PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

A Description of the Skull and Skeleton of a Peculiarly Modified Rupicaprine Antelope (Myotragus balearicus, Bate), with a Notice of a New Variety, M. balearicus var. major

Chas. W. Andrews

Phil. Trans. R. Soc. Lond. B 1915 **206**, 281-305
doi: 10.1098/rstb.1915.0006

VI. *A Description of the Skull and Skeleton of a Peculiarly Modified Rupicaprine Antelope* (Myotragus balearicus, *Bate*), *with a Notice of a New Variety*, M. balearicus *var.* major.

By Chas. W. Andrews, *D.Sc., F.R.S.* (*Brit. Mus. Natural History*).

(Communicated by permission of the Trustees of the British Museum.)

(Received June 4,—Read June 18, 1914.)

[Plates 19–22.]

In the spring of 1909, during a short visit to the Balearic Islands in search of fossil vertebrates, Miss D. M. A. Bate discovered in some cavern deposits in Majorca the remains of the remarkable ungulate to which she afterwards gave the name *Myotragus balearicus*.* Subsequent visits led to the accumulation of more material and to the discovery that the animal also occurred in Minorca, where its remains were found associated with those of a very large land tortoise which has recently been described† under the name of *Testudo gymnesica*. In both Majorca and Minorca the bones were usually found in cave breccias, laid down in caverns which in nearly all cases have been more or less destroyed by the sea, only fragments of the original deposits remaining. An excellent account of these caves and the mode of occurrence of the fossils has recently been published by Miss Bate.‡

In her paper on *Myotragus* Miss Bate§ gave a brief but accurate description of the principal features of the skull, mandible and dentition, together with some remarks on the peculiar metacarpals and metatarsals. In the present communication it is proposed to supplement this account and to give a somewhat detailed description of the whole skeleton of this remarkable form, together with comparisons with the skeletons of other ruminants, with the object of, if possible, determining its affinities. Fortunately the collection is a very extensive one, including many skulls and mandibles, more or less complete and of all ages, together with numerous specimens of nearly all the bones of the skeleton. This abundance of material is especially fortunate, since from its examination the very great range of individual variation occurring in this species can be detected: in some cases no doubt the differences may be due to age or sex, but, allowing for this, the range of variability is exceptionally

* 'Geol. Mag.,' [5], vol. 6, p. 385 (1909).
† 'Geol. Mag.,' [6], vol. 1, p. 100 (1914).
‡ 'Geol. Mag.,' [6], vol. 1, p. 337 (1914).
§ 'Geol. Mag.,' [5], vol. 6, p. 385 (1909).

 [Published, June 30, 1915.

great, affecting in some cases not only the absolute size but also the relative proportions of some parts of the skeleton.

Skull (Plates 19–21).—In the original account of the skull Miss Bate remarks that "although the molars approach in size those of the common goat, the whole skull is characterised by what may be described as a general 'shortening' both before and behind the orbit, the position of which is very high, while its margin is slightly prominent. The lachrymal is short and wide and the portion of the malar situated in front of the orbit is greatly reduced, causing the eye to be placed very far forwards. The opening of the auditory meatus is extremely small. Two roughened projections occur on the upper border of the foramen magnum. The horns, which arise entirely from the frontals, are short and circular in section, the one preserved in the figured specimen (M. 10942) measuring 49 mm. (incomplete at tip) in length and 50 mm. in circumference at its base."

It is now proposed to expand this general description and compare the skull with that of several possibly related forms, including more especially *Capra*, *Ovis*, *Nemorhædus*,* and *Budorcas*. At the same time it does not seem necessary, in most cases, to give a detailed description of the several bones, since in its general structure the skull is that of a typical member of the Bovidæ.

The occipital surface (Plate 19, fig. 4), which is narrower in proportion to its height than in *Capra*, makes an obtuse angle with the plane of the parietals, and, when the basicranial axis is horizontal, slopes slightly forwards, though to a less extent than in *Nemorhædus*. The portion of the lambdoidal crest borne by the supraoccipital is very strongly developed and much roughened, especially in those individuals which are regarded as being probably males. In these also the upper border of the foramen magnum is produced into a pair of blunt prominences, overhanging the opening, and no doubt serving for the attachment of a strong ligament.

The occipital condyles (*oc. c.*) are large and their outer angles are sharply defined, fitting into a corresponding notch in the condylar surfaces of the atlas; the whole arrangement being such as to allow of a maximum degree of flexion of the head downwards, a character perhaps dependent on the manner in which the horns were used. In most specimens the condyles are continuous with one another in the middle ventral line, while in *Capra*, *Nemorhædus*, and in other forms examined they are separated by a greater or less interval, and may pass forward a little on to the hinder face of the posterior basioccipital tuberosities.

The paroccipital processes (*p.p.*) are large and project a little below the level of the condyles: towards their ventral end they are curved inwards and, narrowing slightly, terminate in a flat facet. At their base they are separated from the occipital condyles by a very deep fossa into which the atlas fits when the head is strongly

* In this paper this generic name is used for the Gorals, as in Lydekker's 'Catalogue of the Ungulate Mammals in the British Museum (Natural History),' vol. 1 (1913).

bent downwards. Internally this fossa is bounded by the posterior basioccipital tuberosities, and into it just above these prominences the foramen for the hypoglossal nerve opens.

The *supraoccipital* (*s. oc.*), or, probably, rather the fused interparietal, extends considerably on to the skull roof and its suture with the parietals is convex forwards. The *parietals* (*par.*), which form most of the gently convex cranial roof, vary greatly in length in different individuals, so that scarcely two specimens are alike in the form of the skull behind the horns. The type specimen (M. 10942) (Plate 19, figs. 1–4) is an example of a skull with long parietals, while in that (M. 10945) figured in Plate 21, fig. 2, they are short. The temporal ridge is continued backwards and upwards on the parietals nearly to the anterior angles of the interparietal. The fronto-parietal suture is slightly convex forward and its most anterior point is nearly opposite the posterior border of the bases of the horns. In *Capra* and *Ovis* it is considerably further back. In this respect *Nemorhædus* approaches *Myotragus* most nearly, while *Rupicapra*, in which the suture is concave forward, is most dissimilar.

The large *frontals* (*fr.*) form a nearly flat forehead which makes an angle of about 110° with the plane of the parietals. The horn cores, which arise far behind the orbit, project backward in almost the same plane as the forehead, curving slightly backwards and diverging a little from one another. They are circular in section and are solid to their base, no prolongations of the frontal sinus extending into them. In *Capra*, *Ovis*, and *Nemorhædus* the horn cores are hollowed to a varying extent, being least so in *Ovis*. *Myotragus* seems to be exceptional in this respect. On the whole except for this peculiarity *Nemorhædus* seems to approach *Myotragus* most nearly in the form and position of its horns, though in it they are not quite so far behind the orbits. The temporal fossæ are very large and the temporal ridges are continued from the parietals on to the frontals, passing just beneath the base of the horns, in front of which they form prominent ridges continuous anteriorly with the posterior border of the post-orbital process. This latter is broader and shorter than in *Nemorhædus*, in this respect resembling the same structure in the sheep but differing from it in looking almost directly outwards instead of outwards and backwards. In most specimens the orbit is nearly circular in outline, but in the type specimen the antero-posterior diameter is rather the longer. The chief peculiarity of the orbit is that it looks much more upward and forward than in any of the genera compared; this seems to result from the great deepening of the alveolar portion of the maxillæ, consequent upon the extreme hypsodonty of the molars. The rim of the orbit is only slightly prominent, but is more so than in *Nemorhædus*. The supraorbital foramina vary in position, they may be just behind the orbit or opposite its posterior third, they are in a line with the horns and a slight groove runs forward from them on to the face, but is not so well marked as in *Nemorhædus*. Anteriorly the frontals join the lachrymals and nasals. The latter (*na.*) are thrust in between the frontals, terminating

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

as a rule in a wedge-shaped point, but in the type specimen in a short transverse suture; their posterior end is situated a little in front of a line joining the middle of the orbits. In front of their wedge-like prolongation between the frontals, the relatively narrow nasals have their sides nearly parallel and unite first with the lachrymals, then for some distance with the maxillæ; there is no lachrymal vacuity, though the bone seems to be very thin where it usually occurs. At their anterior end the nasals overhang the nasal opening in a small median prominence, and laterally widen out, sending down a process which unites in suture with the upper edge of the facial process of the premaxillæ. This peculiarity, which seems to be connected with the necessity for an unusually rigid support for the premaxillæ, is apparently confined to *Myotragus*. In *Budorcas* and *Nemorhædus* the nasals have little or no contact with the maxillæ and are widely separated from the premaxillæ. In *Rupicapra* they are more similar in being narrow and remaining nearly the same width throughout, they also have a long suture with the maxillæ, but remain widely separated from the premaxillæ; in *Oreamnus* the relations of the nasals to the maxillæ and premaxillæ are similar. In *Ovis* the premaxilla does not, as a rule, quite reach the nasals but in *Capra* it does for a short distance.

Lönnberg* considers that the reduction of the premaxillæ in *Budorcas*, *Nemorhædus*, *Oreamnus*, and *Rupicapra* is consequent upon their habit of using the thick lips for grazing and not biting against the premaxillaries. On the other hand, from the firmness with which the premaxillaries are held between the nasals and maxillæ in *Myotragus* it might be inferred that they were used in biting, and this is confirmed by the very large size of the median incisors in the lower jaw, which, growing from a persistent pulp, must have undergone constant attrition against the hard pad borne by the premaxillaries, which would thus require more extensive support than is found in the other genera.

Probably in correlation with the shortening of the face the *lachrymal* (*lac.*) has a much smaller extension on the facial surface than on *Capra* or *Nemorhædus*.

The *premaxillæ* (*pmx.*) are slender and lightly built bones, but at the same time their facial processes are relatively large and, as above noted, are supported by a suture with the maxillæ behind and at their upper ends with the nasals in front. The anterior region which bore the pad against which the lower incisors bite is somewhat expanded and the edges slightly turned up; there seems to have been a slit-like median foramen between the two halves of this anterior expansion. Posteriorly, the palatine processes separate the pair of oval incisive foramina, which do not extend so far forwards as usual, *e.g.*, in *Nemorhædus*, *Rupicapra*, *Ovis*, etc., the expanded pad-bearing region being relatively smaller in those genera. Behind the incisive foramina the ends of the palatine processes expand a little and are wedged in between the maxillæ. Although there is no doubt that the peculiarly

* 'Zool. Soc. Proc.' (1900), p. 706.

modified lower incisors bit against a hard pad as in the ordinary Bovidæ, it is interesting to note that in one of the three complete examples of the premaxillary region there is a distinct shallow oval alveolus (Plate 20, fig. 2, *al.*) situated on the border of the left premaxilla about where the last incisor might be expected to be situated. No trace of an alveolus is found on the opposite side in this specimen or on either side in the others.

The *maxilla* (*mx.*) in correlation with the shortening of the face and reduction in the number of premolars is short from before backwards, but at the same time is very deep in consequence of the extreme degree of hypsodonty attained by the molar teeth. On the facial surface of the maxilla above *m* 2 is a well-marked maxillary tuberosity from which the masseteric ridge runs back along the lower border of the jugal, becoming continuous posteriorly with the lower border of the zygomatic arch. The infraorbital foramen is situated rather high up and over the interval between *pm* 4 and *m* 1; usually it is above the second or third premolar, although in *Budorcas* and in *Ovibos* it may be over the last premolar: in *Nemorhædus* it is over *pm* 3. In front of the premolars the palatal region of the maxilla is greatly narrowed, and is bounded by sharp ridges which first converge, then diverge again near the union with the premaxillæ; between these ridges the palatal surface is reduced to a narrow rounded groove. These ridges occur in Ruminants generally but do not seem to be so prominent in other genera, and at the same time the palate between them is not so deeply grooved; in this respect *Oreamnus* seems to approach *Myotragus* most nearly. Between the cheek-teeth the palatal surface is gently concave from side to side. The *palatines* (*pal.*) send a wedge-shaped plate between the maxillæ, their anterior point being opposite the anterior lobe of *m* 2; a little further back the suture between the two bones is interrupted by a pair of rather large, oval posterior palatal foramina, behind which it is continued back to the inner side of the posterior angle of the socket for *m* 3. The posterior palatine notch is nearly opposite the hinder border of the last molar, but in the middle line the united palatines carry the narrow internal narial passage some distance behind the dental series. In *Nemorhædus* the posterior palatine notches extend to the middle of the last molar, and the narial passage, which is relatively wide, opens opposite the hinder end of the tooth series. In *Budorcas*, on the other hand, both the notches and the narial opening are behind the teeth, but *Myotragus* seems to be peculiar in the prolongation backwards of the narial passage and in the narrowness of its opening. The *pterygoids* are not preserved in any specimen. The *jugal* (*j.*) has a much smaller extension on the face in front of the orbit than in *Capra* or *Nemorhædus*; beneath the orbit it is deep, its lower border joining the masseteric ridge already referred to. The post-orbital process is short and broad, and behind it the zygomatic portion bears a strong ridge parallel to its upper border; the bone terminates a little behind the level of the anterior edge of the glenoid surface of the squamosal. This

articular surface, which might have been expected to have undergone some modification in consequence of the change in the lower incisors, shows no special peculiarity. It is gently convex in all directions, and wider from side to side than from before backwards: there is a small post-glenoid foramen. The whole structure of the articulation for the lower jaw is closely similar to that seen in *Nemorhædus*.

The *tympanic bulla* (*tymp.*) is strongly compressed and postero-externally is firmly united to the paroccipital process. This compressed form of tympanic is regarded by Winge* as primitive, and is given by him as one of the chief characters of his *Nemorhædus* group, a division in which he includes not only the forms usually placed there (*Nemorhædus*, *Capricornis*, *Budorcas*, *Rupicapra*, *Oreamnus*), but also *Bos*, *Capra*, *Ovis*, and *Ovibos*. The auditory meatus was narrow and in the type specimen its walls are thick, so that the auditory opening is small. Immediately below the inner end of the auditory meatus the external face of the tympanic bulla is deeply grooved by the fossa for the tympano-hyal. The general form of this region of the skull is much as in *Ovis* and *Budorcas*; in *Nemorhædus* the bulla is scarcely at all inflated.

The basicranial axis makes an angle of 160–165° with the palate, much as in *Ovis* and *Oreamnus*; in *Budorcas* the deflection of the face is considerably greater. The posterior tuberosities of the basi-occipital are strongly prominent, nearly transverse ridges, and it appears that in some cases the articular surface for the atlas is continued on to their anterior face. In front of them the bone is not broad and quadrate, as in the sheep, but narrows gradually forwards, the middle line being grooved longitudinally; the groove deepens a little between the anterior muscular tuberosities, which form very slight rugose prominences, oval in outline. In the basisphenoid region the ventral face of the basis cranii becomes narrow and gently convex from side to side. In its general form the basis cranii of *Myotragus* is most nearly similar to that of *Oreamnus*, from which that of *Nemorhædus* does not differ greatly. In *Budorcas* the region in front of the posterior tuberosities is strongly convex, both from side to side and from before backwards.

* "Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa, Minas Geraes, Brazilien." 'E Museo Lundii,' vol. 3, p. 127 (1906).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The dimensions (in centimetres) of the skull are :—

	A. (M. 10942.)	B. (M. 10945.)	C. (M. 10946.)	D. (M. 10962.)
Length in straight line from middle of lambdoid ridge to posterior angle of the nasals	9·1	—	9·6	10·5
Greatest width of occipital surface	5·8	6·0	5·8	7·2
Greatest height of occipital surface	4·0	3·8	4·2	4·7
Width between outer angles of occipital condyles	4·1	3·7	3·7	4·8
Height from basis cranii to middle of fronto-parietal suture	5·1	4·9	4·8	6·2 (approx.)
Width of narrow posterior region of palate	1·0	—	1·2	1·4
Width of palate at middle of *m* 2	2·8 (approx.)	—	3·0	3·6 (approx.)
Least width of snout in front of cheek teeth	1·9	—	2·0 (approx.)	2·2
Antero-posterior diameter of orbit	2·6	2·5	2·6	2·8
Vertical diameter of orbit	2·2	2·4	2·5	2·5
Width of skull at base of horns	4·9	5·3	4·7	6·3
Width of skull between the orbits	3·4	—	3·2	3·7
Length of horns	5·9 (approx.)	—	5·6	8·2
Diameter of horns at base	1·5	2·0	1·5	2·2
Length of molar-premolar series	5·1	—	4·1	—
Length of molar series	3·5	3·0	4·7	6·3

A is the type specimen, D a skull from Minorca showing the larger dimensions.

Upper Dentition (Plate 19, figs. 2 and 5, and Plate 20, figs. 3, 5, and 6).—The small slender premaxillæ, as usual in the group, bear no incisors, the lower teeth having bitten against a hard pad. In one specimen (Plate 20, fig. 2) referred to above there is, about the middle of the alveolar border of the left premaxilla, a small alveolus-like depression (*al.*), which seems to indicate that occasionally small and probably quite transitory incisors may develop, but this, no doubt, is a rare individual peculiarity. In the sheep it is stated that no trace of the enamel organ of any of the upper incisors is formed, and I can find no record of the occurrence of these teeth in any member of the Bovidæ. The canines, as usual, are entirely absent. The cheek teeth present in the adult are *pm* 3–4 and *m* 1–3, the second premolar present in nearly all the other members of the group having been lost. At the same time the third and fourth premolars are greatly reduced and vary much in size, both according to the state of wear and also in different individuals. *Pm* 3 in most specimens is a small columnar tooth, much curved, the convexity being directed forwards and outwards; as a rule it narrows considerably towards the root. The outer face is slightly grooved vertically, and the wear surface is very oblique. In other specimens *pm* 3 is reduced to a small styliform peg, lying close against the anterior face of *pm* 4 and evidently functionless.

Pm 4 is likewise a columnar tooth and is composed of an outer and an inner crescent; the tooth as a whole is somewhat strongly curved. The antero-external

angle of the crown forms a slightly prominent ridge and there is a trace of a similar ridge at the postero-external angle. The outer cusp forms a very slight prominence on the external face of the tooth. The median valley is simply crescentic in form without any spurs projecting from its walls. In advanced wear the crown of the tooth becomes much shortened from before backwards and all trace of pattern disappears.

The first molar (*m* 1) is remarkable for its extreme hypsodonty, surpassing in this respect the first molar of any other member of the family. In a young individual in which the last milk molar (Plate 20, fig. 3, *mm* 4) is nearly worn out, the root of the first permanent molar is situated nearly on the level with the lower border of the nasal bone or not far below the level of the top of the orbit. In a sheep in which the teeth are in approximately the same state of wear the root of the molar does not extend half so far up the face and is a little below the level of the lower border of the orbit. Moreover in the sheep, the skull of which is more than twice the size of that of the young *Myotragus*, the first molar is absolutely smaller. The tooth itself is columnar and very strongly curved, the convexity being outwards; it narrows greatly towards the root. In an early state of wear the crown shows the usual four crescents and is much longer than wide. In an advanced state of wear the crown becomes square in outline or even wider than long; at the same time all trace of the pattern is lost, the only trace of the original structure being a remnant of the median valley on the inner side and of the mesostyle on the outer. In *Capra* and *Ovis*, in which the molars are very hypsodont, though to a less extreme degree, similar changes in the tooth pattern take place in course of wear, but not to such a remarkable extent.

On the outer face of the first molar the mesostyle is strongly developed, forming a sharp ridge extending up nearly to the root: the antero-external angle (parastyle) likewise forms a sharp ridge but does not extend so far up. At the posterior end of the crown the metastyle forms a sharp angle projecting backwards. The antero-external cusp (paracone) forms a slight convexity on the outer face of the tooth but the outer side of the postero-external cusp (metacone) is nearly flat. The inner crescents are rounded internally and the valley between them extends up nearly to the neck of the tooth. In a very young individual the postero-internal crescent (hypocone) is separated by a notch from a small lobe of the hinder wall of the tooth (? a hypostyle), but in wear they soon become continuous. The anterior valley is crescentic but spurs projecting from its wall cut off a small portion of its posterior end and give rise in course of wear to a separate island which is situated opposite the inner end of the vertical inner groove. The posterior crescent likewise may have a small spur projecting from the hinder part of its outer wall, but in *m* 1 this is frequently wanting.

The general form of *m* 2 is very similar to that of *m* 1: it also is very hypsodont and narrows towards its root. In *m* 3 the mesostylic ridge converges on the anterior (parastylic) ridge towards the root of the tooth; at the same time the posterior lobe widens out by the increasing prominence of its postero-external angle, which forms a well-marked column. The consequence of this is that

while in the young the grinding surface of *m* 3 is much like that of *m* 2, in later life the column described forms a sort of talon.

Upper Milk Dentition (Plate 20, figs. 3 and 3A, M. 10949).—There seem to have been three upper milk molars, *mm* 2 being a very small tooth, represented in the specimens by a broken root only: in some individuals it may have been absent, and in any case had no successor. The second (*mm* 3) consists of four crescentic cusps, the internal rounded, the external forming scarcely any projection on the outer side of the tooth. The parastyle and mesostyle are well developed. The last milk molar (*mm* 4) is similar but considerably larger and the antero-external cusp forms a slightly stronger ridge on the outer face of the tooth. In both *mm* 3 and *mm* 4 the crown narrows rapidly towards the roots. Apart from the high degree of hypsodonty and the reduction of the premolar series the upper cheek teeth do not present any striking differences from those of the Ægodontia generally, and comparison with the dentition of other genera does not afford the assistance that might be expected in settling the precise affinities of *Myotragus*. In a general way the teeth are very similar to those of *Capra*, but this likeness is largely due to the great height of these crowns. The presence or absence of spurs on the inner walls of the crescents seems to depend a good deal on the state of wear, some of these projections only appearing in much worn teeth. The spurs at the posterior end of the anterior crescent, cutting off from it a separate island as wear advances, occur in all the genera with which comparison has been made: the separate island is especially large and distinct in *Budorcas*. The spur in the posterior crescent is less constant; it seems to be absent in *Capra*; it appears during wear in *Ovis* and is present in *Nemorhædus* and *Rupicapra;* in *Budorcas* it is slightly developed in *m* 2 and *m* 3.

Mandible (Plate 19, figs. 1, 7, 8, and Plate 20, figs. 7–10).—Except for the modifications resulting from the great enlargement of the anterior incisors, the mandible differs in no important character from that of a goat or an antelope. The coronoid process is high, slender and strongly recurved. The articular surface, in which some modifications of form might have been expected, is almost identical with that found in the goat, though perhaps it is proportionately a little narrower from side to side. In *Budorcas* and *Nemorhædus* the articular surface slopes a little more downwards towards its inner end, but is otherwise similar. The angle of the jaw is rounded, and the prominence on the outer side for muscle attachment is very strongly developed. The horizontal ramus is shorter and stouter than is usual in members of the group, the shortening being particularly marked in the region of the diastema between the cheek teeth and the incisors. This shortening of the mandible is accompanied by the reduction of the premolars, of which usually only *pm* 4 is present: in one small and slender specimen, and perhaps in the type, the socket for a very small *pm* 3 is present.

The mental foramen in situated a little in front of the fourth premolar. Owing to the absence of the canines and lateral incisors the symphysial region does not form the broad expansion usual in the Bovidæ, but remains comparatively narrow with

parallel sides. The symphysis is strong, but seems to have remained open even in very old individuals.

Lower Dentition.—It is in the arrangement of the lower incisors (Plate 19, fig. 8) that *Myotragus* is most remarkable, differing entirely in this respect from any other Artiodactyle ungulate. Usually in the Bovidæ the symphysial portion of the mandible bears three pairs of incisors and a pair of incisiform canines, which form a closed series of more or less procumbent cutting teeth. In *Myotragus* the canines and the two lateral pairs of incisors are lost, and the series is functionally replaced by the greatly enlarged middle incisors (Plates 19 and 20, fig. 8). These are greatly elongated curved teeth growing from persistent pulps: they extend back in the jaw to a different degree in different individuals, but may reach the level of the hinder lobe of *m* 2. Each incisor has nearly parallel sides and is slightly twisted spirally: the anterior (lower) face is convex from side to side, and is covered with a thick coat of enamel, the surface of which is raised into more or less strongly marked longitudinal ridges (Plate 20, fig. 8). The posterior (upper) surface is deeply channelled and without enamel. At their distal ends the two incisors are in close contact in the middle line, and their common surface of wear is crescent-shaped (Plate 19, fig. 8) and nearly parallel to the grinding surface of the molars: its anterior convex edge is kept sharp by the presence of the enamel in that region. The size of these teeth varies to a remarkable degree in different individuals, being especially much more slender in some than in others.

There can be no doubt that the enlarged incisors are the middle pair, and it seems certain that they belong to the permanent and not to the milk dentition. Fortunately the collection includes numerous mandibles of very young individuals, some probably only just born. In these the large median pair of incisors was already present, and in specimens in which the first molar is just appearing they may extend back in the jaw as far as the level of the third milk molar. At this stage there is a small socket for a second incisor situated immediately above and behind the alveolus for the large median tooth: this small tooth probably belongs to the milk series, and it might be supposed that the median pair did also, but in one specimen a small aveolus first occurs immediately above the large socket, and seems to indicate that these teeth had milk predecessors, lost at a very early age and probably never functional. In these young individuals, as noted above, the median incisor may extend back to the level of the third milk molar, but in some cases it only reaches to about the hinder end of the symphysis. The great extension of these teeth in the adult seems to be the result of their growth backwards in the jaw as the premolars and anterior molars become worn and shortened. In one specimen the small lateral incisor persisted until the second molar was in wear and the fourth premolar just being cut.

The peculiar character of the incisors described above has no parallel among the Artiodactyle ungulates, and the steps by which it was acquired can only be surmised.

It is notable that in many antelopes, *e.g.*, the Gazelles, the median incisor is considerably larger than the lateral ones. Moreover, in some genera, *e.g.*, *Ovis*, the middle incisors acquire a very considerable degree of hypsodonty. Probably the antelope from which *Myotragus* has descended combined both these peculiarities and possessed enlarged and at the same time hypsodont median incisors, from which the form of tooth seen in *Myotragus* might arise.

In the lower jaw there is usually only one premolar (*pm* 4), but in a few specimens a small alveolus shows that a greatly reduced *pm* 3 was sometimes present. In the Bovidæ generally there are usually three premolars, which are reduced to two in a few genera (*e.g.*, *Connochætes*, *Pantholops*, *Saiga*, *Antedorcas*), but as far as I can find the reduction is never carried further.

The fourth premolar in an unworn condition consists of a high anterior crescentic cusp, the anterior and posterior angles of which bear prominent tubercles on their inner side. The hinder part of the tooth is formed by a small crescent, much lower than the anterior one : its anterior end is in contact with the outer face of the main cusp, while posteriorly it forms the hinder wall of the tooth and joins the postero-internal angle of the main cusp. In wear the pattern is quickly lost, and the surface becomes rhomboidal in outline, rather wider posteriorly than in front.

The first molar is an extremely hypsodont columnar tooth, consisting of the usual two pairs of crescents. Like the upper first molar, it decreases in antero-posterior diameter towards the root, though to a less degree ; at the same time it widens from side to side, so that when first coming into wear the outline of the crown is very different from that seen in an old tooth, in which it is very short from before backwards and without any trace of pattern. The pillars formed by the inner cusps project very little on the inner face of the tooth, which is nearly flat except at the anterior and posterior angles, which form slight ridges ; the posterior ridge projects a little behind the anterior border of the next tooth. The outer face of the outer column is rounded ; there is no trace of an accessory column. The valleys form simple crescents without any spurs projecting into them.

The second molar is very similar to the first, but the third, as usual, differs in possessing a large posterior lobe, the wear surface of which is oval, or, rather, semi-circular, the outer face being nearly flat and separated from the rest of the tooth by a well-marked vertical ridge.

The height of the crown of the lower molars is so great that when one of the series is just coming into wear its lower end forms a strong prominence or even a distinct tuberosity on the ventral border of the mandibular ramus, and is only covered by a very thin wall of bone. This condition is well shown on Plate 20, fig. 9, where a portion of a mandible is figured in which *m* 3 is just coming into wear, and its lower end forms the prominence marked *t*. As wear proceeds, remarkable changes in the form of the mandibular ramus take place, until in extreme old age, when the last molar is worn close down to its roots, the lower portion of the mandibular ramus

beneath the molars is to a great extent absorbed and may be reduced to the condition shown on Plate 20, fig. 10, where *m* 3 is seen worn to the roots while the ventral portion of the ramus is reduced to a thin sharp-edged plate of bone, the outer face of which is deeply concave from above downwards; at the same time the bone becomes thin and brittle. Although, of course, changes commonly take place in the form of the mandibular ramus when highly hypsodont teeth are worn down, no case has been observed in which the change is so extreme as in *Myotragus*.

Lower Milk Dentition (Plate 20, fig. 7).—The occurrence of milk incisors has already been referred to above. The milk molars present are the third and fourth. The third is a small two-rooted tooth, the crown of which is triangular in section with a small, imperfectly separated anterior column; this tooth usually has no successor. The fourth milk molar is of the elongate trilobate form usual in the group. The inner face is nearly flat, the cusps forming very slight projections; the antero-external and postero-external angles, on the other hand, form well-marked ridges. Towards its root the crown of this tooth narrows considerably from before backwards, as in the sheep. It is replaced by the premolar before the last molar is cut; in the sheep the reverse seems to be the case.

The remarks made as to the value of the upper dentition for determining the affinities of *Myotragus* apply with even greater force to the lower teeth. The dentition as a whole seems to have been subjected to extraordinarily hard wear; this is shown not only in the permanently growing incisors, but also in the cheek teeth. Thus, in an adult in which the first molar is almost worn out, the third may have already lost almost all trace of pattern on its crown. At this and in earlier stages the tooth crowns are worn into strong transverse or slightly oblique ridges, showing that the movement was from side to side, as in an ordinary ruminant, and not from before backwards, as might perhaps be expected from the condition of the incisors; the normal ruminant form of the condyle of the mandible also shows that the movement of the lower jaw was lateral, and that the cutting edge of the peculiar incisors was used in just the same way as that formed by the united edges of the three pairs of incisors and the canines in the ordinary ruminant.

The dimensions (in centimetres) of some mandibular rami are given below :—

	A. (M. 10942.)	B. (M. 10963.)	C. (M. 10964.)
Length from posterior angle to tip of incisor	12·7	13·7	12·2
Depth of ramus beneath *m* 3	3·1	3·0	3·0
Depth at middle of diastema	1·5	1·4	1·2
Width of condyle	1·7	2·1	1·7
Length of crowns of molar-premolar series	4·7	4·0 (approx.)	4·1 (approx.)
Length of crowns of molar series	3·9	3·5	3·5
Width of incisor	1·0	0·8	0·6

A is the mandible of the type specimen.

The antero-posterior lengths (in millimetres) of the crowns of the cheek teeth in several mandibles are—

	A.	B.	C.	D.	E.
pm 4	6·0	5·5	5·0	7.0	—
m 1	8·5	7	8·5	8·0	7·0
m 2	12·0	10	11·5	10·5	11·0
m 3	20·0	19	16·0	18·0	17·5

The lengths (in millimetres) of the crowns of the milk molars in three specimens are—

mm 3	5·0	4·0	—
mm 4	14·5	12·5	14·0

Vertebral Column.—Like the rest of the skeleton, the vertebræ vary much in size and details of structure. No associated series is known, but from the large number collected by Miss BATE it has been possible to make an assemblage which probably nearly represents a complete vertebral column.

The *atlas* (Plate 22, fig. 5), of which several specimens, besides that belonging to the type specimen, are found in the collection, varies very greatly in size and form. Speaking generally, it is of normal bovine form. The cups for the occipital column are separated into upper and lower lobes by notches at their outer angles: into these notches the outer angles of the condyles fit. Comparison with the atlas of other forms shows that there is great likeness to the atlas of *Budorcas* (except in size) and to that of *Nemorhædus*. The chief point in which the atlas of the latter differs is that in it the condylar surfaces are not continuous in the mid-ventral line, and the hypapophysial prominence is situated about the middle of the centrum and not on its posterior border. The atlas of *Ovis* differs considerably in the form of the condylar cup and in the presence of a strong prominence in the mid-ventral line of the anterior face. In *Rupicapra* the vertebra is longer and the hypapophysis situated some distance in front of the hinder border.

The *axis* (Plate 22, fig. 6) is very variable, some specimens being much wider in proportion to their length, and at the same time possessing shorter but stouter transverse processes. The articulation for the atlas is of the spout-like form usual in the group. The neural spine is not very high, it slopes gently up from before backwards, thickening in the same direction. In *Budorcas* it is very high, sloping rapidly upwards. In *Nemorhædus* the spine projects behind the posterior zygapophysis, and the ventral border of the spout is notched. In *Rupicapra* the spine is much as in *Myotragus*, but the vertebra as a whole is proportionately longer and more slender. In the sheep the neural spine projects farther forward, and the spout is

notched. The remaining cervicals are deeply opisthocœlous, and the last three at least have neural spines of increasing size. The first seven or eight dorsals have high backwardly sloping spines, behind this they shorten and then at about the twelfth become upright; in the lumbar region the spines are very short and broad, more so than in *Nemorhædus*, *Ovis*, or *Capra*. In the sacral region the spines become still shorter, and as usual pass into a continuous ridge. Except in the extreme shortness of the spines the sacrum does not differ notably from those with which it has been compared. The *ribs* in proportion to the size of the animal were stout, and the *sternum* also was proportionately heavy.

No complete specimen of the scapula is preserved, but so far as it is known it does not differ in any important respect from that of a sheep or goat, except that the coracoid process is proportionately rather larger.

The *humerus* (Plate 22, figs. 1, 1A, 1B) is short and stout, its upper end being especially massively constructed. The head is large and strongly convex from before backwards, and considerably less so from side to side; posteriorly it projects some distance behind the shaft. The outer tuberosity (*o.t.*) is large and rises as a hook-like process considerably above the head, curving inwards over the bicipital groove (*b.g.*) Externally this process is separated by a notch from a strongly marked prominence for the attachment of a muscle, probably the infraspinatus. The inner tuberosity (*i.t.*) is small and laterally compressed, while the bicipital groove is wide and smoothly convex from above downwards. Beneath the head the shaft is somewhat compressed laterally and on its anterior face bears a strongly developed deltoid crest, from which a ridge runs upwards and outwards. On the postero-internal face of the middle of the shaft is a prominent rugosity for the insertion of the *teres major*. Beneath this the shaft first narrows slightly, then widens out to the distal articulation. The trochlear surface (*t.s.*) is oblique and projects strongly towards the outer side; the intercondylar ridge (*i.c.r.*) is low and rounded, and is situated at about the middle of the outer half. The anconeal fossa is rather shallow, but the supra-trochlear fossa is very deep, though there is no perforation of the bone. The inner condyle is large and projects considerably beyond the trochlea.

This humerus is very like that of an ox, resembling it both in its general proportions and in the prominence of the deltoid crest and of the rugosity for the *teres major*. In its shortness and stoutness it differs from the humerus in *Capra* and *Nemorhædus*, in which, moreover, the rugosity for the *teres major* is absent or slightly marked. The prominence of the deltoid crest and its greater distance from the proximal end also distinguishes this bone from the humerus of *Ovis*, *Capra*, and *Nemorhædus*. On the other hand, in the form of the outer tuberosity, the strong deltoid crest, and the well-marked surface for the *teres major*, it is similar to the humerus of *Budorcas*, which, however, is more slender, and differs also in a number of other characters.

The dimensions of five specimens of the humerus (in centimetres) are given below :—

Length (to summit of greater tuberosity).	Width at upper end.	Width of shaft at narrowest.	Width of distal end.
13·1	3·8	1·6	2·9
12·4	3·5	1·7	3·0
11·4	3·5	1·7	2·3
11·0	3·3	1·4	2·6
10·5	2·9	1·4	2·4

Considering the shortness and stoutness of the humerus, the *radius* (Plate 22, figs. 2 and 2A) and *ulna* are relatively slender bones, though less so than in *Ovis*, *Rupicapra*, *Nemorhædus*, etc. Another peculiarity is the straightness of the radius ; in the genera mentioned there is a slightly marked sigmoid curve in the shaft when seen from the front ; this is also absent in *Budorcas*. The olecranon process (*o.p.*) of the ulna is large, while distally the bone becomes very slender, and the distal internal angle is less produced than in the genera with which it has been compared, the articular surface for the cuneiform being relatively small, and apparently allowing a greater degree of flexion of the carpus upon the bones of the forearm, so that the metacarpus can take a position at right angles to the radius.

In *Budorcas* a similar degree of flexion is possible, but here the distal articular surface of the ulna is broader, and the cuneiform is very wide and short. In adult specimens all the muscle impressions are very strongly marked.

The dimensions of six specimens of the radius (in centimetres) are given below :—

Length.	Width at upper end.	Width of shaft at narrowest.	Width of distal end.
15·5	3·4	1·7	2·8
15·3	3·1	1·7	2·8
14·5	3·0	1·8	2·8
12·5	2·9	1·4	2·6
12·0	2·7	1·4	—
11·8	2·7	1·4	2·3

In the *carpus* (Plate 21, fig. 3) the proximal row of bones are not shortened in the direction of the axis of the limb as they are in *Budorcas*, but resemble those of an ordinary goat or sheep, except for the reduction of the cuneiform (*cu.*). This bone has a relatively small articular surface for the ulna, and is also reduced distally so that it does not overlap the unciform to the usual extent. In correlation with the reduction of the cuneiform the proximal articular surface of the lunar (*l.*) is increased so that it extends nearly to the inner edge of the radius. The distal carpals are

considerably shortened in the direction of the axis of the limb, and the unciform has a comparatively small surface for the cuneiform.

The *metacarpus* (Plate 21, fig. 4, *mc.*) is one of the most characteristic bones of *Myotragus*, differing widely from the usual form common in the group. It is very short and broad, and at the same time considerably compressed from before backwards. The surface for the trapezoid and magnum (*m.*) is very large, and posteriorly is separated from the surface for the unciform (*u.*) by a deep pit continued posteriorly on to the posterior face of the bone and leading down to the usual foramen which marks the original line of separation of the metacarpals. The anterior face of the shaft is gently convex from side to side, the posterior nearly flat except towards the upper end, where a groove runs up to the interosseous foramen; there is also a small distal interosseous foramen just above the interdigital notch. The line of union of the distal epiphyses with the shaft is marked by a strong transverse ridge, especially on the anterior face. The articular surfaces for the phalanges are of the normal form, but perhaps are proportionately rather narrow and with less strongly defined grooves than usual.

No lateral metacarpals are preserved, but they were present, though, judging from the size of the facets for their support, and of the roughened surfaces on the cannon-bone, they were small. Probably they were similar to the lateral metacarpals in *Budorcas* (Plate 21, fig. 5), in which they are short rods of bone, rounded at the extremities, and not reaching to the middle of the cannon-bone.

In its shortness and stoutness the metacarpus is astonishingly like that of *Budorcas* (Plate 21, fig. 5), which, except in size, differs only in having its surface for the trapezoid-magnum smaller in proportion to that for the unciform, from which it is not separated by a posterior pit. The articular surfaces for the phalanges also differ in details.

The next nearest approach to this type of metacarpus is that of the Rocky Mountain Goat (*Oreamnus*), but in this the shortening is much less marked, as is also the case in *Ovibos*.

The dimensions of six specimens of the metacarpus (in centimetres) are given below:—

Length.	Width at upper end.	Width of middle of shaft.	Width across articular surfaces for digits.
6·3	2·3	2·2	2·6
6·0	2·5	2·2	2·5
5·8	2·2	2·1	2·4
5·5	2·3	2·1	2·5
4·7	2·1	2·6	2·5
4·3	1·9	1·8	2·1

The *phalanges* are short and stout. The distal surface of the second for union

with the hoof is very oblique, looking inwards towards the middle line of the foot, a peculiarity which is also strongly marked in *Budorcas*. The effect of this obliquity of the articulations is that when the limb is extended, the hoofs being flexed downwards are at the same time rotated outwards away from one another. When the weight of the animal is thrown on the foot, the hoofs are automatically bent upwards and brought nearer together, which must give considerable assistance in obtaining a grip upon rough ground.

The ungual phalanges (Plate 21, figs. 3 and 3A) are short and stout: when their anterior angles are in contact their rather broad plantar surface forms a horseshoe-shaped area. They are somewhat similar in form to the ungual phalanges of *Ovibos*, and differ considerably from the narrow sharp-pointed type found in *Capra* and *Ovis*. In *Budorcas* the plantar surface is broad, but the points of the phalanges do not converge, and in *Oreamnus* they are similar.

The proportions of the bones of the fore-limb in *Myotragus*, as compared with the proportions in the genera with which it is compared, are shown in the following Table; in all cases the length of the radius is taken as 100:—

	Humerus.	Metacarpus.
Myotragus	85·3	36·7
Budorcas	97·0 approx.	41·0
Oreamnus	87·3	42·0
Ovibos	109·0	58·0 approx.
Nemorhædus	103·0	74·0
Rupicapra	100·0	80·0 approx.
Ovis	95·0	83·0

It will be seen that the only animals in which the relative shortness of the metacarpus at all approaches that found in *Myotragus* are *Budorcas* and *Oreamnus*; in the latter, however, the bone is more slender in proportion to its length. In *Oreamnus* the proportions of the humerus also approximate to those of *Myotragus*. It may be noted that both *Budorcas* and *Oreamnus* are climbers rather than jumpers, and live much of their time on rough talus-strewn slopes and steep cliff faces.

The lengths of the limb-bones of *Myotragus* have been taken from the average size of a considerable number of specimens.

Pelvis.—No complete os innominatum is preserved, but from several fragments most of the characters can be determined. The neck of the *ilium* is shorter than usual in the group; the anterior end is greatly expanded, and is nearly flat on its outer face; on the inner side the surface for union with the sacrum is very strongly marked. In its general form this ilium resembles that of *Budorcas* more nearly than any other with which it has been compared.

The acetabular cup is very large and is remarkable for the great size of the

cotylar notch, which in one specimen interrupts the posterior part of the rim for nearly a quarter of its length. In all the pelves with which comparison has been made the lips of the notch approach one another very closely, so that the rim is interrupted for a very short distance only; it is possible that this peculiarity may have given greater freedom of movement to the femur than usual.

The *pubis* is comparatively slender, and the obturator foramen is shorter and broader than in any of the other pelves, that of *Budorcas* being the most like. The *ischium* is not completely preserved in any specimen. The pelvis, as a whole, is shorter and broader than is usual in the goats and antelopes.

Hind-limb.—The *femur* (Plate 22, figs. 3, 3A, 3B), like the humerus, is very short and stout, the ridges and tuberosities for the attachment of muscles being strongly marked. The head, which is nearly hemispherical, is directed somewhat upwards, and the pit for the ligamentum teres is circular and deep. The greater trochanter (*g.t.*) is much smaller than in any bovine femur with which it has been compared and it does not rise to the level of the summit of the head (*h.*). The lesser trochanter (*l.t.*) varies greatly in size in different individuals; it is situated nearly on the inner border of the bone and projects less posteriorly than usual. The digital fossa (*d.f.*) is deep but very narrow, and, in consequence of this and of the position of the lesser trochanter, the upper portion of the bone appears somewhat compressed from before backwards. Beneath the lesser trochanter the straight shaft widens gradually towards the distal articulation; except that the posterior face is slightly flattened, the shaft is nearly circular in section. There is a slightly marked *linea aspera* running obliquely across to the inner border of the greatly roughened but slightly depressed plantar fossa.

The distal articulation is large and massive; the rotular surface (*r.s.*) is broad and rather shallow and at the same time is shorter than in the femora of other forms, not extending so far up the front of the bone; at the same time its inner border is thicker and more rounded, while the outer forms a prominent crest. The articular condyles and intercondylar groove lie somewhat obliquely to the long axis of the bone. The chief characters distinguishing this femur from all those with which it has been compared are its shortness and stoutness, the massiveness of its distal end and the relatively small size of the greater trochanter. The straight and rather stout femur of *Budorcas* comes nearest in its general proportions, but is still proportionately much more slender.

The dimensions (in centimetres) of four specimens are given below:—

Length.	Width of upper end.	Width of shaft at narrowest.	Width of distal end.
13·3	4·4	1·7	3·8
12·5	3·8	1·6	3·4
12·3	4·3	1·6	3·2
11·4	3·8	1·5	3·5

Except that it is rather stouter in proportion to its length, the *tibia* (Plate 22, figs. 4 and 4A) does not differ in any important respect from those with which it has been compared, though the fossa for the reception of the outer part of the articulation of the *astragalus* is rather deeper. The bone is very variable in size and in some minor points of structure, thus in some specimens the internal malleolus is almost wanting.

The dimensions (in centimetres) of six specimens of the tibia are given below :—

Length.	Width of upper end.	Width of shaft at narrowest.	Width of distal end.
14·9	3·5	1·4	2·4
14·4	3·4	1·4	2·5
14·1	3·3	1·4	2·2
12·1	2·9	1·2	2·0
11·7	2·8	1·0	2·0
11·5	2·8	1·0	2·1

The *fibula* is reduced to the extent usual in the goats and antelopes.

The *astragalus* differs very slightly from those of *Capra*, *Rupicapra*, etc., with which it has been compared. The outer half of the articular surface for the tibia seems to be larger and rises a little more above the inner ; the distal portion of the bone is perhaps a little smaller in proportion to the proximal than usual.

The *tuber calcis* of the *calcaneum* is shorter than in the genera compared and its end bears a very strongly developed surface for the attachment of tendons. The sustentacular process is relatively large, the surface for articulation with the *astragalus* being extensive. The fibular facet is small and that for the cuboid much shorter than usual.

The distal tarsals present a peculiar condition, since in the adult they are all fused with one another and also with the metatarsus (Plate 21, figs. 6 and 6A). This fusion sometimes occurs very early, even before the distal epiphyses have united. Amongst ruminants all the distal tarsals are fused with one another in *Hyæmoschus* and *Tragulus*, but in no case has fusion with the metatarsus taken place. In the goats and antelopes the cuboid and navicular fuse with one another, but not with the cuneiforms : this is the case in *Budorcas*, but here, although no actual fusion takes place, the distal tarsals and metatarsus are so closely united by strong ligaments that in a macerated skeleton in which the other bones are all separated they remain in union, the whole very closely resembling the tarso-metatarsal complex of *Myotragus* (Plate 21, fig. 7). The form of the articular surfaces for the astragalus and calcaneum presents no special peculiarity.

The *metatarsus* (Plate 21, fig. 6), though less shortened and compressed than the metacarpus, is nevertheless exceptionally short and stout, being closely similar to the metatarsus of *Budorcas* alone among the genera compared. The bone is somewhat

flattened from before backwards, and on its anterior face the original line of separation of the third and fourth metatarsals is marked by a broad groove, deepening towards the distal end. The posterior surface has a deep groove at its upper end, running down from the interosseous foramen, but distally it is nearly flat, widening a little towards the articulations. As in the metacarpus the line of union of the distal epiphyses forms a prominent ridge. The articulations for the phalanges present no special peculiarities.

Greatly reduced remnants of the upper ends of the second and fifth metatarsals are present as thin splints of bone closely fused at their upper ends with the posterior face of the third and fourth metatarsals respectively, but with the distal pointed extremities free. In some specimens these lateral metatarsals are either missing or so intimately fused as to be indistinguishable. It is interesting to note that while in the Pecora generally lateral metatarsals are wanting, in *Budorcas* quite considerable remnants are found, very similar and similarly situated to those of *Myotragus* but shorter, only extending at most down the upper third of the canon-bone, while in *Myotragus* they may reach beyond the middle.

The following are the dimensions (in centimetres) of five specimens of the metatarsus. The length given includes the fused distal tarsals :—

Length (to the upper angle of the fused navicular).	Width of upper end.	Width of shaft at narrowest.	Width of distal articulation.
8·6	2·0	1·8	2·4
8·4	2·2	2·6	2·3
8·0	2·2	1·9	2·3
7·3	2·0	1·8	2·3
6·5	1·8	1·5	2·0

Three specimens with which the distal tarsals had not yet fused were 6·3, 5·8, 5·7 cm. long.

The proportions of the bones of the hind limb in *Myotragus* as compared with the proportions found in the genera with which comparison has been made are shown in the following Table. The length of the tibia is taken as 100 :—

	Femur.	Metatarsus.
Myotragus	93·2	46·6
Budorcas	95·0 approx.	38·2 approx.
Oreamnus	93·0 approx.	45·5
Nemorhœdus	83·6	57·4
Ovibos	106·7	57·0 approx.
Rupicapra	78·4	63·0
Ovis	81·8	65·2

It will be seen from the above Table that in *Budorcas* alone the metatarsus is actually relatively shorter than in *Myotragus*, while in *Oreamnus* it is about the same as in that genus, but it is proportionately more slender. Thus in the hind as in the fore limb *Budorcas* and *Oreamnus* approach *Myotragus* most nearly in the proportions of their limb bones.

The posterior phalanges seem to have been very similar to those of the fore foot. It has not been found practicable to distinguish the hind from the front hoofs with certainty.

From the above description and comparisons it will be seen that *Myotragus* is almost certainly an aberrant member of the Rupicaprine (Nemorhædine) group of Antelopes. In its skull, particularly in the form and position of the horns, it approaches *Nemorhædus* most closely, while in the structure of its limbs it resembles *Budorcas* and to a less degree *Oreamnus*. It must, however, be noted that, while the characters of the skull may be good evidence of relationship, those of the limbs may be merely the consequence of convergence due to adaptation to a similar mode of life, but in the case of *Budorcas* and *Myotragus* the similarity of the foot structure is so complete and is supported by so many small points of resemblance in other parts of the skeleton that a near relationship between the two genera must be regarded as highly probable. At the same time the peculiarities of *Myotragus* are so great that probably it should be referred to a distinct sub-family the *Myotraginæ*.

Species and Distribution of Myotragus.

In spite of the considerable variation occurring among the individuals collected in Majorca there can be no hesitation in referring them all to a single species. The specimens from Minorca on the other hand are in most cases considerably larger and with proportionately larger horns. Furthermore, the roof of the skull in the parietal region is usually shorter from before backwards than in the Majorcan specimens, and at the same time is flat or even slightly concave in the same direction. These differences being associated with a difference of habitat seem to justify the separation of the Minorcan form as at least a local variety, under the name *Myotragus balearicus* var. *major:* when this form is better known it may be necessary to accord it specific rank.

Recently M. Dehaut has described* the frontlet and horn-cores of an antelope from a cave-breccia at Cape Figari in the north of Sardinia. This animal, which was named *Antelope melonii*, has been doubtfully referred to *Nemorhædus* by M. Dehaut but it seems to have been very similar to *Myotragus* and may prove to be identical with it. The horns are similarly rounded in section and run straight back in a line with the forehead : the orbit also seems to have been similarly situated.

A natural brain cast probably belonging to the same animal was collected by

* 'Matériaux pour servir à l'Histoire Zoologique et Paléontologique des Iles de Corse et de Sardaigne. Fasc. III.—Animaux Fossiles du Cap Figari,' p. 57, Plate 2 (1911).

M. DEHAUT in the same breccia, and has been presented by him to the British Museum (Natural History). This agrees very closely with brain casts made from skulls in Miss BATE'S collection. If further material should prove the identity of the Sardinian animal with *Myotragus*, it would appear that that genus had formerly a wide distribution in the Mediterranean region, and may have been a member of the Tyrrhenian quaternary fauna,* some members of which, *e.g.*, *Myolagus sardus*, are closely similar to species occurring in the Middle Miocene of Sansan and Oeningen. By this it is not suggested that *Myotragus* is likely to have existed in its present form since the Miocene, but that perhaps its ancestral form is to be sought in European deposits of that age. None of the antelopes of Pikermi or Samos, which are probably almost all of African origin, seem to stand in any near relationship with *Myotragus*, while probably the Nemorhædine or Rupicaprine Antelopes, as defined by WINGE,† and including *Myotragus*, are of northern origin.

Summary and Conclusions.

Myotragus is without doubt the most peculiarly specialised and aberrant member of the Bovidæ that has hitherto been described, and the question of whence and why this peculiar type arose is a very difficult one. The specialisation undergone may be regarded as twofold, one bringing about the peculiar modification of the dentition, the other that of the limbs, the two not necessarily, though probably, being in some way correlated with one another. Considering first the modification of the limbs it appears that in *Myotragus* adaptation for climbing on steep crags and talus slopes has been carried to a degree equalled in no other animal. This adaptation, as WINGE‡ has pointed out, is manifested especially in the shortening of the metacarpus and metatarsus, and probably also in the broadening of the hoofs. The nearest approach to this type of foot structure is found in the Takin (*Budorcas*) and the Rocky Mountain Goat (*Oreamnus*), both of which are animals specially adapted for climbing on steep crags and screes. *Budorcas* is said to live in small herds and spends most of its time, at least in summer, on "the stone-scattered slopes and battlemented crags that tower above the rhododendron groves and thickets"§ on the mountain sides. In winter they feed on bamboo and willow, in summer on birch shoots, elm, grass, and other plants—the food being of such a kind that no special modification in the form of the dentition such as occurs in *Myotragus* has been necessary.

* FORSYTH, Major, "Die Tyrrhenis.—Studien ueber Geographische Verbreitung von Thieren und Pflanzen im Westlichen Mittelmeergebiet," 'Kosmos,' vol. 7, p. 1 (1883).

† "Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa, Minas Geraes, Brazilien," 'E Museo Lundii,' vol. 3, p. 126 (1906).

‡ "Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa, Minas Geraes, Brazilien," 'E Museo Lundii,' vol. 3, p. 124 (1906).

§ WALLACE, H. T., 'The Big Game of Central and Western China,' London (1913), chap. ix–x. See also LYDEKKER, 'Proc. Zool. Soc.,' vol. 2, p. 795 (1908).

The Rocky Mountain goat also lives on precipitous cliffs and steep talus slopes, where many are destroyed by avalanches and rock-slides. It browses on buds and twigs of the forest which extends up to the crags among which it lives. In this case the feet are not so extremely modified as in *Budorcas*, the metapodials being relatively more slender and less compressed from before backwards. Here also the character of the food has not brought about any special modification of the dentition, and it is the absence of such modification in any recent form that makes the peculiarities of the dentition in *Myotragus* the more difficult to account for. No doubt some great change in the nature of the food had taken place, and it may be suggested that for some reason or other, so far as *Myotragus* was concerned, the supply had become restricted to lichens, mosses and other small plants growing on the rocks among which the animal lived. If when it became necessary to adopt this kind of food the ancestor of *Myotragus* already possessed enlarged and high crowned median incisors such as occur in some antelopes (*e.g.* Gazella), these teeth might develop these characters still further until they displaced the lateral incisors and canines altogether and became permanently growing or rootless. Such an incisor would be very well adapted for gnawing and scraping lichens and mosses from rock-faces, and that the food was exceptionally hard and intractable is shown by the extremely hard wear to which the hypsodont cheek teeth must have been subjected; possibly the inclusion of fragments of the rocks with the food may have added to this effect. This manner of use of the incisors might also lead to the shortening of the mandible and consequently of the facial region of the skull also. If this explanation is accepted it still remains difficult to explain why the food supply should have been so restricted. The association of *Myotragus* in Minorca with a giant species of *Testudo* makes it impossible to suppose that the climate was a very cold one. On the other hand it may have been extremely arid, so that vegetation was stunted, especially on the crags among which the animal lived.

The great variability among the individuals of *Myotragus* seems to show that it had not yet arrived at a position of stable equilibrium; probably its peculiar characters were rapidly acquired and at the time of its extinction it was not an ancient type.

[*Note.*—Freudenberg* has recently made the suggestion that the peculiar incisors of *Myotragus* were adapted for stripping off the bark from the stems of heath-like bushes. It has also been suggested that the food may have consisted of the bark of trees and tough woody fibre. In the kangaroos, which feed on grass and other herbage, the lower incisors are somewhat similar in form to those of *Myotragus*, but, though very long, do not grow from persistent pulps.]

* 'Geol. u. Pal. Abhandlungen,' vol. 12, p. 489 (1914).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

EXPLANATION OF PLATES.

Plate 19.

Myotragus balearicus.

Fig. 1.—Skull and mandible from side, $\frac{2}{3}$ natural size.

Fig. 2.—Skull from below, $\frac{2}{3}$ natural size.

Fig. 3.—Skull from above, $\frac{2}{3}$ natural size.

Fig. 4.—Skull from behind, $\frac{2}{3}$ natural size.

Fig. 5.—Right upper cheek teeth, natural size.

Fig. 6.—Right lower cheek teeth, natural size.

Fig. 7.—Inner side of right ramus of mandible, $\frac{2}{3}$ natural size.

Fig. 8.—Anterior end of mandible with incisors, seen from above, natural size.

All the above figures are drawn from the type specimen, M. 10942.

con., condyle of mandible; *cor.*, coronoid process; *d.f.*, dental foramen; *f.m*, foramen magnum; *fr.*, frontal; *i.*, lower incisor; *j.*, jugal; *lac.*, lachrymal; *m.* 1–3, molars; *mx.*, maxilla; *na.*, nasal; *oc.c.*, occipital condyles; *pal.*, palatines; *par.*, parietals; *pm.* 3–4, premolars; *p.p.*, paroccipital process; *s.oc.*, supraoccipital; *sym.*, symphisis of mandible; *tymp.*, tympanic bulla.

Plate 20.

Myotragus balearicus.

Fig. 1.—Anterior portion of skull from right side (M. 10947), natural size.

Fig. 2.—Anterior portion of skull from below (M. 10948), natural size.

Fig. 3.—Side view of the anterior portion of a young skull showing the milk molars and first molar (M. 10949), natural size.

Fig. 3a.—Crowns of the same teeth, $1\frac{1}{2}$ natural size.

Fig. 4.—Base of skull (M. 10942), natural size.

Fig. 5.—Sections of crowns of the upper cheek teeth to show the pattern (M. 10951), natural size.

Fig. 6.—Inner side of cheek teeth to show their hypsodont character (M. 10950), natural size.

Fig. 7.—Left ramus of very young mandible with milk teeth (M. 10952), natural size.

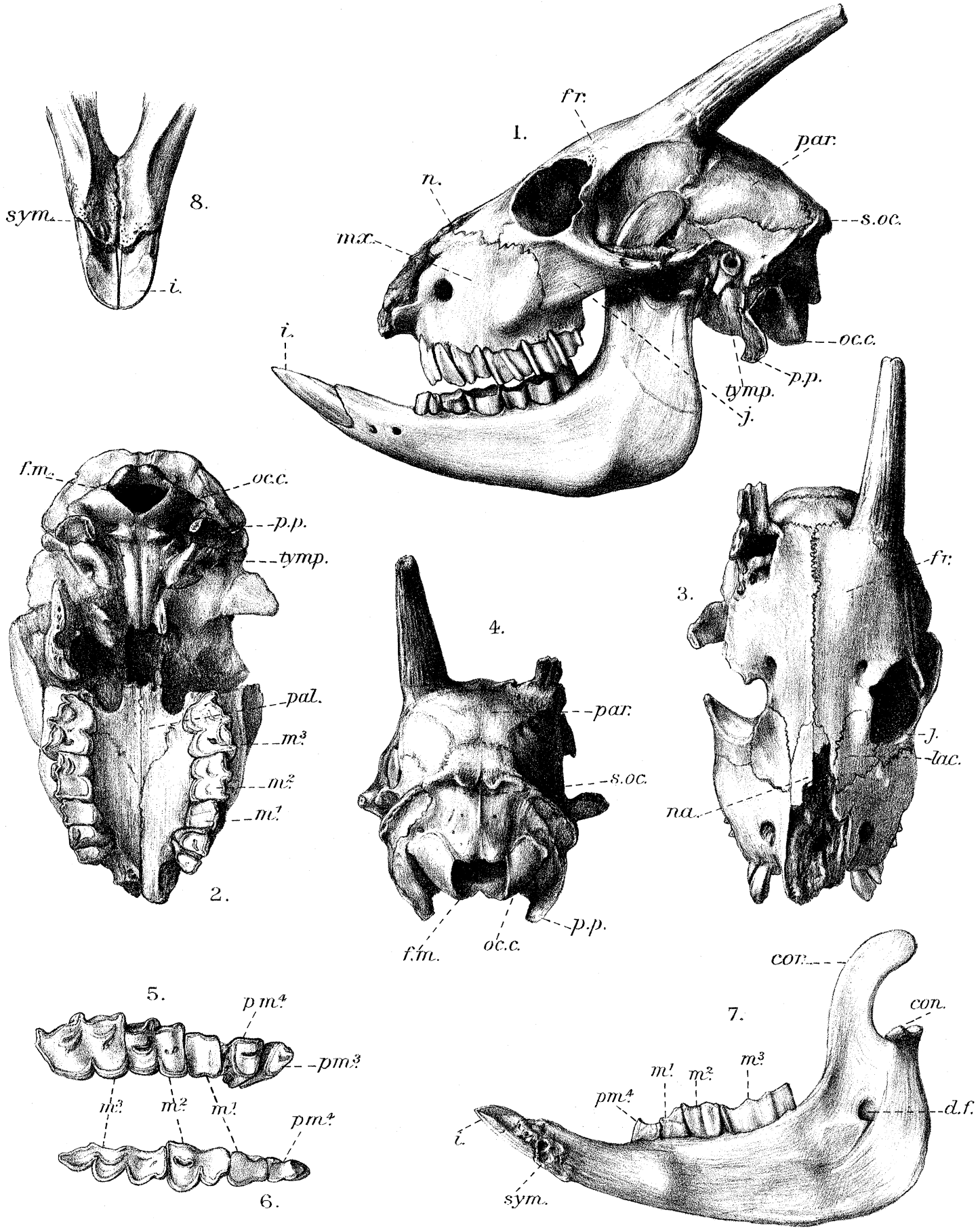
Fig. 8.—Left lower incisor (M. 10955), natural size.

Fig. 9.—Posterior portion of mandibular ramus with *m*3 just coming into wear (M. 10953), natural size.

Fig. 10.—Imperfect mandibular ramus of a very old individual in which *m*3 is worn to the roots (M. 10954), natural size.

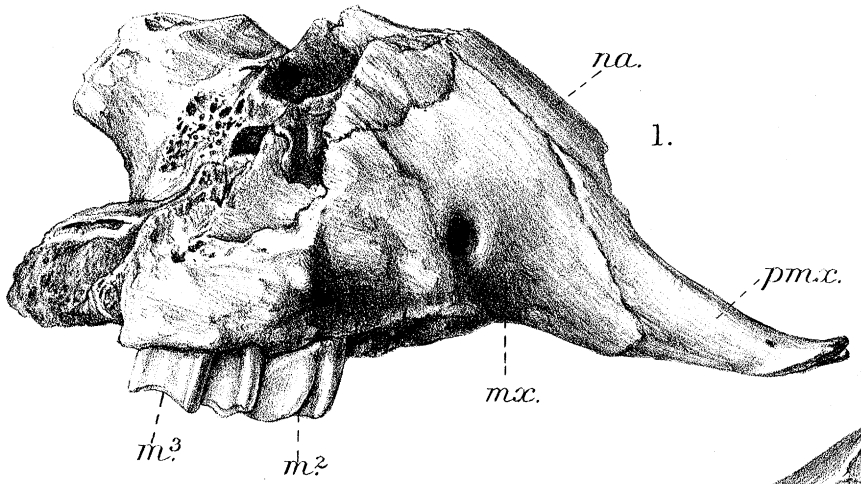
al., ? alveolus for upper incisor; *d.i.*, alveolus for first deciduous incisor; *i.*, alveolus for first permanent incisor; *m.* 1–3, molars; *mm.* 3–4, third and fourth milk molars; *mx.*, maxilla; *na.*, nasal; *oc.c.*, occipital condyles: *pmx.*, premaxilla; *p.p.*, paroccipital processes; *t.*, tuberosity on the lower border of the mandible caused by the root of the young molar.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

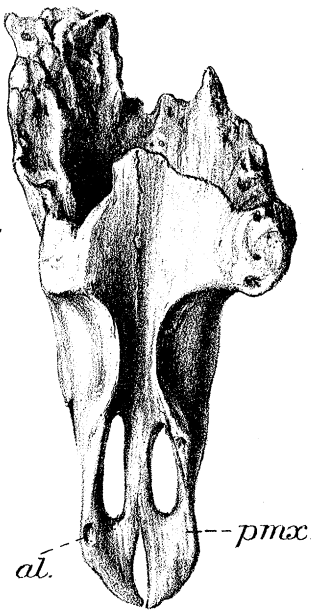


G.M. Woodward del. et lith. Huth imp.

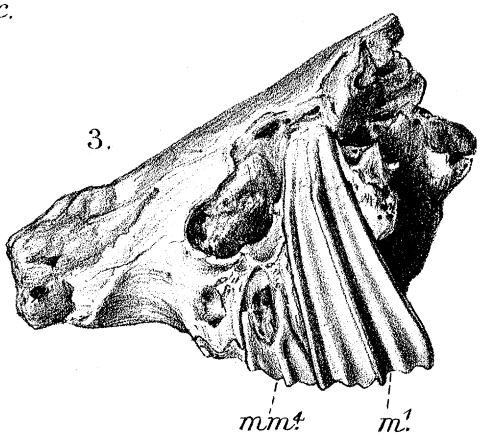
MYOTRAGUS BALEARICUS.



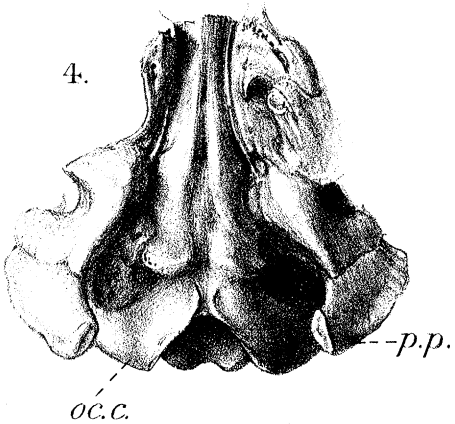
1.



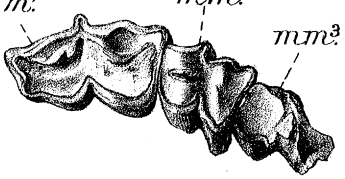
2.



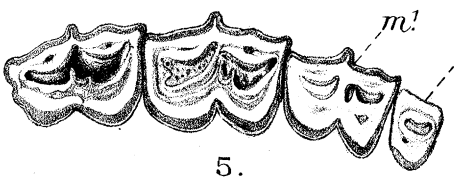
3.



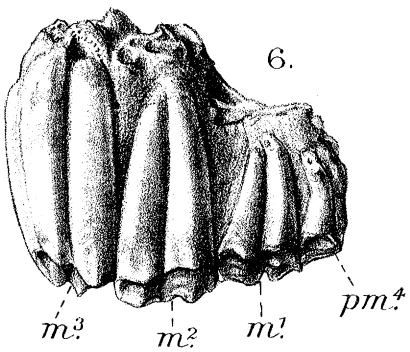
4.



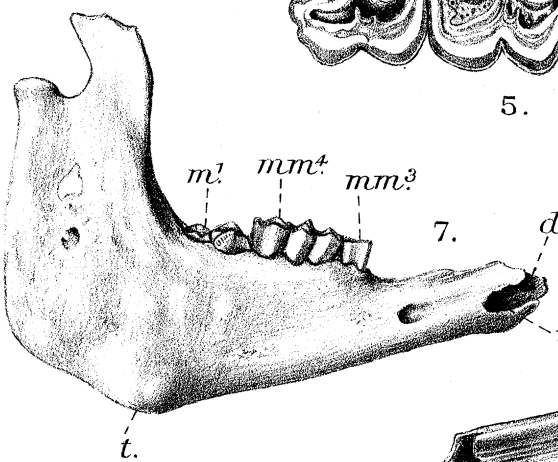
3a.



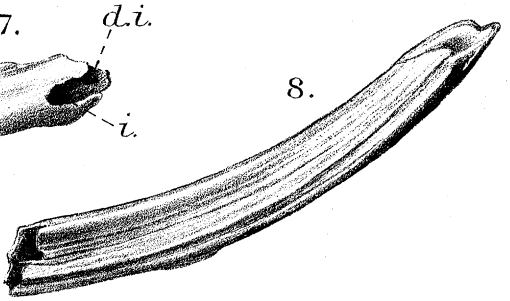
5.



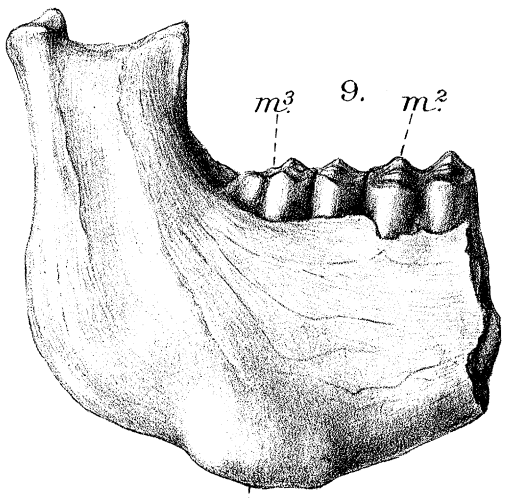
6.



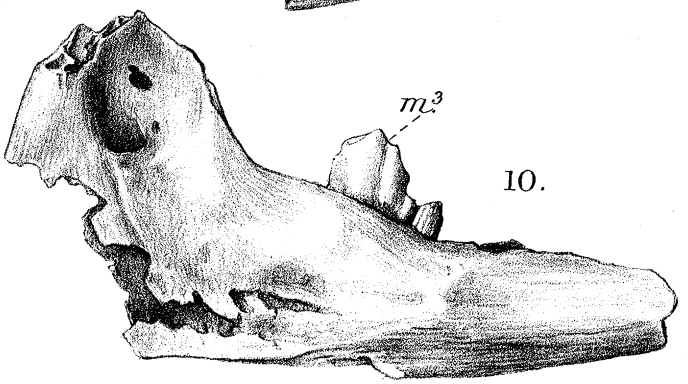
7.



8.



9.

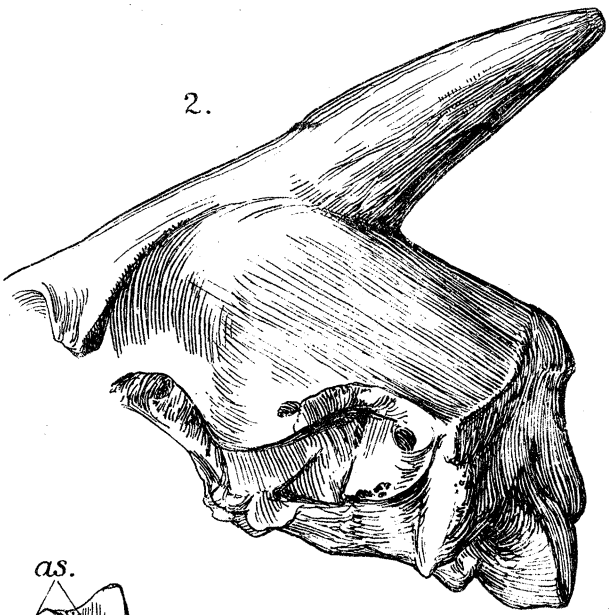


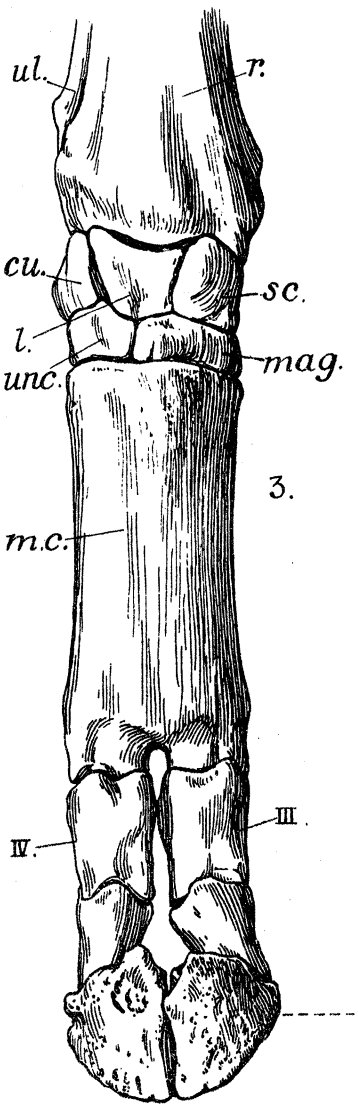
10.

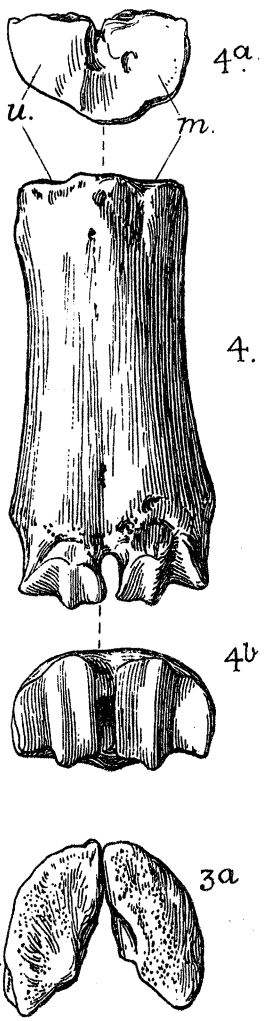
G.M.Woodward del. et lith.

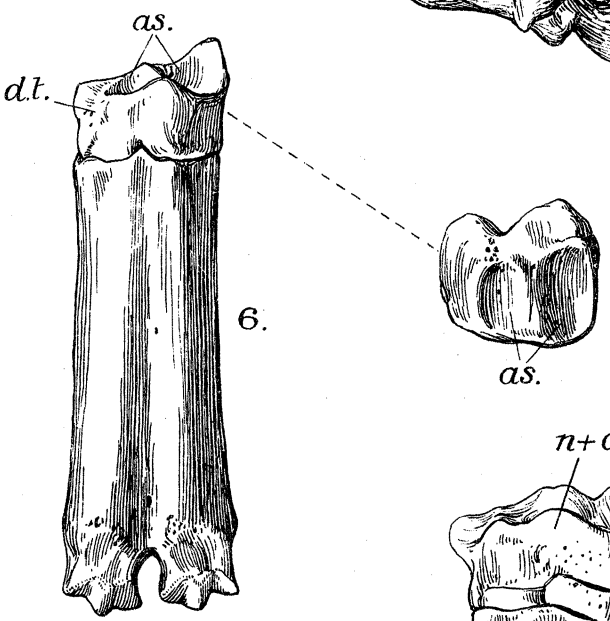
Huth imp.

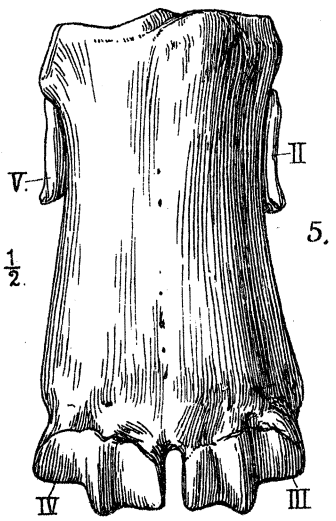
MYOTRAGUS BALEARICUS.

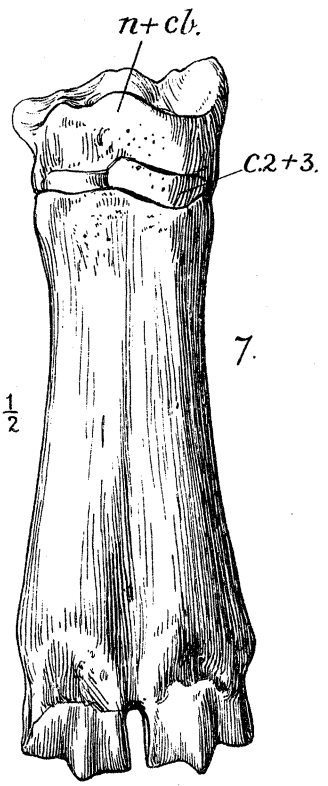










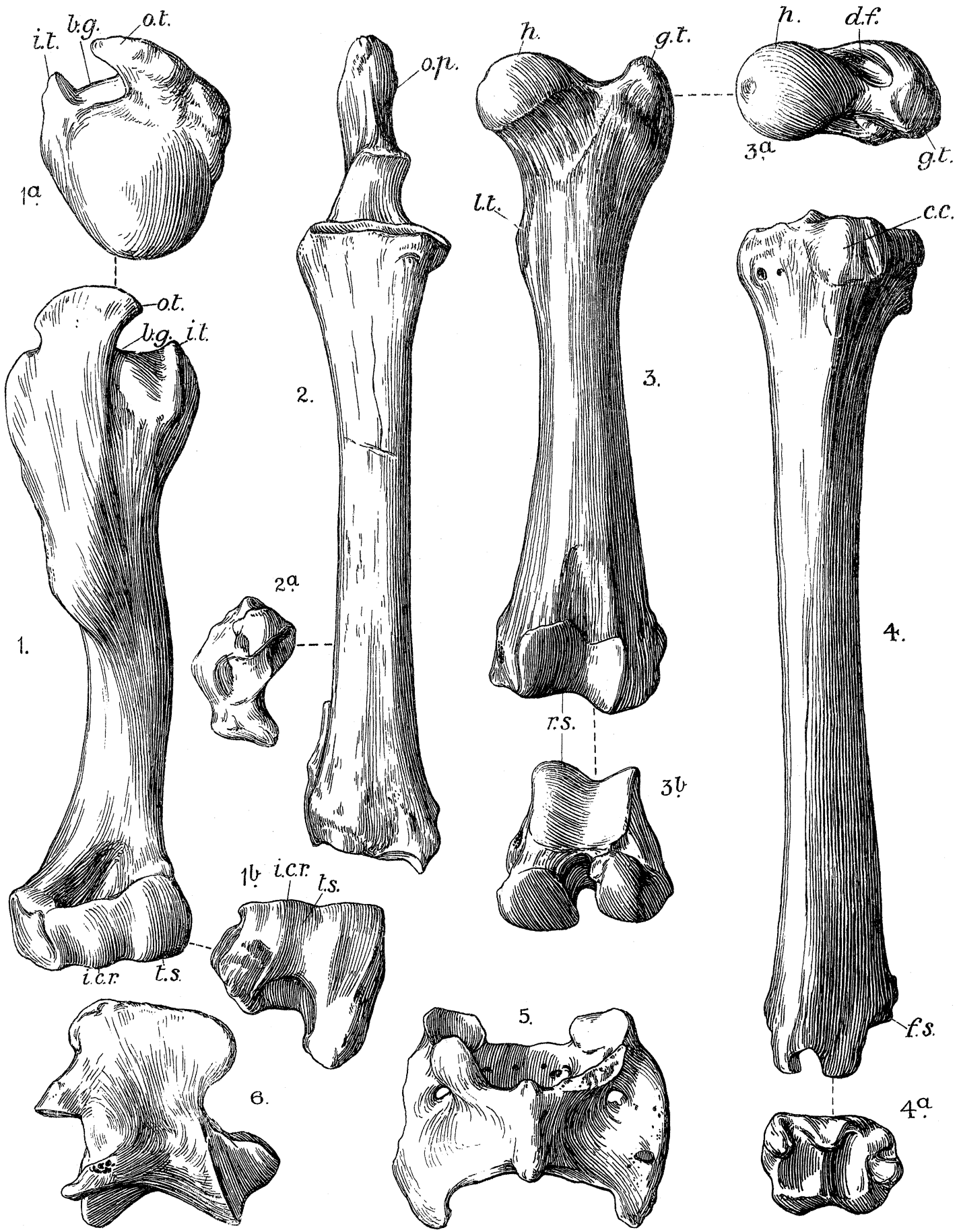


G.M.Woodward.del.

Huth photo-lith.

MYOTRAGUS BALEARICUS.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



G. M. Woodward, del.

Huth photo-lith.

MYOTRAGUS BALEARICUS.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Plate 21.

Fig. 1.—*Myotragus balearicus.* Posterior portion of skull (M. 10946) from the side.
Fig. 2.—*M. balearicus.* Posterior portion of skull (M. 10945) from the side.
Fig. 3.—*M. balearicus.* Lower portion of right fore-limb from front.
Fig. 3a.—*M. balearicus.* Plantar surface of ungual phalanges.
Fig. 4.—*M. balearicus.* Right metacarpals from front.
Fig. 4a.—*M. balearicus.* Right metacarpals, upper articular surface.
Fig. 4b.—*M. balearicus.* Right metacarpals, lower articular surface.
Fig. 5.—*Budorcas taxicolor.* Right metacarpals from front.
Fig. 6.—*M. balearicus.* Right metatarsals with the fused distal tarsals, from front.
Fig. 6a.—*M. balearicus.* Fused distal carpals, showing the surface for the astragalus.
Fig. 7.—*B. taxicolor.* Right metatarsals with distal tarsals, from front.

a.s., surface for astragalus; *c.* 2+3, fused second and third cuneiforms of tarsus; *cu.*, cuneiform; *d.t.*, fused distal tarsals; *l.*, lunar; *m.*, surface for magnum; *mag.*, magnum; *mc.*, metacarpals; *n.*+*cb.*, fused navicular and cuboid; *r.*, radius; *sc.*, scaphoid; *u.*, surface for unciform; *ul.*, ulna; *unc.*, unciform; II–V, second to fifth metacarpals.

All the figures are natural size except Nos. 5 and 7, which are half.

Plate 22.

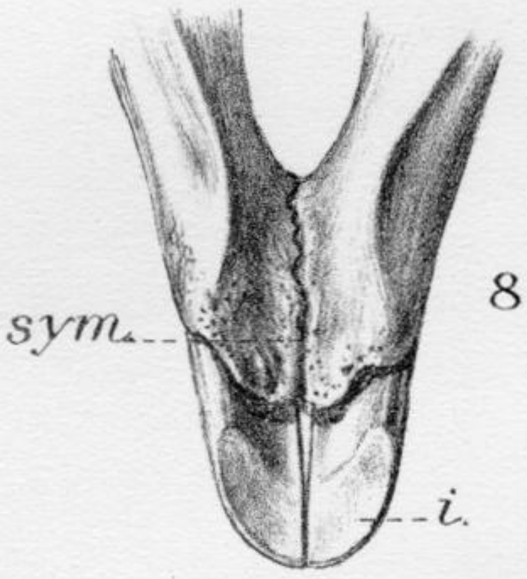
Myotragus balearicus.

Fig. 1.—Right humerus from front.
Fig. 1a.—Upper end of humerus.
Fig. 1b.—Lower end of humerus.
Fig. 2.—Right radius and ulna from front.
Fig. 2a.—Distal end of ulna.
Fig. 3.—Left femur from front.
Fig. 3a.—Upper end of femur.
Fig. 3b.—Lower end of femur.
Fig. 4.—Left ulna from front.
Fig. 4a.—Distal end of ulna.
Fig. 5.—Atlas vertebra from below.
Fig. 6.—Axis vertebra from right side.

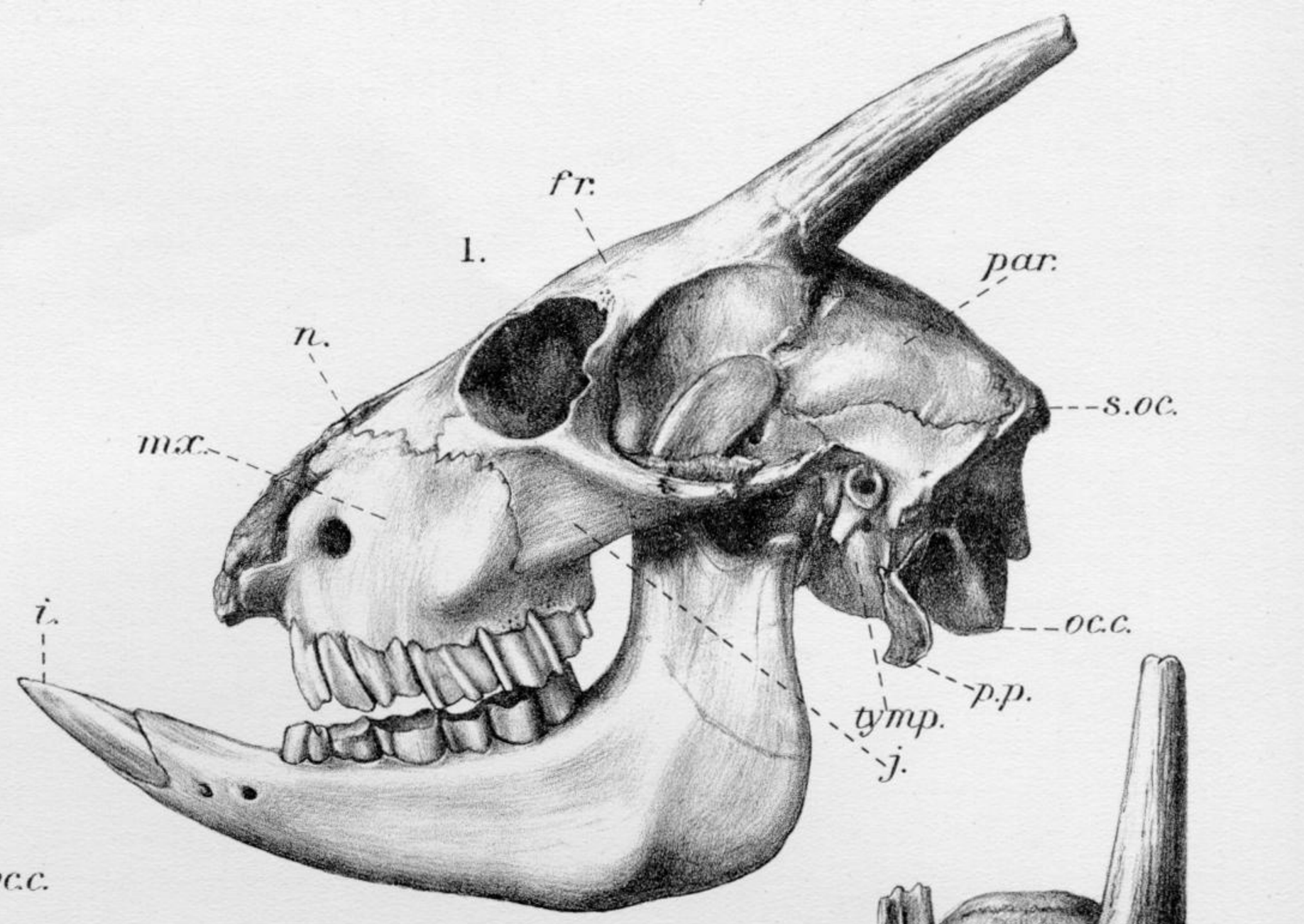
b.g., bicipital groove; *c.c.*, cnemial crest; *d.f.*, digital fossa; *f.s.*, surface for fibula; *g.t.*, great trochanter; *h.*, head of femur; *i.c.r.*, intercondylar ridge; *i.t.*, inner tuberosity; *l.t.*, lesser trochanter; *o.p.*, olecranon process; *o.t.*, outer tuberosity; *r.s.*, rotular surface; *t.s.*, trochlear surface.

All the figures are natural size.

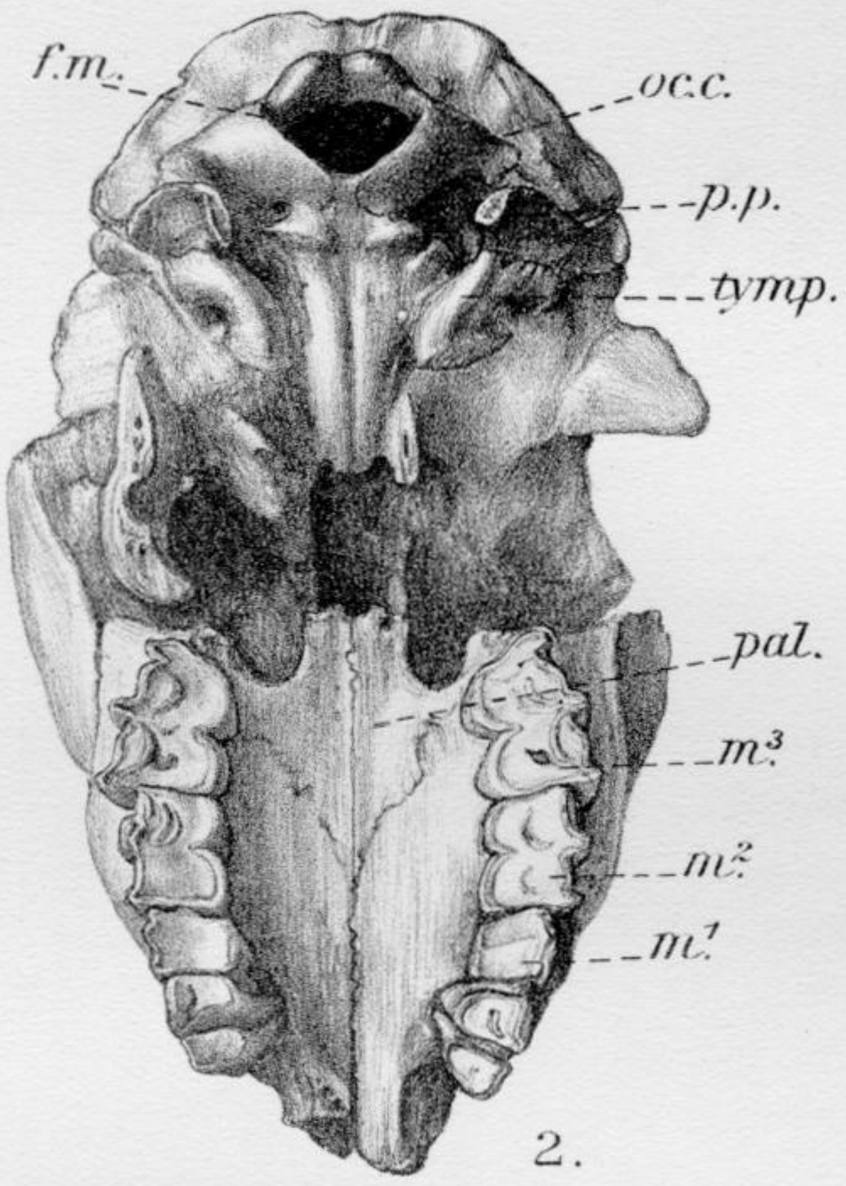
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



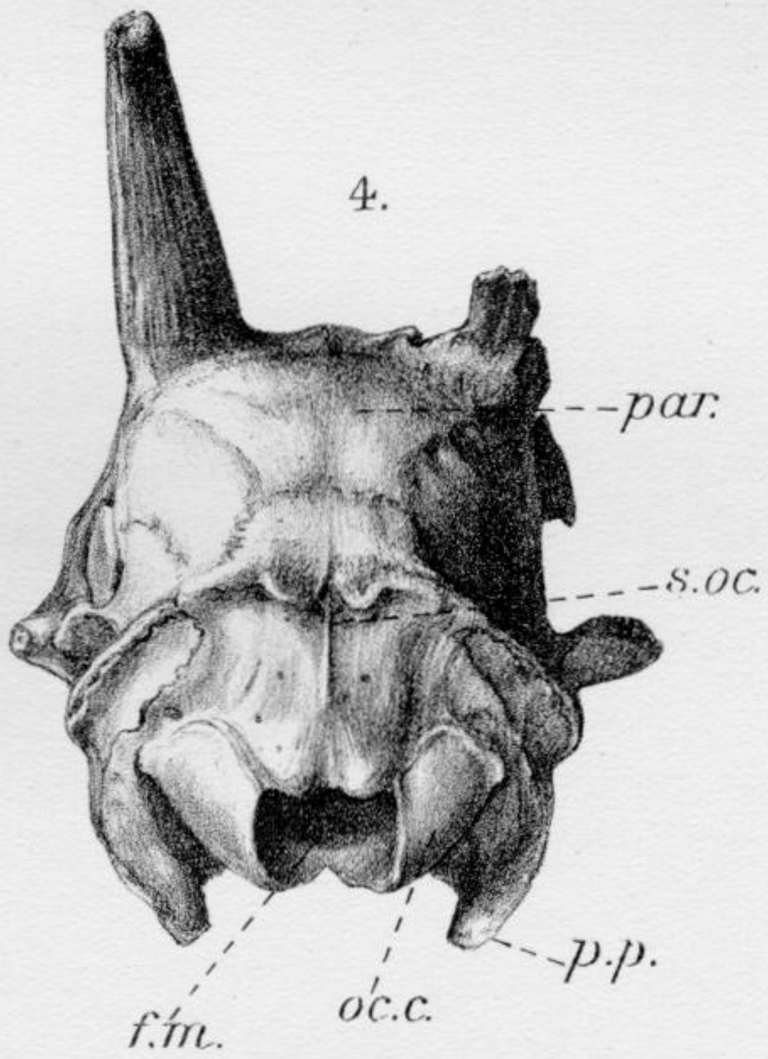
8.



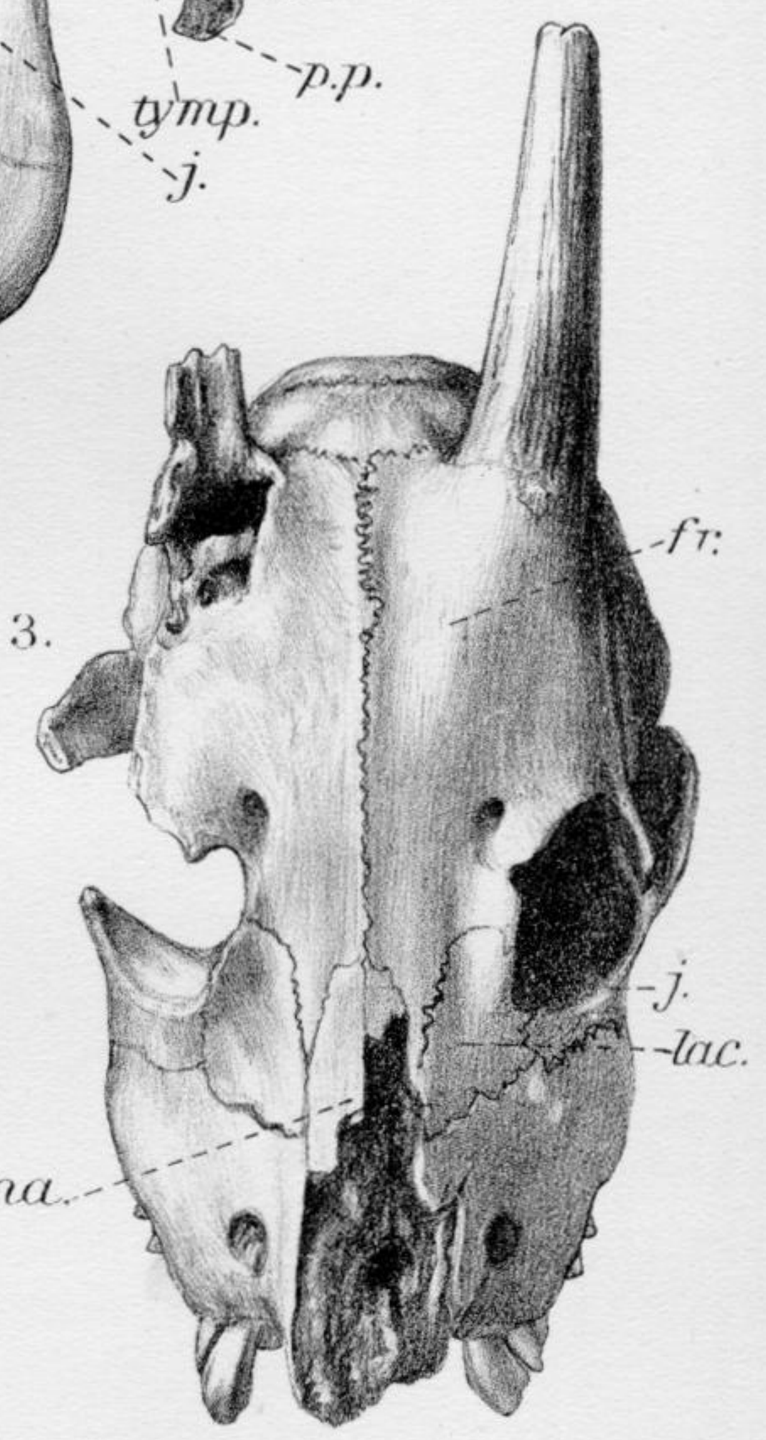
1.



2.



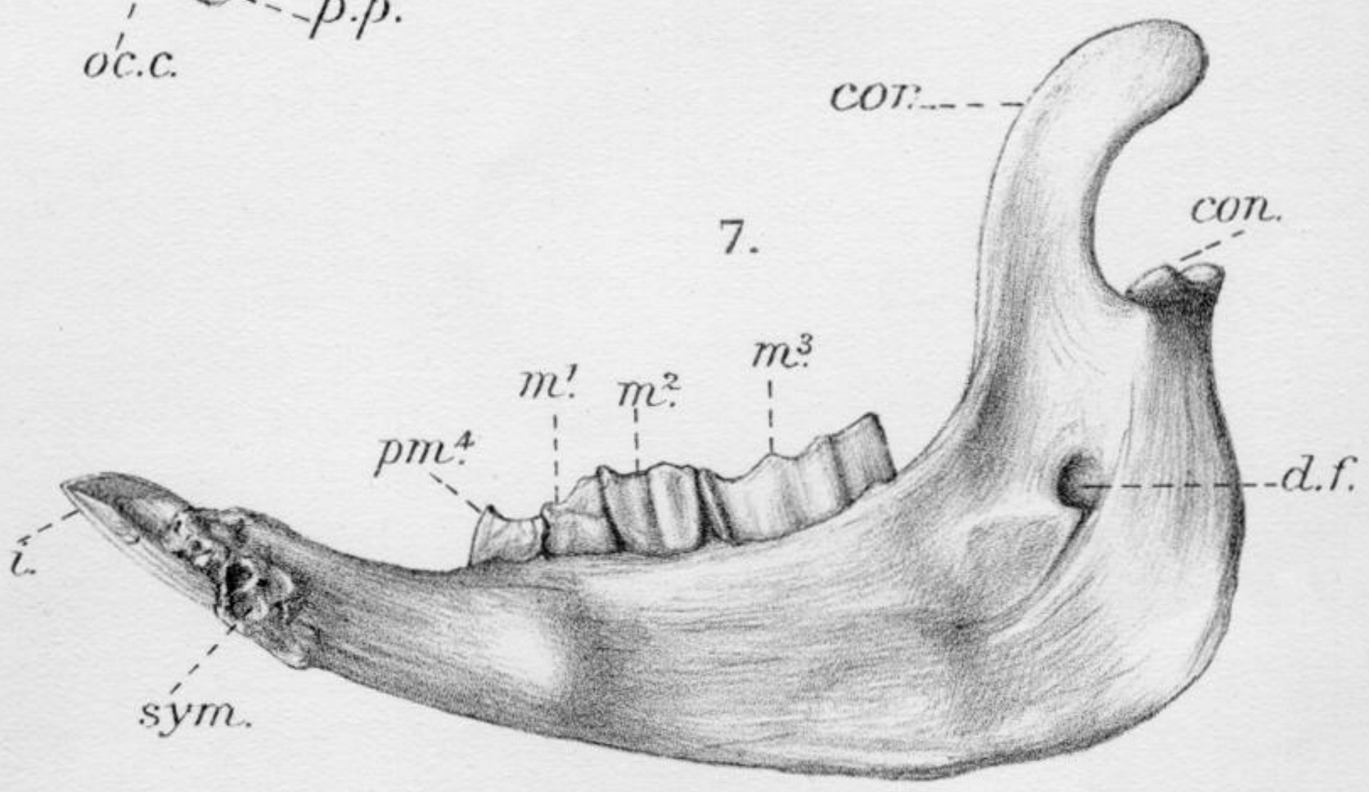
4.



3.

5.

6.



7.

Plate 19.

Myotragus balearicus.

Fig. 1.—Skull and mandible from side, $\frac{2}{3}$ natural size.

Fig. 2.—Skull from below, $\frac{2}{3}$ natural size.

Fig. 3.—Skull from above, $\frac{2}{3}$ natural size.

Fig. 4.—Skull from behind, $\frac{2}{3}$ natural size.

Fig. 5.—Right upper cheek teeth, natural size.

Fig. 6.—Right lower cheek teeth, natural size.

Fig. 7.—Inner side of right ramus of mandible, $\frac{2}{3}$ natural size.

Fig. 8.—Anterior end of mandible with incisors, seen from above, natural size.

All the above figures are drawn from the type specimen, M. 10942.

con., condyle of mandible; *cor.*, coronoid process; *d.f.*, dental foramen; *f.m.*, foramen magnum; *fr.*, frontal; *i.*, lower incisor; *j.*, jugal; *lac.*, lachrymal; *m.* 1–3, molars; *mx.*, maxilla; *na.*, nasal; *oc.c.*, occipital condyles; *pal.*, palatines; *par.*, parietals; *pm.* 3–4, premolars; *p.p.*, paroccipital process; *s.oc.*, supraoccipital; *sym.*, symphisis of mandible; *tymp.*, tympanic bulla.

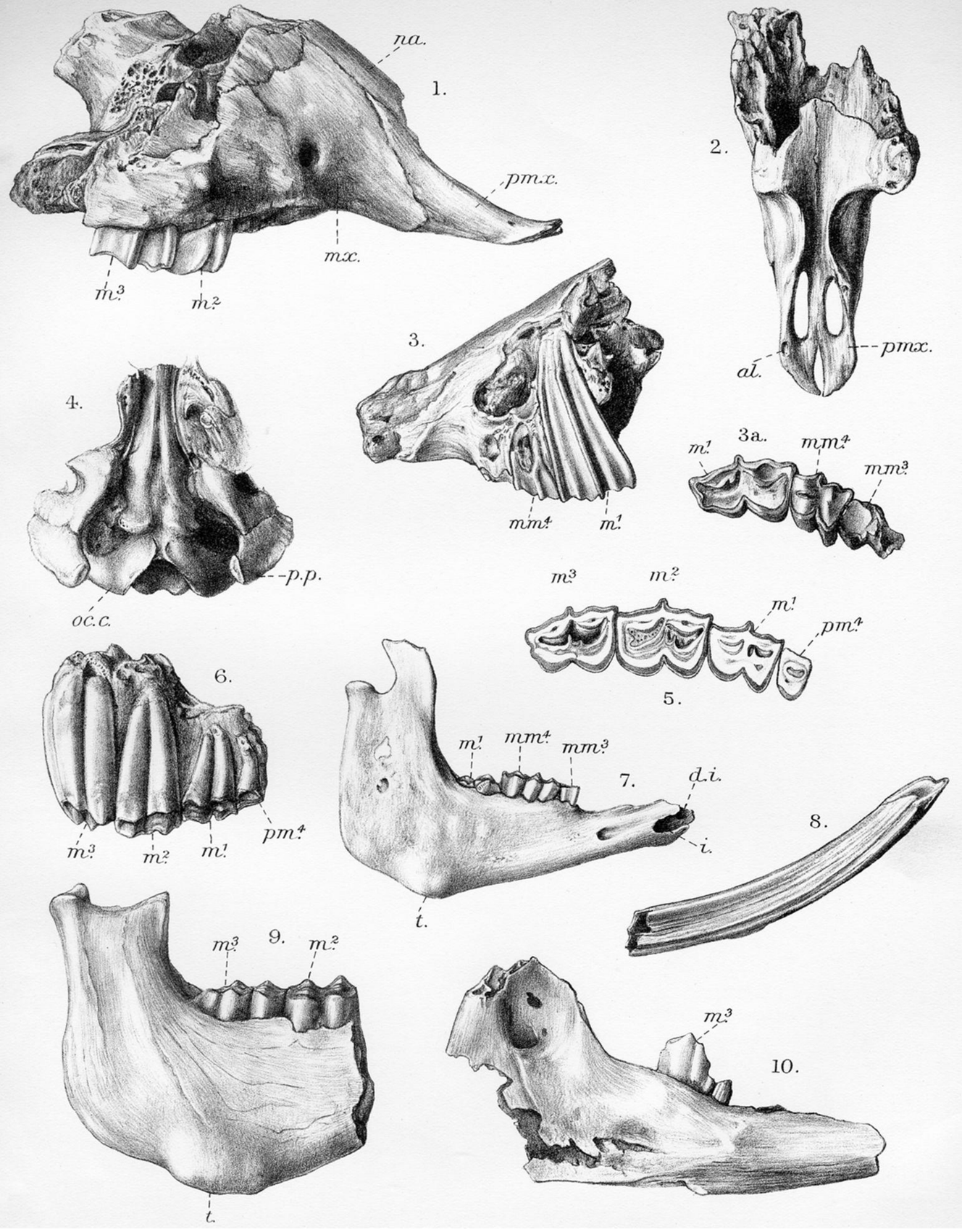


PLATE 20.

Myotragus balearicus.

FIG. 1.—Anterior portion of skull from right side (M. 10947), natural size.

FIG. 2.—Anterior portion of skull from below (M. 10948), natural size.

FIG. 3.—Side view of the anterior portion of a young skull showing the milk molars and first molar (M. 10949), natural size.

FIG. 3A.—Crowns of the same teeth, $1\frac{1}{2}$ natural size.

FIG. 4.—Base of skull (M. 10942), natural size.

FIG. 5.—Sections of crowns of the upper cheek teeth to show the pattern (M. 10951), natural size.

FIG. 6.—Inner side of cheek teeth to show their hypsodont character (M. 10950), natural size.

FIG. 7.—Left ramus of very young mandible with milk teeth (M. 10952), natural size.

FIG. 8.—Left lower incisor (M. 10955), natural size.

FIG. 9.—Posterior portion of mandibular ramus with *m*3 just coming into wear (M. 10953), natural size.

FIG. 10.—Imperfect mandibular ramus of a very old individual in which *m*3 is worn to the roots (M. 10954), natural size.

al., ? alveolus for upper incisor; *d.i.*, alveolus for first deciduous incisor; *i.*, alveolus for first permanent incisor; *m.* 1–3, molars; *mm.* 3–4, third and fourth milk molars; *mx.*, maxilla; *na.*, nasal; *oc.c.*, occipital condyles: *pmx.*, premaxilla; *p.p.*, paroccipital processes; *t.*, tuberosity on the lower border of the mandible caused by the root of the young molar.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES