Article IV.—ON THE OSTEOLOGY OF AGRIOCHŒRUS.

By J. L. WORTMAN.

PLATE I.

Although the genus *Agriochœrus* has been known for many years, and has always been abundantly represented in our collections by numerous complete skulls, yet it was not until the past year that we have obtained any information regarding the remainder of its skeletal structure. The first intelligence of the very curious organization of its feet was published by Professor Osborn and myself in the description of a remarkable hind foot[1] from the Protoceras layer of the White River beds, obtained by the Museum Expedition in 1892. On account of the large claw-like ungual phalanges, and in the complete absence of teeth, we referred it to the order Ancylopoda, established by Cope, and considered it to represent a distinct subdivision of this group (Artionychia). Professor Scott, upon careful examination of the specimen, shrewdly surmised that the foot probably pertained to a species of *Agriochœrus*.

The explorations of the past year have demonstrated the correctness of this surmise, and he has added to our knowledge of the genus by a description of a portion of the fore limb.[2] He has also, in the same paper, discussed at some length the systematic position of the genus within the Artiodactyla. Another important addition to our knowledge of the probable ancestral genus has recently been made by Professor Marsh in the description of a new form (*Hyomeryx breviceps*) from the older Uinta beds.[3]

During the past year the expedition from the American Museum into the White River beds, near the same locality where the hind foot was found, was fortunate enough to discover a more or less complete skeleton of *Agriochœrus latifrons*, together with numerous skulls and other important parts of the skeleton of different individuals of other species, so that the materials are now

[1] 'Artionyx, a New Genus of Ancylopoda,' Bull. Amer. Mus. Nat. Hist., Feb., 1893, pp 1-18.
[2] 'Notes on the Osteology of Agriochœrus,' Amer. Philos. Soc., May, 1894, pp. 244-251.
[3] 'Description of Tertiary Artiodactyles,' Amer. Jour. Sci., Vol. XLVIII, Sept., 1894, pp. 259-274.

at hand to enable me to give a tolerably thorough account of the osteology of one of the species at least. Another considerable addition to the materials that I was fortunate enough to obtain, was found in the Cope Collection, which the Museum has recently acquired, consisting of a complete skull associated with numerous limb bones and vertebræ of a single individual, collected by myself in 1879 in the John Day Basin in Oregon. This specimen has aided me materially in supplying the missing parts in making the restoration. It may be added here that the association of the large claw-like terminal phalanges with the teeth, in at least two of our White River specimens, leaves no room for doubt as to the correctness of the determination that this type of ungual phalanx belongs to *Agriochœrus.*

It is the object of the present paper, therefore, to present as complete an account as possible of the osteology of this group, together with a critical review of the species which have been described as belonging to it. Following this I will take up the question of the systematic position of the group.

Osteology.

Skull.—This part of the osteology has been so thoroughly described by Leidy, Cope, and Scott, that little remains to be said concerning it. It may not be amiss, however, to recall some

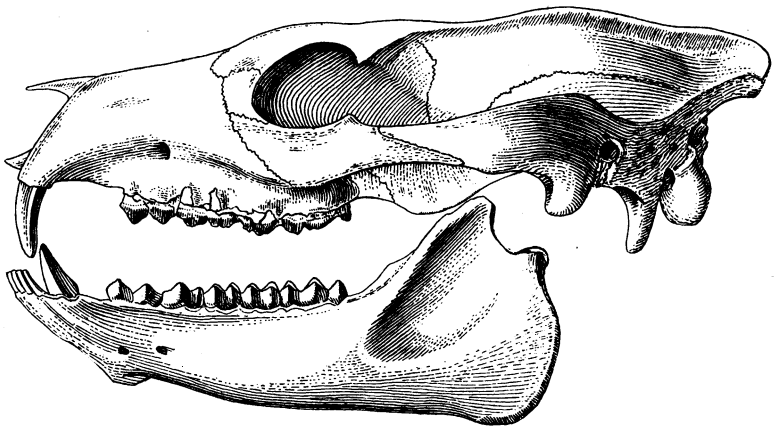


Fig. 1. Side view of skull of *Agriochœrus major.* One-third natural size.

of the more important characters in which it differs from its nearest cotemporary selenodont allies—the Oreodontidæ—as well as those characters in which it resembles them. The general outline of the skull is very much like that of the earlier Oreodonts, especially *Oreodon culbertsoni*, with which Leidy compared it in his original description. It is rather elongated and narrow, with moderately elevated, compressed, overhanging occiput. The face is but little bent down on the basicranial axis, and the form and relationship of the facial bones, with the notable exception of the premaxillaries, are practically the same as in *Oreodon*. The otic bullæ are always inflated, they are not filled with cancellous tissue, and the foramina at the base of the skull are similarly disposed as in *Oreodon*. An apparently constant exception to this latter correspondence, however, is seen in the presence of a moderate sized foramen, generally equal to or slightly larger than the *foramen opticum*, which opens just in front of the sphenoidal spine, in *Agriochœrus*. It is situated above and a little posterior to the *foramen opticum*. The office of this foramen, as well as its homology, is difficult to determine, but judging from its size and direction I am inclined to regard it as the *foramen rotundum*.

The principal characters in which the skull of *Agriochœrus* differs from that of *Oreodon* may be enumerated as follows: In *Agriochœrus* the premaxillaries are reduced and practically edentulous. In our collections there are three skulls of different species, in which these bones are in a good state of preservation, and they show that the premaxillaries were not in contact in the median line; they are small and project but little in advance of the canines. There is a single, small, shallow alveolus upon either side from which the incisors had apparently been shed early during life. In all the cotemporary Oreodonts, on the other hand, the premaxillaries are well developed; they are in contact in the median line, and always bear their full complement of incisors. Some of the later forms, however, show a marked tendency to incisor reduction.

In *Agriochœrus* the posterior rim of the orbit is not enclosed by bone, whereas in *Oreodon* the bony ring of the orbit is complete, and there is always a distinct preorbital pit or fossa which is absent in *Agriochœrus*. In the more primitive Oreodont genus,

Protoreodon, however, the orbit is open posteriorly as in *Agriochœrus*, and there is no lachrymal pit.

The dentition of *Agriochœrus* presents some striking resemblances to the true Oreodonts ; in other respects it more nearly approximates *Hyopotamus*, while in others still it possesses characters peculiarly its own. The most characteristic Oreodont feature is seen in the enlargement of the first inferior premolar into a caniniform tooth, while the true canine is small, incisiform, and so placed as to form a continuous series with the incisors. The upper canine is large, considerably curved, and has a characteristic D-shaped pattern on cross section, as is seen in all the Oreodonts. The characters in which the dentition of *Agriochœrus* departs from that of *Oreodon* are especially seen in the presence of a diastema between the canines and premolars in the upper jaw and between the caniniform first premolar and the second premolar in the lower jaw. In *Oreodon* all the teeth are arranged in a continuous series.

The structure of the molars presents many important differences from those of *Oreodon ;* the crowns are lower, less selenodont, the valleys are much more open, and the angles of the superior teeth more rounded off. In *Oreodon* the external median buttress is compressed from before backwards into a vertical plate, whereas in *Agriochœrus* it forms a wide loop. If it were not for the absence of the anterior intermediate cusp, the molars of *Agriochœrus* would resemble those of *Hyopotamus* very closely. The only genus known to me in which the structure of the superior molars is strictly comparable is *Merycopotamus* of the Indian Miocene, and it would not indeed be surprising to find, when the osteology of this latter genus is more fully known, that the two are quite closely related.

The Vertebræ.—There is no single specimen in our collection which contains a complete vertebral column, so that the exact number of vertebræ cannot be made out with certainty. In one, however, in which the limbs are more or less complete, the posterior five dorsals, all the lumbars, the sacrum, and nineteen of the caudals are preserved. In this specimen there are six lumbars, and if we allow thirteen as the number of the dorsals, we will

then have the highly characteristic dorso-lumbar formula for all the known Artiodactyla.

The *atlas* presents the same general outline as that seen in the Artiodactyla. The articular cavities for the condyles of the skull are deep and spacious and are overhung by the anterior superior part of the arch. In *Oreodon* and all the recent genera this part of the arch is interrupted by a wide notch which shortens its fore and aft extent. In *Agriochœrus* this notch is very narrow, and is continued upwards and backwards as a deep groove which separates the spine into two low indistinct tubercles. The transverse processes are well extended laterally, somewhat broader in front than in *Oreodon*, and project backwards further behind the facets for the axis. They are perforated by moderate sized foramina for the passage of the vertebral artery, which does not appear to be the case in any specimen of *Oreodon* which I have examined. Anteriorly, the foramen for the exit of the suboccipital nerve is large and conspicuous, while the inferior tubercle is small. The facets for the axis are more transverse, and not so oblique as in *Oreodon*, resembling more nearly the sheep or deer in this respect.

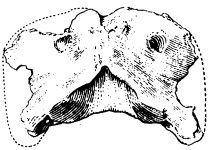


Fig. 2. Top view of atlas of *Agriochœrus guyotianus*. Two-fifths natural size.

The *axis*, as described by Scott,[1] differs from that of *Oreodon*. This is especially to be seen in the character of the spine. In *Agriochœrus* it is unusually high and prolonged in front, so as to overhang the odontoid slightly, while behind it is not so produced, reaching no further than the extremity of the posterior zygapophyses. In *Oreodon* the spine is much lower, but little produced in front, but greatly thickened and extended posteriorly. The odontoid, as already well known, is intermediate between the peg-like form of the pig and the hollow half-cylinder of the higher forms. In some of the larger specimens in our collection

Fig. 3. Side view of axis of *Agriochœrus guyotianus*. Two-fifths natural size.

[1] Beiträge zur Kentniss der Oreodontidæ, p. 361. It is also stated in the same paper (p. 322) that the atlas of *Oreodon* has the transverse processes perforated by the vertebral canal. In all the specimens in our collection the transverse processes are imperforate, but the position of the canal is frequently indicated by a pit of variable dimensions.

the odontoid is almost as highly developed as in any of the living genera. The remaining cervicals are very much like those of *Oreodon;* they are provided with prominent hypopophyses and moderately developed neural spines, which increase rapidly in length from before backwards.

The *dorsals* resemble those of *Oreodon* very closely, so far as can be determined from our somewhat imperfect material of this region. The spine of the first dorsal, however, is much longer than that of the corresponding vertebra of this genus. The posterior six have rather elongated, slightly keeled centra, with nearly flat oval faces. In the ninth, tenth, eleventh and twelfth, the zygapophyses are nearly flat, while those of the thirteenth begin to assume the tongue and groove pattern of the lumbars. The neural spine of the ninth is high and backwardly directed, that of the tenth being more nearly vertical. From this point backwards the spines have a more forward direction. The transverse processes begin at the eleventh and become more and more prominent posteriorly. Metapophyses are fairly well indicated on the last two dorsals.

Fig. 4. Front view of cervical of *Agriochœrus guyotianus.* Two-fifths natural size.

Fig. 5. Side view of cervical of *Agriochœrus guyotianus.* Two-fifths natural size.

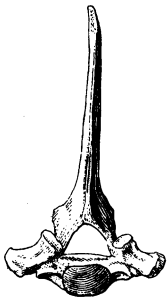


Fig. 6. Anterior view of first dorsal of *Agriochœrus guyotianus.* Two-fifths natural size.

Fig. 7. Side view of first dorsal of *Agriochœrus guyotianus.* Two-fifths natural size.

The *lumbars* are six in number. The second, third and fourth have moderately strong ventral keels, the two last being practically without this structure. The centra increase in size and length from before backwards, the last two being markedly flattened vertically; the central faces exhibit a slight convexity both in front and behind, except that of the last lumbar, where it joins the sacrum, which is nearly flat. The spines are broad and elevated, and the metapophyses well developed. The zygapophyses

exhibit a well-marked double tongue and groove articulation, a feature so highly characteristic of the Creodonts. In *Oreodon* this tongue and groove is always apparently single, at least all the specimens I have examined fail to show any trace of the double structure.

Fig. 8. Side view of second lumbar of *Agriochœrus latifrons*. One-third natural size.

The *sacrum* is composed of three vertebræ, and resembles that of *Oreodon* as nearly as can be determined.

The number of the *caudals* cannot be stated with certainty; there are, however, nineteen preserved in one specimen, and if one is permitted to judge from the way in which they would ordinarily taper, at least three or four should be added to this number. The proximal ones are short with well-developed neural arches and zygapophyses; these latter structures disappear in the fourth or fifth caudal, while the arch continues to the seventh or eight. They lengthen rapidly towards the middle of the tail, after which they again become shorter. There is no evidence of chevrons having existed, although it is not at all improbable that they were present.

The *ribs* do not present any characters worthy of especial mention, further than to say that the anterior ones were stout and considerably flattened. The middle ones were larger, indicating a spacious chest, while towards the posterior end of the series they become more rounded and smaller.

The *sternum* is represented in the collection by a single segment, which I take to be the second sternal bone. It may be described as an elongated bar, expanded at either extremity and greatly constricted in the middle. It is grooved upon its ventral aspect, and exhibits at either antero-inferior angle a prominent process; posteriorly it is not so broad as it is in front. Upon either side about midway of the bone, in a deep salcus, is seen a facet for a rib, presumably the second. In all the recent forms of the Artiodactyla the cartilaginous ribs join the sternum at the point where the segments meet, except the first, which is located near the anterior extremity of the manubrium. If our specimen is to be homolo-

Fig. 9. Ventral view of second (?) sternal bone of *Agriochœrus latifrons*. One-third natural size.

gized with the manubrium or anterior sternal bone, then the relatively great expansion of its anterior extremity is peculiar. I have not seen a specimen of this part of the sternum of *Oreodon*, so that I am unable to state whether there is any resemblance or not.

Fore Limb.[1]—The fore limb of *Agriochœrus* is found to differ from that of *Oreodon* in many important particulars when the two structures are carefully compared. Aside from the great differences seen in the character of the ungual phalanges and carpus, presently to be described, the limb is both relatively longer and more robust than in any of the Oreodonts. While *Agriochœrus latifrons* is nearly of the same size as the larger specimens of *Oreodon culbertsoni*, yet the long bones are more than one-third longer; this disproportion extends also to the elements of the manus, but the whole foot, especially the metapodials, are more nearly equal to those of *O. culbertsoni*.

The *scapula* of *Agriochœrus latifrons* in our collection is represented only by its distal third, including the glenoid cavity, coracoid, acromion and part of the spine, in good state of preservation. In a smaller specimen of *A. guyotianus*, from the Oregon beds, however, the whole bone is sufficiently preserved to admit of a determination of its more important characters. Its general proportions are very similar to those of *Oreodon culbertsoni*, with some slight exceptions. The spine divides the dorsal surface into two subequal fossæ, of which the supraspinous is slightly the larger. The acromion is prominent, somewhat thickened and pointed, and projects in such a way as to overhang the neck of the bone. As in *Oreodon*, a small though distinct metacromion process is present. In *Oreodon* this process is narrow and terminated by a point, while in *Agriochœrus* it is placed relatively further back from the acromion, being at the same time more extended along the crest of the spine and not so distinctly pointed. It is interesting to note that this process has almost entirely disappeared in the later selenodont Artiodactyles, being represented only by a slight thickening of the crest of the spine,

[1] Scott has described a part of the fore limb of one of the larger species of this genus ('Notes on the Osteology of *Agriochœrus*,' Amer. Philos. Soc., May, 1894, pp. 243–251), but as his materials were not complete, I have thought best to give a description of our specimen in full.

which is located far back near its middle. In the Suellines, on the other hand, it is strongly developed, but situated at a still greater distance from the glenoid cavity. The coracoid is small and less distinctly constricted off from the rim of the glenoid cavity than in *Oreodon*. The glenoid cavity is more oval in form than in *Oreodon*, its greatest diameter being in the transverse direction. While the neck of the bone is relatively shorter and thicker than in *Oreodon*, the axillary and coracoid borders exhibit practically the same relations to the rest of the bone. The vertebral border is not well preserved in any of our material.

The *humerus*, as already remarked, is proportionately much longer and to a slight extent more robust than the corresponding bone in *Oreodon*. The head has nearly the same shape, but does not overhang the shaft to the same extent. The greater tuberosity is prominent and distinct, but it does not rise above the articular surface to the same extent as is seen in either *Oreodon* or any of the recent forms of the Artiodactyla; its antero-posterior extent, however, is considerable, and its posterior portion is as much elevated as its anterior, which is, apparently, not true of any other form with which I am acquainted. The lesser tuberosity is large and prominent, but does not rise above the level of the articular surface as it does in *Oreodon*, the pig, camel, sheep and deer. The bicipital groove is wide, deep and single, and the inconspicuous deltoid crest reaches far down the shaft in marked contrast to its proximal position in many of the recent genera.

Fig. 10. Head of humerus, top view, *Agriochœrus latifrons*. One-third natural size.

The characters of the distal end of the humerus appear, at first glance, so remarkable that one would hesitate to place it in the ungulate series, but a more careful study reveals the fact that its nearest affinities are in all probability with the primitive Artiodactyla. That which causes it to appear so remarkable at the first glance is its great breadth as well as the unusual size of the internal condyle. Another marked feature, which gives to it a distinctly carnivorous appearance, is the cylindrical form of the shaft and its decided antero-posterior flattening as it approaches the distal end. What may be described as an extremely constant

and highly characteristic feature of the recent Artiodactyle humerus is its very straight internal border, together with the lateral flattening of the shaft. If a line be drawn down this border it will just cut the inner edge of the distal articular surface. This is exemplified in its greatest perfection in the Bovidæ and Cervidæ, although it is almost equally true of the camels and pigs. In all these forms the internal condyle has quite completely disappeared, which gives to the whole distal end of the bone a laterally compressed appearance. Now in *Oreodon* we meet with some important deviations from this type of humerus; the internal border is not so straight, the shaft is not so compressed laterally, and there is an internal condyle of moderate proportions present. It can readily be seen, however, on placing the humerus of a deer and an *Oreodon* side by side that these parts of the two bones are very much alike, and it is also to be remarked that in those particulars in which *Oreodon* departs from the deer, in these respects it approaches *Agriochœrus*.

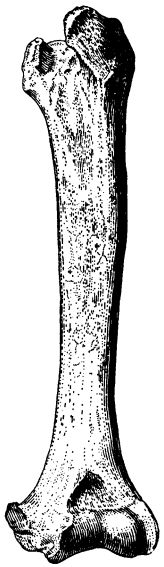


Fig. 11. Humerus of *Agriochœrus latifrons*. Front view. One-third natural size.

The distal end of the humerus of *Oreodon* and all the recent genera differs from *Agriochœrus* not only in the size of the internal condyle and the relative breadth, but also in the peculiar and characteristic way in which the comparatively thin internal border of the anconeal fossa is prolonged downwards so as to form the most dependent part of the bone. The camels furnish an exception to this rule, the flange of the inner trochlea reaching as low or a trifle lower than this process. In *Agriochœrus* the inner border of the anconeal fossa is thick, rounded off below, and passes into the internal condyle, the most dependent part of the bone being formed by the flange of the inner trochlea.

The distal articular surface of the bone presents a number of interesting characters which are quite in keeping with the other peculiarities already noted. The surface is rather imperfectly divided into an internal and external trochlea by a low, thick,

inconspicuous carina, which is placed nearer the outer than the inner side. It results from this that the inner trochlea is much the larger of the two, as is so markedly the case in all the recent forms of Artiodactyles, but not so in *Oreodon.* The inner boundary of this trochlea is indicated by a prominent flange, which does not extend more than halfway around to the posterior side. When looked at from below, the upper or anterior profile of the surface is seen to descend at first greatly towards the middle, then more abruptly to form the principal groove of the internal trochlea, after which it rises again to correspond with the carina. The external trochlea is deeper, narrower and terminated externally by a prominent flange. The whole distal end of the bone more nearly resembles that of a bear than an Ungulate. A marked difference, however, is seen in the comparatively deep anticubital fossa, which in the bear is but slightly developed. As compared with *Oreodon*, the main differences are seen in the disparity in size between the two trochleæ and the weaker development and breadth of the carina. In *Oreodon* the two trochleæ are subequal, whereas in the recent genera the internal greatly exceeds the external in breadth, as in *Agriochœrus.*

The *radius* is long and rather slender in proportion to its size. The proximal articular surface is divided into three facets, which when applied to the humerus, cover a large part of its distal extremity. The innermost of these facets is placed somewhat obliquely to the head of the bone, is slightly cup-shaped, and looks upwards and inwards. In conjunction with the inwardly projecting shelf-like facet on the ulna, it covers the inner part of the internal trochlea of the humerus when the bones are placed in apposition. It is separated from the median or central facet by an inconspicuous ridge ; this latter facet forms a wide shallow depression, being limited in front by the thickened, prominent edge, which is fashioned into an indistinct tubercle. When applied to the humerus, this surface serves to receive the carina of that bone. The outer of the three facets is of a lunate pattern,

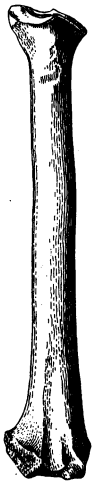


Fig. 12. Radius of *Agriochœrus latifrons.* Anterior view. One-third natural size.

beginning in front near the middle of the head and passing outwards and backwards to terminate at its postero-external angle. It presents a curious bevel, so that its surface looks upwards, forwards and outwards, being at the same time slightly concave from side to side. When the radius is placed in its natural position, and the fore arm extended, a wide space is left between the anterior part of this facet and the outer trochlear surface of the humerus. It is only when the forearm is strongly flexed that it engages with its proper articular surface of this latter bone, and it is a matter of no little interest to note that the mechanism of the joint is such that when this extreme flection is made the outer border of the whole manus is rotated to that extent that the palmar surface looks almost directly inwards. If there is anything in the hypothesis, that the particular way in which the foot has been used is responsible for its modification, then we have a very distinct reason why the fourth digit should have been equally developed with the third, so as to produce the paraxonic type. That part of the head of the radius which is applied to the ulna is greatly flattened, and is provided with a long, narrow, transverse facet reaching entirely across the bone. There can be no doubt, therefore, that the radius was capable of considerable movement upon the ulna, but owing to the flattened character of the facet this movement was not a rotary one.

The shaft is, in its proximal third, considerably flattened from before backwards, but towards its distal portion becomes thicker and more angulated. The distal end is expanded and marked upon its anterior surface by distinct tendinal grooves for the extensor muscles. The facets for articulation with the scaphoid and lunar are distinct, although this is not plainly indicated in front. Posteriorly the scaphoid facet is produced into a rounded transverse ridge, which is received into a corresponding depression of this bone. The facet for the head of the lunar is excavated, as is the anterior part of the scaphoid articulation. Neither of these facets present any marked obliquity.

The *ulna* is long and slender, and shows no tendency to that extreme reduction seen in the later Artiodactyla. The olecranon is relatively short, stout and thick, and is provided with a distinct groove at its posterior end, as in *Oreodon*, *Protoceras*,

Leptomeryx, and in the Carnivora. The office of this groove was probably for the accommodation of the tendon of the triceps during extreme flexion of the forearm upon the humerus. The sigmoid cavity is of moderate depth, and its inferior boundary rises up into a rudimental coronoid process. The internal part of the articular surface of this cavity projects as a considerable ledge, which is not covered by the radius when these bones are articulated. The shaft is stout and heavy in its proximal portion, but is decidedly flattened and thinner in its middle and distal portions. It is deeply grooved upon its outer and inner sides. The distal end is expanded somewhat, and displays an antero-posteriorly rounded surface for articulation with the cuneiform, and a distinct postero-external facet for articulation with the pisiform.

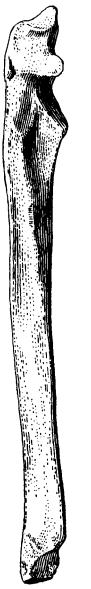


Fig. 13. Ulna of *Agriochœrus latifrons*. Anterior view. One-third natural size.

A comparison of the ulna and radius of *Agriochœrus* with those of *Oreodon* shows a great number of similarities. The head of the radius in *Oreodon* is not so broad, but at the same time covers the ulna more completely; this results principally from the less developed internal shelf which forms the floor of the sigmoid cavity. The inner side of the shaft of the ulna is not grooved in *Oreodon*, whereas it is deeply grooved in *Agriochœrus*. The distal end of the radius is slightly different in the two genera, but not to such an extent as to indicate a very wide separation. The distal end of the ulna in *Oreodon* shows no distinct facet for the pisiform, being very much rounded from before backwards; in *Agriochœrus* it is thicker, not so rounded, and has a distinct facet for the pisiform.

The Manus.—The carpus of *Agriochœrus* is in many respects exceedingly primitive for that of an artiodactyle Ungulate. If the serial arrangement was the primitive one for the Ungulata, as Cope has suggested, then the shifting of the proximal upon the distal row has made less progress in this respect than in almost any other Artiodactyle yet described. The cuneiform rests exclu-

sively upon the unciform, the lunar almost wholly upon the magnum, while the scaphoid is largely supported by the trapezoid and trapezium ; it has, however, developed a considerable contact with the magnum as well, but not to the same extent seen in the large majority of other members of the order. Another striking feature of the carpus is the vertical flattening of many of its elements, especially the scaphoid.

The *scaphoid*, as just observed, is chiefly remarkable for its great width in proportion to its height. In the Artiodactyla in general this is a high and narrow bone, but in *Agriochœrus* it may be described as flat and broad. When viewed from above it presents a subcircular outline, somewhat more narrowed upon its inner than its outer side. The radial facet is cup-shaped, with the anterior lip rounded off. Upon its distal surface there is a narrow, antero-posteriorly directed, internal facet for articulation with the magnum, and a larger external oblique facet for articulation with the trapezoid. *There is no facet for the trapezium*, although this bone is present and of considerable size.

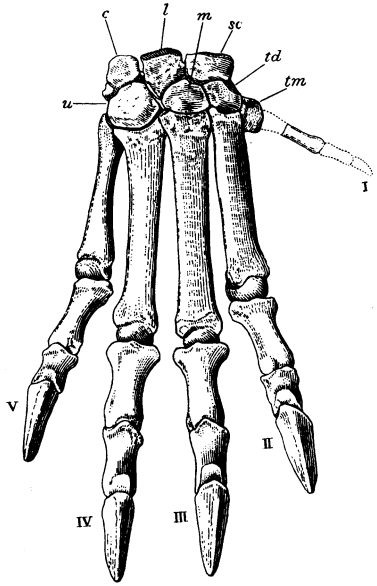


Fig. 14. Fore foot of *Agriochœrus latifrons*. One-half natural size.

The facet for the magnum is divided into two parts, an anterior, nearly plane, and a posterior, concave portion for the articulation with the head of this latter bone. Upon the outer side this facet passes into the surface by which the scaphoid articulates with the lunar. The internal or trapezoid facet is much the larger of the two, and is also divided into two parts, separated from each other by an indistinct oblique ridge ; the posterior of these is concave, like that for the head of the magnum, and serves to receive the posterior elevation of the trapezoid. The anterior part of the

facet is nearly flat, with but a slight concavity. Near the middle of the distal surface of the bone, where the anterior and posterior divisions of these two facets meet, is a prominent tubercle.

A comparison of the scaphoid of *Agriochœrus* with that of *Oreodon* shows many important differences in detail. In *Agriochœrus* it is unusually low and flat, whereas in *Oreodon* it is relatively high and narrow, approaching more nearly in shape that of the modern type as seen in the pig, deer, sheep and camel. In *Agriochœrus* the radial facet is concave with the anterior lip comparatively little rounded off, while in *Oreodon* it consists of a prominent, transversely convex, and a posterior, deeply concave portion of nearly equal extent. In *Agriochœrus* the magnum facet has little obliquity, and is almost as broad in front as behind; in *Oreodon* this facet is very oblique and is much broader in front than behind. Another important difference is seen in the relative size and shape of the trapezoid facet. In *Agriochœrus* it displays a posterior convex and an anterior nearly flat surface, while in *Oreodon* there is but a single division, which is saddle-shaped. In *Oreodon*, again, there is a distinct facet for the trapezium, notwithstanding its reduced size, whereas in *Agriochœrus* this facet is completely wanting.

The *lunare* is quite as characteristic as the scaphoid; it has the same general shape as that of the Oreodonts, but its relationship to the surrounding bones is very different. It differs from all the recent forms, and agrees with the Oreodonts in the great development of the anterior wedge-shaped process which projects downwards in front between the unciform and magnum. The length and size of this process gives the bone a high and narrow appearance, the head being strongly convex from before backwards. The facet for articulation with the scaphoid is narrow and elongated; that for the cuneiform is flat and vertical, and becomes continuous with a vertical articular face upon the ulnar side of the wedge-shaped process where it touches the unciform. The distal surface is made up of a deep, transversely excavated, posterior part for articulation with the head of the magnum, and an anterior, more or less flattened, oblique portion which rests upon the inner oblique shelf of the same bone. Upon the ulnar side of this excavated facet, and more or less continuous with it, is a

small facet which receives a spur-like lateral process from the unciform. It results from this arrangement that the lunar rests almost wholly upon the magnum, the contact with the unciform, with the exception of the small lateral spur just mentioned, being vertical. In *Oreodon*, on the other hand, this arrangement is just reversed, the vertical contact being with the magnum instead of the unciform, upon which the lunar principally rests. There is, however, a small oblique facet posteriorly which serves to receive the head of the magnum. So different, indeed, is the lunar in the two genera that one would readily mistake the one from the right side of one as pertaining to the left side of the other, and conversely.

The *cuneiform* is relatively smaller than in *Oreodon*, and of considerably less extent; its ulnar facet is deeply concave from before backwards, and the facet for the pisiform is of much the same shape and proportions as in *Oreodon*. The facet for the unciform is single, more or less cup-shaped, and differs from that of *Oreodon*, in which there is an additional facet at the postero-external angle of the bone.

The pisiform resembles that of *Oreodon* in its general form, but it is relatively longer, heavier and with a more expanded distal extremity. The two facets are subequal, whereas in *Oreodon* that for the cuneiform considerably exceeds that for the ulna.

The *unciform*, while it resembles that of *Oreodon* in a general way, nevertheless exhibits a number of striking differences. The prominent posterior hook projects backwards, downwards, and slightly outwards. The cuneiform surface is very convex from before backwards, and the postero-internal angle terminates in a lateral spur which projects under the lunar. Just in front of this spur is an almost vertical, concave facet with the concavity directed inwards, which articulates with the anterior descending process of the lunar already mentioned; at a considerable distance behind this facet, at the base of the hook, is a small, indistinct articular surface, which is the only point where the magnum touches the unciform. The distal face is occupied by three facets—an outer one, greatly elongated from before backwards, for the support of the fifth metapodial; a middle larger one for the fourth, and an inner oblique one for the outer process of the

third. As compared with *Oreodon* the posterior hook projects less strongly outwards, and the proximal surface is much less oblique. The internal spur in *Oreodon* is swollen into a large process, which forms the chief support for the lunar, having usurped the principal function of the head of the magnum. The cuneiform facet is relatively much smaller than in *Agriochœrus*, and is, moreover, double. The facet for the articulation of the descending process of the lunar is much larger and less vertical, while that for the articulation with the magnum is a small vertical circular area, upon the radial side of the inwardly projecting spur.

The *magnum* differs widely from the corresponding bone in *Oreodon*, almost if not more than *Oreodon* does from the modern type, as seen in the pig, camel and deer. It is proportionally larger and stronger than in *Oreodon*, and has a much greater posterior breadth. Upon its proximal surface the prominent, strongly convex head rises abruptly from the scaphoid and lunar facets in front; it is divided by a faint ridge into two portions for articulation with these two bones, of which that for the lunar is much the larger, and displays a marked obliquity from without inwards. In *Oreodon* the head is placed much nearer the anterior margin, is strongly keeled in front, and its obliquity is from within outwards—just the reverse of that seen in *Agriochœrus*. In *Agriochœrus* the lunar facet in front is broad and transverse, while that for the scaphoid is small and more or less vertical. In *Oreodon* again this condition is reversed, the scaphoid facet being broad and transverse, and that for the lunar being small and vertical. In *Agriochœrus* the posterior part of the magnum is as broad as the anterior, and it is terminated behind by a stout rounded process. In *Oreodon* the bone narrows very rapidly behind and terminates in a slender, inwardly projecting, hook-shaped process, which winds around the head of the second metacarpal, developing a distinct facet in this situation. Were it not for the presence of this hook, one might easily be led to mistake the two bones of the same side in these genera for the opposite bones of the same species. The distal surface for the support of the third metacarpal does not present any characters worthy of especial remark.

The *trapezoid* is nearly double the size of the corresponding bone in *Oreodon*. It articulates with the magnum by two distinct facets, a larger, anterior, and a smaller, posterior one; its facet for the scaphoid is broad and nearly flat in front, but rises into a prominent tubercle behind. Upon the radial side there is a small though distinct facet where it articulates with the trapezium; its distal surface is saddle-shaped, and is occupied entirely by the head of the second metacarpal. The only noticeable difference between *Agriochœrus* and *Oreodon* as regards this bone, is seen in the relative size and the facet for its articulation with the magnum. In *Oreodon* there is but a single facet.

The *trapezium* of *Agriochœrus*, at least in the species under consideration, is not only remarkable for its connections, but what is still more surprising, it gives evidence of having supported a more or less opposable pollex. It is the smallest of the carpal elements and considerably reduced in size, but not so much so as to have been entirely functionless. Its proximal part bears two distinct facets for articulation with the trapezoid and the second metacarpal. One of the surprising features about it is that it has no connection with the scaphoid. Distally it displays a distinctly saddle-shaped facet for articulation with the metapodial of the pollex. Taking into consideration the fact that the bones of both sides are preserved, and that when placed in position they fit accurately, there can be no mistake regarding the *more or less opposable position, at least, of the first digit.* It differs from that of *Oreodon*, in which the trapezium is small, nodular, and articulates with the scaphoid; the direction of its metacarpal facet, moreover, indicates that the pollex projects in the same line as the other digits.

The *metacarpals* are somewhat longer and more slender than those of *Oreodon*, and the difference in length between the third and fourth is less marked. When the phalanges are added, however, the third digit is seen to be a little longer than the fourth. In length, the third metacarpal exceeds the others, after which come the fourth, second, fifth and first in the order named. In the matter of robustness, the second surpasses all the others, the fifth being smaller and decidedly more slender. With the notable exception of the pollex the metacarpals are articulated in the

same way as those of *Oreodon*, as is also the case in the manner in which they are supported by the various carpal elements. The distal ends of the metacarpals, like those of the metatarsals, are very rounded and prominent, especially upon their dorsal surface, in this respect resembling the Carnivora much more than the Ungulates; in this they differ markedly from those of *Oreodon*. In all there is a strong keel, which is confined to the palmar aspect of the extremity. The metacarpal of the pollex is represented in the collection by only its distal portion, which is imbedded in matrix in such a manner in connection with the metacarpal of the second digit as to leave no room for doubt as to its presence; it is relatively larger than the corresponding bone in *Oreodon*, and is much compressed laterally. Its proximal end is not preserved, but judging from the saddle-shaped facet at the distal end of the trapezium, it is fair to presume that it had a corresponding surface.

The *phalanges*, especially those of the proximal and median rows, are decidedly longer and more slender than those of *Oreodon*, having at the same time the heads much more laterally expanded. This feature is indeed so strongly marked that one would readily mistake any of the proximal phalanges for those of a cat; this likeness is not confined to the head alone, but extends to the distal extremity as well, where the narrow, deeply-grooved facet is very feline in appearance. The median phalanges are high and strongly compressed from side to side, in marked contrast to those of *Oreodon*, in which they are broad and depressed; their proximal ends are more deeply grooved than in this genus, and the dorsal extremity of the articular facet is produced into a prominent overhanging spine, which is but faintly indicated in *Oreodon*. The distal articular facets are carried much further back upon the dorsum of the phalanges than they are in *Oreodon*, a fact which points to a much greater flexibility of the ungues and constitutes a nearer approach to the modern condition found in so many of the Artiodactyla. It is, however, in the ungual phalanges that the most striking peculiarity of *Agriochœrus* is seen, and did not the remainder of the skeleton bear the unmistakable stamp of its ungulate affinities, one would be led to place it in another order. So remarkable is their shape

Fig. 15. Ungual phalanges. Side and top views. 1 and 4, *Agriochœrus latifrons*; 2 and 3, *Oreodon culbertsoni*. One-half natural size.

that they merit the name of claws rather than that of hoofs. They are high, compressed, and curved, ending in a blunt downwardly projecting point; the dorsum is strongly keeled and much curved, while the plantar aspect is broader and less curved. The proximal articular surface is deeply excavated to fit the strongly convex surfaces of the median phalanges. The ungual phalanges of *Oreodon* are simply hoofs of the ordinary primitive Artiodactyle type, so that no comparison is necessary.

The Hind Limb.—There is no great disproportion in length between the fore and hind limbs of any of the species of *Agriochœrus*, so far as our material will permit one to judge. The femur slightly exceeds the humerus in length, the tibia is a trifle longer than the radius, and the manus and pes are subequal.

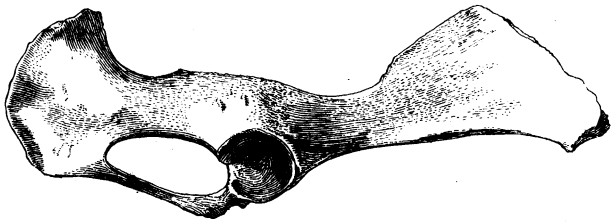


Fig. 16. Pelvis of *Agriochœrus guyotianus*. Two-fifths natural size.

The *pelvis* in its general form closely resembles that of *Oreodon*. The ilium is prolonged in front of the acetabulum somewhat more than the ischium is behind it, the disparity in length between the two bones being about equal to that seen in *Oreodon*. It is considerably expanded, and its anterior inferior angle is produced into a prominent hook-shaped spine. The narrow contracted portion, just in advance of the acetabulum, is of moderate length, and the transition into the expanded portion is more gradual than in *Oreodon*, where it is quite sudden. In the pig, deer and sheep, the concavity of the ilium is divided into a superior and an inferior portion by a longitudinal ridge, which terminates at the

anterior border in a well-marked tuberosity. No trace is seen of this in the camel, as is also the case in *Agriochœrus* and *Oreodon.*

The ischium, again, resembles that of *Oreodon* more closely than any form with which I have compared it. Its posterior border is thin and of considerable vertical depth, passing by a well-rounded border into the pubis below. It, however, exhibits three thickenings, one of which is superior, one posterior, and one inferior. In the pig the ischium terminates posteriorly in a stout trihedral bar of bone, which is directed upwards at a considerable angle. The plate which bounds the obturator foramen posteriorly, however, exhibits a considerable thickening upon its lower edge. In the sheep, camel and deer, the ischium has near its posterior termination a stout transverse spur projecting outwards; in the camel the ischial tuberosity is at the base of the spur, while in the sheep and deer it is considerably behind its base. *Agriochœrus*, therefore, resembles the pig more in this respect than any of the Selenodonts.

The pubis is short and rather weaker than in *Oreodon.* The ileo-pectineal eminence is well marked, and the pubic symphysis short; the obturator foramen is of moderate size and has an oval form. The acetabulum is deep, and the cotyloid notch is rather wide and backwardly directed.

Of the *femur*, the head is very globular and is more exserted from the neck than in any of the recent Artiodactyla. The great trochanter does not rise as high as the top of the head of the bone, the digital fossa is deep, and the intertrochanteric line rather indistinct. The neck is rather more elongated than in recent forms, and the whole proximal end of the femur has rather more of a carnivorous than ungulate appearance. The shaft is nearly straight, almost circular in section, and displays but a faint development of the *linea aspera.* The distal extremity has considerable antero-posterior extent, and does not exhibit the fore and aft flattening noticed by Professor Osborn and myself in our

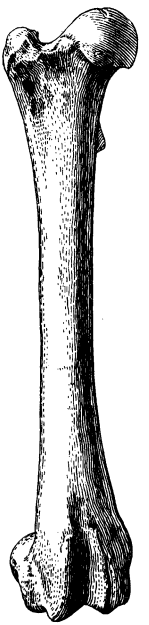


Fig. 17. Femur of *Agriochœrus latifrons.* One-third natural size.

original description. A comparison of the original specimen with our present material shows that this feature of the distal end of the femur was altogether due to crushing, and does not represent the natural shape of this part of the bone. The whole distal extremity rather closely resembles that of *Oreodon*, the differences being of comparatively little importance.

Tibia and Fibula.—The latter of these bones is represented in the collection by only its articular extremities, so that a complete description cannot be given. The head of the tibia presents the usual Artiodactyle pattern, and differs little from that of *Oreodon*, the sheep or camel. The shaft is relatively more slender and elongated than that of *Oreodon*, and the cnemial process is not extended so low down. The remainder of the description of the two bones I take from our original statement :

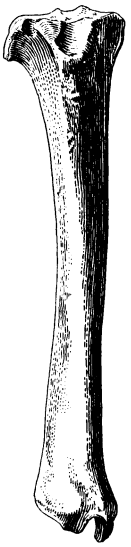


Fig. 18. Tibia of *Agriochœrus guyotianus*. Two-fifths natural size.

" The internal malleolus is remarkable for its development and the manner in which it articulates with the astragalus. It is long, stout, and slightly hook-shaped, reaching at least half-way down the inner side of the astragalus when the bones are placed in position. The hook is directed to the outer side of the ankle, and is received into a deep excavation upon the inner face of the ankle bone. In the pig the internal malleolus is small and overlaps the inner side of the astragalus but slightly, but in *Oreodon* it is much larger and overlaps the astragalus considerably. It also has a tendency to become hook-shaped in this form. The remainder of the articular surface is shaped very much as in the pig, being deeply grooved to receive the condyles of the astragalus, with a median tongue or ridge which fits accurately into the intercondylar groove of this latter bone.

" The shaft of the fibula, so far as it is preserved, is slender and much flattened. Its distal extremity is expanded to a greater extent than in the pig, and, as in all the Artiodactyla, it articulates with both the astragalus and calcaneum. The articular

surface, by means of which it joins the astragalus, consists of a beveled edge upon the upper outer surface of the external condyle of this bone, anteriorly. In the Artiodactyla, owing to the vertical dimensions of the astragalus, the fibula overlaps it considerably, so that the articulation between these two bones is confined entirely to the outer side of the astragalus.

"*Tarsus.*—The tarsus presents so many striking resemblances to that of the Artiodactyle Ungulates that its description is perhaps best accomplished by instituting a comparison between it and some generalized members of this order, of which the pig is a good example.

"The *astragalus* is relatively broader and of less vertical depth than that of the boar. This results from the shortness of the neck and the inward extension of the navicular portion of the head. Its superior or trochlear surface presents two unequal condyles, strongly convex from before backward, and separated by a deep groove. The external condyle, the larger of the two, is limited in front by a deep transverse notch which separates it sharply from the cuboidal facet, in front or below. This notch is much more pronounced than in the astragalus of the pig. The inner condyle is smaller and presents a somewhat sharper crest, owing to the excavation of its inner side for articulation with the internal malleolus. In its lower or anterior extremity it is well rounded, and of a somewhat scroll-like pattern, terminating abruptly in a distinct overhanging ledge, which separates it from the navicular facet. This ledge is absent from the astragalus of the boar, as is also the scroll-like appearance of the lower part of the condyle, but traces of it are to be seen in *Oreodon*. The distal extremity or head of the astragalus is occupied by two facets for articulation with the cuboid and navicular. It joins the trochlear portion by a short neck, and is placed quite as obliquely upon this part of the bone as in that of the suillines. The cuboid and navicular facets are strongly convex from before backwards, and in their articulation with these bones form as perfect a ginglymus as is to be seen in any of the Artiodactyla. They are sharply separated from each other by a prominent fore and aft ridge, which passes backwards to form the inner boundary of the

sustentacular facet behind. The cuboid facet is the smaller of the two, and can be said to have but a limited extension backwards. It narrows greatly at the middle of the under or anterior surface, and become continuous with the sustentacular facet behind. In the pig, and to a somewhat less extent in *Oreodon*, it is continued well around to the posterior surface, but it is separated from the sustentacular facet by a well-marked ridge. This facet, while it is strongly convex from before backwards, is little or not at all concave from side to side. The navicular facet on the other hand is not only very convex fore and aft, but presents first a convexity and then a marked concavity laterally from within outwards, as in the pig. One feature in which it differs markedly from the astragalus of the pig, and for that matter, of all the Artiodactyla, is its great backward extension, reaching as far as the middle of the posterior surface of the bone. By reason of this backward extension of the navicular facet, the facet for the *sustentaculum tali* is very oblique and beveled considerably externally. It covers the larger part of the posterior surface of the bone.

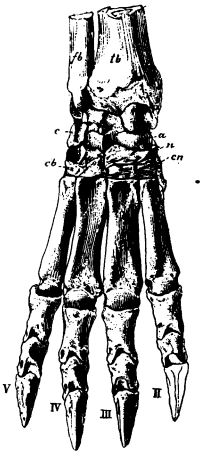


Fig. 19. Hind foot of *Agriochœrus major*. Front view.

"The *calcaneum* resembles the corresponding bone of the pig very closely. This is especially noticeable in the small sustentaculum, the narrow distal extremity where it articulates with the cuboid, together with the prominent articular face by which it articulates with the fibula. As compared with that of the pig, the tuber is relatively shorter, the distal end is somewhat narrower, and the fibular facet has a greater antero-posterior extent. Upon the outer side just below the fibular facet is a prominent bony ridge for the attachment of the external lateral ligament, beneath which is a shallow fossa, which is scarcely indicated in the calcaneum of the boar. Upon the end of the tuber is seen a well-marked groove, located somewhat to the inner side, which serves for the passage of the tendon of the *plantaris* muscle.

"The *cuboid*, as compared with that of the pig, is much depressed. Posteriorly it bears a process of moderate dimensions as in the Artiodactyla in general. Upon its upper surface are the two facets for the calcaneum and astragalus, that for the calcaneum being almost flat and inclined downwards and forwards, while the astragalar facet is strongly concave. Distally two facets can be distinguished for articulation with the fourth and fifth metapodials respectively. They are relatively broad and flat. At the posterior edge of these articular surfaces, immediately beneath the backwardly projecting bony process, is to be seen a slight groove for the passage of the long peroneal tendon as it crosses the plantar surface of the foot. This groove is especially well developed in the pig, being almost completely converted into a foramen. In *Oreodon* it is less developed.

"The *navicular* is also much flattened from above downwards, resembling in this respect the corresponding bone of the Perissodactyla, rather than that of Artiodactyla. It is strongly cup-shaped above to receive the convex navicular portion of the head of the astragalus, and much flattened below where it articulates with the coössified ecto- and meso-cuneiforms. Upon its inner face is seen a moderately weak *tuberculum*, to which the tendon of the anterior tibial muscle (*tibialis anticus*) is attached. Its chief peculiarity is found, however, in the enormous hook which is developed upon its posterior surface. This hook is broad, much flatttened from behind, and completely overhangs the ecto-meso-cuneiform, as well as the proximal ends of the neighboring metapodials. Although less prominent it appears to be universally present in the Artiodactyla and as universally absent in the Perissodactyla.

"*Features of the Double Ginglymus.*—It is interesting to note in this connection, and a matter of no slight significance, that a similar hook is developed upon the navicular of the lagomorph rodents. In this widely separated group we also find that the foot is of the paraxonic type, that the fibula articulates with the calcaneum, and that there is a distal ginglymus present (astragalo-navicular). It would thus appear that these characters, arising as they have independently, in at least two distinct and widely

separated orders, are necessary concomitants, and dependent upon the same or similar causes for their production.

"The *ecto-* and *meso-cuneiforms* are completely coössified, there being no trace of the suture visible. This compound bone is broad and flat, and rests upon the second and third metapodials. The articulation with these bones is by a broad flattened surface, which is also true of the articular surface by which it supports the navicular."

The ento-cuneiform is a long slender styliform nodule articulating by a double facet with the navicular and compound cuneiform ; upon its anterior internal face is seen another elongated facet by which it joins the posterior surface of the head of the second metatarsal. When in place, it lies anterior and internal to the navicular hook. In our original description we erroneously supposed that a hallux was present, but our present material shows that this bone did not support a metatarsal. The hallux was therefore absent. The general shape and connections of the bone are similar to that of *Oreodon.*

The Metatarsus.—"Of the metatarsals, the two median ones, mts. III and IV, are almost if not quite equal in size and length. The lateral ones, mts. II and V, are practically so, the disparity in their length being slightly greater than that found in the pig. While the outer one (mt. V) is a little the longer of the two, the inner one (mt. II) is the stronger. This appears also to be true of all the more generalized Artiodactyla in which four toes are present. In the rabbit, on the other hand, mt. II, is both longer and stronger than mt. V, and this is also true of the median pair, the inner one slightly exceeding its fellow in size and length.

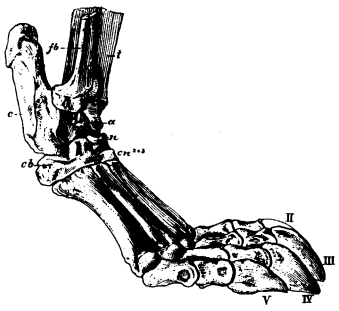


Fig. 20. Hind foot of *Agriochœrus major.* Side view.

"The two outer metatarsals (IV and V) are supported wholly by the cuboid, while the two inner ones (II and III) are supported by the compound cuneiform. Just as in the lower

Artiodactyla and in the rabbit there is no tendency to displacement of any of the metapodials. The distal ends of the metapodials have prominent well-rounded articular heads, very similar to those of the digitigrade Carnivora. These facets are continued well backward upon the dorsal surface, and are constricted off from the shafts by deep grooves, indicating that the main flexure of the foot took place at this point, as figured by Gaudry in *Chalicotherium*, and that the animal was truly digitigrade. Distal keels are present, but are confined to the plantar surface.

"*The Phalanges.*—The proximal phalanges are quite remarkable for the character of the articular surfaces by which they join the metapodials. When looked at from the side these surfaces are seen to be directed more upwards than backwards, almost to the same extent as represented by Gaudry in *Chalicotherium*. This indicates two things, viz.: that the proximal ends of the metapodials were raised from the ground, and that the distal end of the phalanx was carried slightly upwards when the bones were placed in their natural position. This view is further carried out by the character of the articular surface at the distal end of the phalanx. It is directed more downwards than forwards, which would give the succeeding phalanx a downward trend again, so that the first two phalanges would describe a gentle curve. This is well exemplified in the cat. The second or median phalanges are shorter than the proximal, and are more compressed from side to side. Distally they exhibit a grooved articular surface almost equally divided between the upper and lower moieties of the bone, for articulation with the large compressed claws or ungues. There is nothing to indicate that the ungues were strongly bent down upon the middle phalanx, as represented by Gaudry. If one can imagine a digitigrade bear it would come very near representing the manner in which the phalanges were articulated in *Artionyx* [*Agriochœrus*].

"The ungues are large, strongly compressed, and considerably arched upon the dorsal surface. They are a little hook-shaped. The proximal ends are deeply excavated (representing almost a semicircle), to receive the distal ends of the median phalanges. There is no trace of a bony sheath or median cleft developed."

The foot described above is from the larger species of the Protoceras Beds. In the smaller *A. latifrons* from the lower beds the foot is longer, more slender; the phalanges are considerably longer and resemble those of the fore foot.

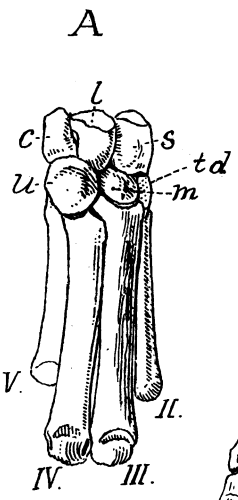


Fig. 21. Fore foot of *Merychyus*. After Scott.

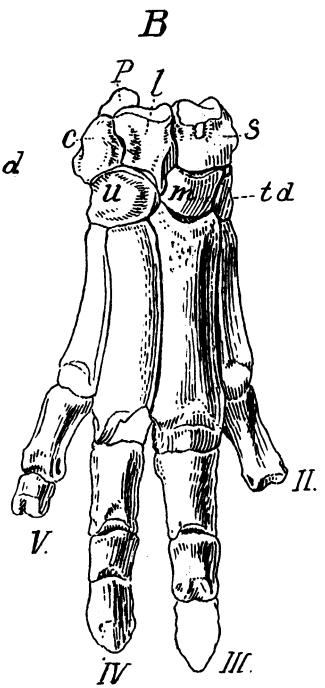


Fig. 22. Fore foot of *Merycochœrus*. After Scott.

Fig. 23. Fore foot of *Oreodon*. After Scott.

Summary of Comparison with Oreodon.

In the foregoing description I have compared the bones of *Agriochœrus* very closely with those of *Oreodon*, and it now remains to summarize the likeness and differences. *Agriochœrus* resembles *Oreodon* in the following important characters: (1) The upper canines are enlarged and have the distinctive D-shaped pattern on cross section. (2) The first lower premolar is enlarged and caniniform, the lower canine being incisiform. (3) The form of the skull is practically the same, and the foramina

have nearly the same arrangement. (4) In the fore limb the scapula, humerus, ulna and radius are very similar in the two genera. (5) The lunar has a prominent downwardly projecting beak which excludes the magnum from contact with the unciform in front. (6) Both have five digits in the manus. (7) In the hind limb the pelvis, tibia and fibula are similar, as is also the case with tarsus. (8) The ecto- and meso-cuneiforms are united.

Agriochœrus differs from *Oreodon* in the following characters, which may be regarded as of equal importance: (1) Loss of incisors in *Agriochœrus*. (2) Molariform pattern of the fourth superior and inferior premolars, and the presence of a diastema in both jaws. (3) The molars are very different in structure. (4) The neural spine of the axis is different, and the transverse processes of the atlas are perforated. (5) There is a double tongue and groove articulation of the lumbar vertebræ. (6) The lunar rests largely upon the magnum instead of upon the unciform. (7) The trapezium does not touch the scaphoid. (8) The pollex has an opposable position and saddle-shaped articular facet. (9) The terminal phalanges are claw-like and not hoof-like.

Comparison with the Anoplotheridæ.

In many of its osteological features *Agriochœrus* resembles the Anoplotheroids. This is seen in the form of the skull, in the humerus, ulna and radius, as well as in the pelvis, femur, tibia and fibula. A very distinctive resemblance to *Agriochœrus* is seen in the molariform fourth premolars of *Dichodon cuspidatus*, while the only approach to the claw-like terminal phalanges is seen in *Diplobune*. Zittel says of them :[1] "Die Endphalangen zeichnen sich durch schmale, seitlich zusammengedrückte, gekrümte, fast Krallenartige Beschaffenheit aus." Another very marked peculiarity of this genus is seen in the way in which the lunar rests almost wholly upon the magnum, and has also a lateral contact with the unciform, just as in *Agriochœrus*. This resemblance between the two forms is further strengthened by the presence of the peculiar beak-like process which wedges in between the magnum and unciform. In the drawing given by

[1] 'Handbuch der Palæontologie,' p. 373.

Zittel the magnum and unciform are represented as being in contact, with the lunar very loosely articulated. It is probable that if a closer fit of these bones were made the unciform and magnum would be separated in front.

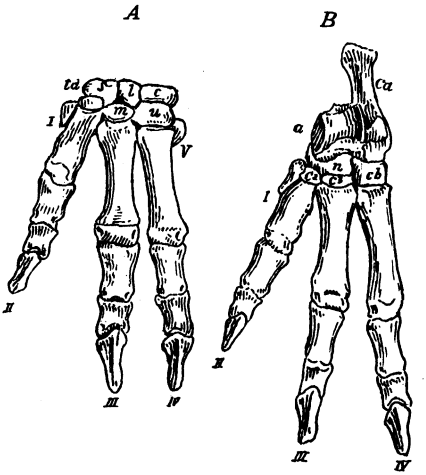


Fig. 24. Fore foot of *Diplobune*. After Zittel

Notwithstanding the resemblances to *Agriochœrus* to be found in these various members of this family, there are at the same time many well-marked differences. The upper canine of the Anoplotheroids is but little elongated, and does not have the characteristic D-shaped pattern on cross section; the first inferior premolar is not caniniform, and the molars have a large and distinct anterior intermediate cusp. The ecto- and meso-cuneiforms are always distinct, and the toes are reduced to two or three. In some instances the reduction of the digits and the elongation of the podial elements has gone almost as far as in any of the modern Pecora.

The Systematic Position of Agriochœrus.

In attempting to discover the more exact relationship of *Agriochœrus*, I think we may safely assume, from what has already been said, that it is a member of the Artiodactyla. We can furthermore exclude the Suillines as being little or no nearer to it than the original or common ancestor of the whole group. There can be little doubt that the Selenodonts early split into two divisions, of which one retained the anterior intermediate cusps of the molars, while the other kept the posterior intermediate cusps. In the higher development of each of these lines the intermediate cusps disappeared, leaving a tetraselenodont molar. According to

Schlosser it was the latter of these lines which gave origin to the modern Selenodonts, while the former became entirely extinct. It is possible, however, that the camels represent an independent off-shoot.

In *Agriochœrus* the molars are tetraselodont, and until we know more of its ancestry it is impossible to say with certainty from which of the two lines it has descended. If, however, we can form any judgment from the great similarity of its skeletal structure with that of the group with the anterior intermediate cusp in the superior molars, viz., the Oreodonts, Anoplotheroids and Anthracotheroids, then we must conclude that its nearest affinities are with these forms. There is one character that opposes itself to this view, and that is the opposable position of the pollex. We probably know the direct ancestors of the true Oreodonts in *Protoreodon* of the upper Eocene, and according to Scott,[1] there is no hint of this position of the pollex seen in the manus of this form. While it tends in a measure to bridge over the differences between *Agriochœrus* and *Oreodon*, it nevertheless is much nearer to the latter than the former in all of its essential characters. The terminal phalanges are quite as distinct hoofs as are those of *Oreodon*, and the scaphoid is high and narrow. The relationship of the lunar to the surrounding bones is also decidedly more oreodont than agriochœrid.

Before we can understand the meaning of the peculiar position of the lunar in *Agriochœrus* it is necessary for us to know what the original arrangement of the carpal bones was in the Artiodactyla. Cope has shown that the arrangement in *Phenacodus* was serial, and he believes that this was the original position of the carpal elements in all the Ungulates. This it may be said is not at all an improbable view, and there is much evidence to support it. Now if this were the case in the ancestors of the Artiodactyla, then we must look upon the Oreodonts as an extreme form in which the lunar has shifted almost completely from the magnum across upon the unciform. In fact, *Protoreodon* furnishes us with very strong presumptive evidence that this is true, for in this ancestral form we find the lunar with a much larger contact with the magnum. *Agriochœrus*, on the contrary, is yet more primitive

[1] Mammalia of the Uinta Formation, pp. 496–499.

in that the lunar has made but a slight advance upon the unciform.

I cannot see that there is any evidence whatever to support the view expressed by Scott,[1] that the lunar of *Agriochœrus* originally rested equally upon the unciform and magnum, and later shifted to the radial side so as to rest almost wholly upon the magnum. The much more probable view, it seems to me, is that *Agriochœrus* is more primitive in this respect than either *Oreodon* or its ancestor *Protoreodon*, and that the lunar, as well as the other bones of the proximal row, had just begun to shift towards the ulnar side. This is a conceivable explanation of the opposable position of the pollex.

Regarding this latter character of *Agriochœrus*, it may be said that it is the only instance of its kind known among the Ungulata. While it is true that the pollex was to a large extent functionless in this Miocene representative, yet at the same time it raises some interesting questions. Is it possible that the remote ancestors of the Artiodactyla had opposable thumbs, and that they were more or less arboreal in habit; or are we to suppose that the position of this digit came to be more or less opposable as a consequence of and during its progressive atrophy? We know of no analogous instance within the whole range of the mammalia. It is hardly conceivable that the thumb could have at first had a position in line with the other digits, then became opposable, and finally reverted to its original condition. Did these characters stand alone I would be tempted to regard them lightly, and as of comparatively little importance, but it must not be forgotten that we have associated with them the remarkable form of the ungual phalanges. The meaning of all this may be more profound than one would perhaps be led to consider after a hasty review. That *Agriochœrus* displays many striking resemblances in the structure of its skeleton to the group already mentioned, there can be no question, but before we construct its phylogeny, and finally determine its position, I think it would be wise to wait until we know a little more of the forms that went before.

The Species of Agriochœrus.

The genus *Agriochœrus* was originally described by Leidy[2] as representing a distinct family. This author referred three species

[1] 'Notes on the Osteology of Agriochœrus,' Amer. Philos. Soc., 1894, pp. 243–251.
[2] Proc. Acad. Nat. Sci. Philad., 1850, p. 121.

to it, all of which were from the White River Miocene deposits of Dakota. Subsequently Cope added three more species from the John Day beds of Oregon, together with another genus under the name of *Coloreodon*, to which he referred two species from the same locality.[1] Within the past year Marsh has described a third genus under the name of *Agriomeryx* from the White River beds.[2] The only characters by which either *Coloreodon* or *Agriomeryx* is distinguished from *Agriochœrus* is the possession of three superior premolars, whereas the typical species have four. In our collection there are two skulls which agree in every particular with Leidy's description of *Agriochœrus latifrons;* in one skull there are three superior premolars upon each side, while in the other there are three upon one side and four upon the other. This character is therefore shown to be variable within the limits of a species, and cannot be used to define a genus. It may be that the three-premolar types have other characters of the skeleton which will separate them into a distinct genus, but as the evidence now stands the names of Cope and Marsh must be regarded as synonyms of the original genus *Agriochœrus*.

The following analysis of the species is somewhat modified after Cope.[3]

I.—Superior premolars, 4.

(*a*) Otic bullæ much inflated, ovoid, and produced in direction of long axis of skull; muzzle short and wide; internal wall of inf. Pm. 4 complete; frequently only three sup. premolars; Oreodon beds, White River.....*A. latifrons* Leidy.

(*b*) Otic bullæ less inflated, more or less quadrate in outline and elongated in same direction as last species; muzzle longer and narrower; internal wall of inf. Pm. 4 not complete; sup. Pms. always 4; Oreodon beds, White River.....*A. antiquus* Leidy.

(*c*) Otic bullæ small, more or less mammiform, triangular in outline, not reaching below point of postglenoid from which it is widely separated, and with large anteriorly projecting process in front at junction with skull; muzzle relatively long and narrow; internal wall of inf. Pm. 4 complete; nasals pointed posteriorly. John Day beds.....*A. guyotianus* Cope.

(*d*) Otic bullæ proportionately much larger than in last species, greatly flattened in front and projecting much below point of postglenoid, which it joins internally; muzzle short, broad and concave above. John Day beds.....*A. trifrons* Cope.

[1] Proc. Amer. Philos. Soc., 1879, p. 375.
[2] 'Description of Tertiary Artiodactyles,' Amer. Jour. Sci., 1894, Vol. XLVIII, p. 270.
[3] 'Synopsis of the Species of Oreodontidæ,' Proc. Amer. Philosoph. Soc., 1884, p. 503–572.

(*e*) Otic bullæ large, quadrate in outline, very obliquely directed and constricted in the middle ; muzzle broad, flattened above ; nasals trucate posteriorly ; postglenoid robust. John Day beds.
A. ryderanus Cope.

II.—Superior premolars, 3.

(*a*) Species large ; otic bullæ greatly inflated, ovoid, and produced in direction of long axis of skull ; nasals narrow and pointed behind ; palatonareal border opposite anterior cusp of third molar. Protoceras beds, White River.....*A. major* Leidy.

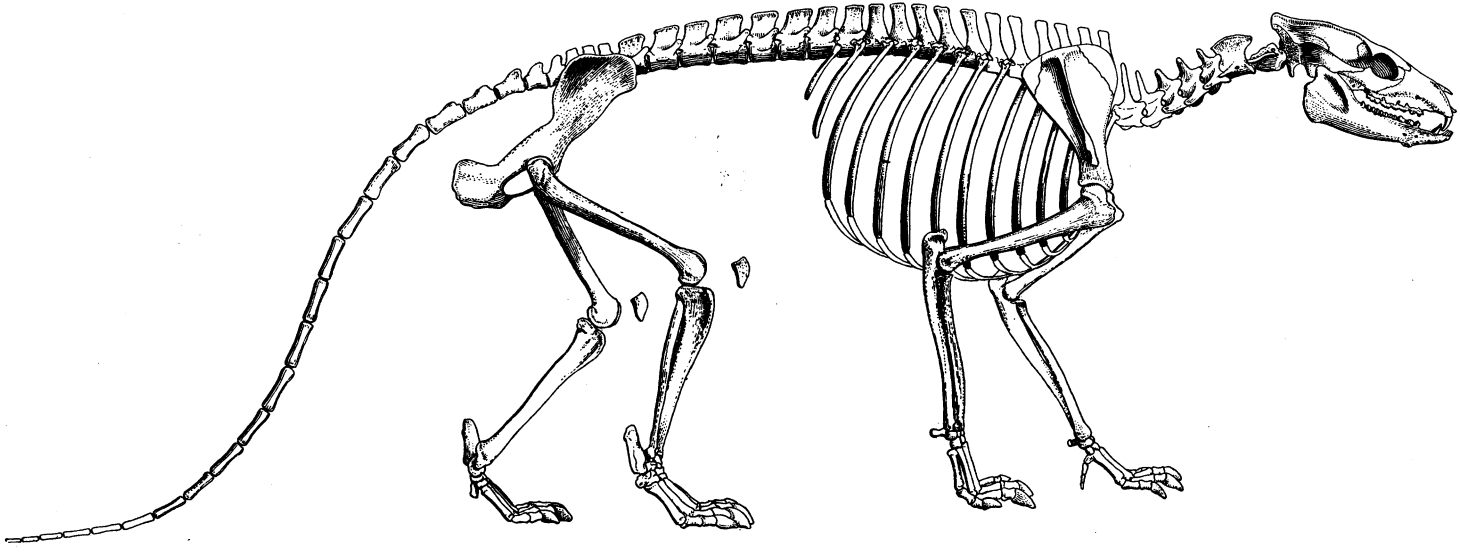
(*b*) Species large ; otic bullæ unknown ; palatonareal border opposite posterior cusp of third molar ; sagittal crest posterior, commencing opposite preglenoid border. John Day beds.
A. macrocephalus Cope.

(*c*) Species small ; otic bullæ unknown ; palatonareal border opposite posterior cusp of second molar ; sagittal crest anterior, commencing opposite optic foramen. John Day beds.... *A. ferox* Cope.

There is a large species found in the Oreodon beds of the White River formation which I have not been able to identify with certainty on account of lack of material ; this may yet prove to be Leidy's *A. major* when more complete material is obtained ; it will then probably become necessary to recognize another species from the Protoceras layer, which I have here called *major*. If this supposition is correct the large species from the upper beds would take the name of *A. gaudryi*, which Osborne and myself have already described.

The succession of the species is natural and easy as we pass from the lower to the upper beds. *A. latifrons* from the Oreodon beds of the White River stands in direct ancestral relation with *A. major* of the Protoceras beds. This is especially seen in the character of the bullæ and the disposition to discard one of the superior premolars. From this three-premolar type we pass by easy steps to *A. macrocephalus* and *A. ferox* of the later John Day horizon. In like manner the four-premolar type with the long narrow muzzle and comparatively little inflated otic bullæ, *A. antiquus*, begins low down in the White River. This form was undoubtedly the progenitor of *A. guyotianus* and its relatives of the John Day.

My especial thanks are due to Professor Marsh for the opportunity of examining his beautiful material relating to the earlier Eocene Artiodactyla, as well as to Professor Scott for the loan of specimens.



RESTORATION OF *Agriochœrus latifrons*.

About one-eighth natural size.