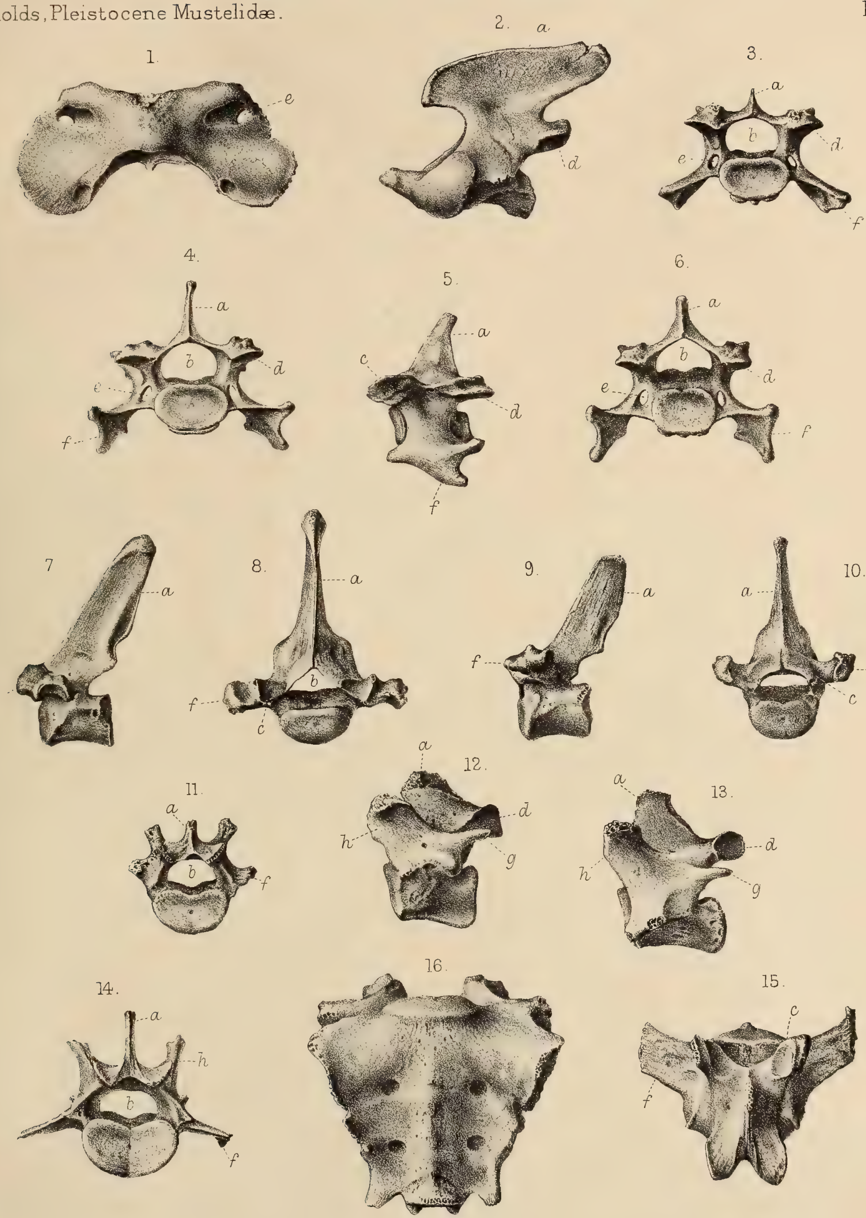
Badger (*Meles taxus*).

(Natural size.)

Fig.		
1.	Atlas, dorsal view	From the British Museum Collection.
2.	Axis, left side view	
3.	Third cervical, posterior view	
4.	Fourth cervical, posterior view	From the collection of Dr. F. Corner, F.G.S., of Poplar.
5.	The same bone, left side view	
6.	Fifth cervical, posterior view	
7.	First thoracic, left side view	From the British Museum Collection.
8.	Dorso-anterior view of the same bone	
9.	Fifth thoracic, left side view	
10.	Dorso-anterior view of the same bone	
11.	Thirteenth thoracic, posterior view	From the collection of Dr. F. Corner, F.G.S.
12.	Fifteenth thoracic, left side view	
13.	First lumbar, left side view	From the British Museum Collection.
14.	Third lumbar, posterior view	
15.	The same bone seen from above	
16.	Sacrum, ventral view	

All these vertebræ are from the Pleistocene of the Happaway Cave, Devon.

a.	Neural spine	Plates VII and VIII.
b.	Neural canal	
c.	Pre-zygapophysis	
d.	Post-zygapophysis	
e.	Vertebrarterial canal	
f.	Transverse process	
g.	Anapophysis	
h.	Metapophysis	



J.Green del.lith.et imp.

BADGER: MELES TAXUS.

Vertebræ.

PLATE VIII.

Pleistocene Mustelidæ.

Vertebræ.

Polecat (*Mustela putorius*), and Otter (*Lutra vulgaris*).

(Natural size.)

Mustela putorius.

Fig.

1. Atlas, dorsal view
2. Axis, left side view
3. Fourth cervical, left side view
4. The same bone, anterior view
5. Sacrum, dorsal view
6. Sixth lumbar, dorsal view

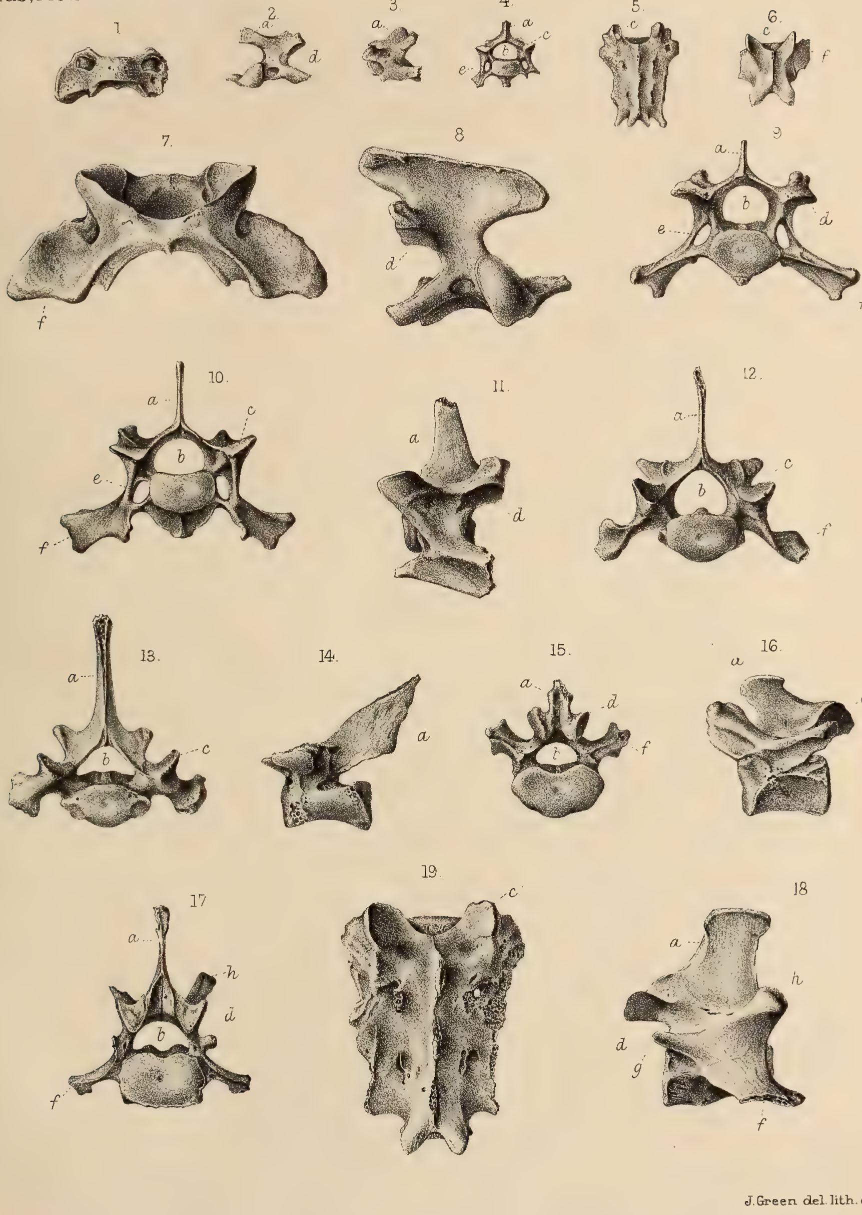
All from the Pleistocene of the Brixham Cave, and preserved in the British Museum.

Lutra vulgaris.

7. Atlas, ventral view.
8. Axis, seen from the right side.
9. Third cervical, posterior view.
10. Fifth cervical, anterior view.
11. Sixth cervical, seen from the left side.
12. Seventh cervical, anterior view.
13. First thoracic, anterior view.
14. Ninth thoracic, seen from the left side.
15. Twelfth thoracic, posterior view.
16. Thirteenth thoracic, seen from the left side.
17. Fourth lumbar, posterior view.
18. Fourth lumbar, seen from the right side.
19. Sacrum, dorsal view.

All the Otter vertebræ figured are from the Prehistoric peat of Burwell Fen, and are preserved in the Sedgwick Museum, Cambridge.

Lettering as in Plate VII.



J. Green del. lith. et imp.

POLECAT: MUSTELA PUTORIUS, & OTTER: LUTRA VULGARIS.
Vertebræ.