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Article I.—ARTIONYX, A NEW GENUS OF ANCYLOPODA.

By HENRY FAIRFIELD OSBORN and JACOB L. WORTMAN.

In the last volume of this Bulletin (IV, pp. 351–371) we described a new Artiodactyl, *Protoceras*, and in the present paper we record the discovery of remains of a mammal of even greater interest. It is, so far as can be judged from the foot structure alone, a Chalicotherioid with an Artiodactyl type of foot; that is, with the astragalus, calcaneum, cuboid, all modified as in the Artiodactyla, with toes in pairs on either side of the median line, and with phalanges like those in the Carnivora. Besides these four functional toes in the hind foot there are portions of the hallux, indicating that this digit, although much smaller than the others, was still of considerable size, and provided with phalanges. Another distinctive feature is that none of the phalanges are cleft, whereas in *Chalicotherium* they are all deeply cleft.

We had anticipated finding skeletal remains of *Chalicotherium* in the Lower Miocene of America, because the teeth have recently been found both in the Lower and Upper Miocene, indicating that this form was distributed over this continent, and this foot was at first supposed to belong to *Chalicotherium*. But a closer examination showed that while *Chalicotherium* may be described as a clawed Perissodactyl, this new form, which we have named *Artionyx*, may with equal fitness be termed a clawed Artiodactyl.

Thus the group Ancylopoda must be enlarged to embrace two distinct subdivisions: the Perissonychia—animals resembling the odd-toed Ungulates in foot structure; and the Artionychia—animals resembling the even-toed Ungulates in foot structure.

It will be remembered that the species of *Chalicotherium* have long been known under two sets of names; one set, under the genus *Chalicotherium*, being applied to its teeth, and the other, under the genera *Schizotherium*, *Macrotherium*, *Ancylotherium* and *Moropus*, being applied to its feet. Filhol, in 1888, first conjectured that these two forms might really be one. We recall also that Filhol confirmed this conjecture by his discoveries in Sansan, and that Forsyth Major arrived at the same conclusions in his explorations of Pikermi beds. Quite recently Depéret has described parts of a skeleton and skull found together at Grive St. Alban, in beds nearly contemporaneous with Sansan. It is probable that a similar confusion has arisen in this country. In 1877 Marsh described three species of *Moropus* (*distans*, *senex* and *elatus*) from the Middle and Upper Miocene of Oregon and Nebraska, considering them as large Edentates. The types consisted of a number of loose phalanges, and the author compared them with those of *Ancylotherium* (now known to be identical with *Chalicotherium*) rather than with any true Edentates; *Moropus* being considered distinct because of the coalescence of its first two phalanges. Undoubted remains of *Chalicotherium* in this country were found later by Garman in the Loup Fork (Upper Miocene), and described by Scott and Osborn. Cope has also described the teeth of a Lower Miocene species (*C. bilobatum*) from the White River beds (Swift Current Creek) of Canada. It is probable that all these species belonged to the order Ancylopoda, and as the distribution of members of this order in America and Europe is known to have been extended at least to the Siwaliks in Asia, we reach the conclusion that this order, which has become very recently known, was widely dis-

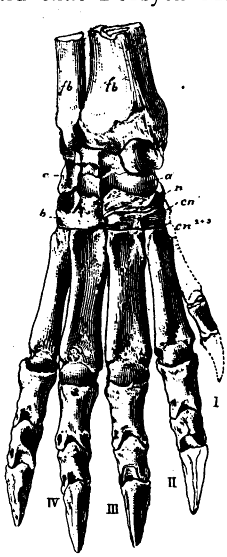

FIG. 1. *Artionyx gaudryi*, front view of right pes.

tributed in the Miocene, and, as proved by the differences between the Sansan and Pikermi forms, and still more by the differences between *Chalicotherium* and *Artionyx*, was highly differentiated. The remains known to us at present indicate, therefore, that we have mere glimpses of a very important order, the remains of which have for some reason been rarely preserved fossil.

In a recent number of the 'Revue Scientifique,'[1] Ameghino has repeated the opinion expressed in 1891[2] that the Homalodontotheridæ are the ancestors of the Chalicotheriidæ. This ancestry is impossible because *Homalodontotherium* has a typical lophodont dentition while *Chalicotherium* is buno-selenodont; it is by no means impossible, however, that this Patagonian genus is a member of the Ancylopoda. Ameghino has pointed out many features of the skeleton in which it strikingly resembles *Chalicotherium*. The carpals and tarsals are alternating or diplarthrous; there are five digits upon the robust fore and hind feet, and the ungual phalanges are shaped as in *Chalicotherium* with deep median clefts. The humerus has an epitrochlear perforation, and in general the limbs are modified as in the Edentates. The calcaneum is described as of the Litopterna type, with a very convex facet for the fibula. The head of the astragalus is extended and convex, with a nearly plane tibial trochlea. If Ameghino's supposition is correct this still further widens the distribution of the Ancylopoda.

The structure of the limbs of *Chalicotherium*, which has been mainly made known by Gervais, Filhol and Depéret, indicates that it was a digitigrade, not a plantigrade, as restored by Filhol. Osborn pointed out the perissodactyl character of the carpus and tarsus. The limbs are now completely known, and indicate that there was little or no prehensile power. It is a peculiarity of both fore and hind feet that they are turned somewhat

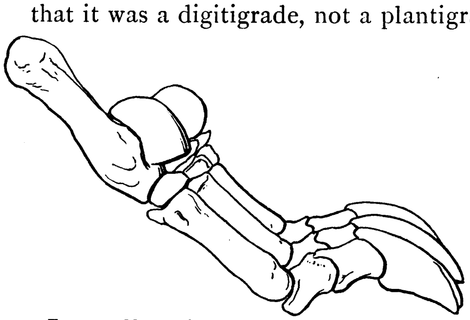

FIG. 2. *Chalicotherium magnum*, outer view of right pes (after Filhol).

[1] Mammiferes Fossiles de la Patagonie Australe. <Revue Scientifique, Jan. 7th, 1893, p. 14.

[2] Nuevos Restos de Mammiferos Fosiles, August, 1891, p. 9.

upon the inner side, and that the outer toes are somewhat enlarged. When *Chalicotherium* was known only by its teeth it was considered unquestionably an Ungulate; later, when the feet were connected with it, it has been considered by Filhol as bridging the gap between the Ungulates and Edentates; by Depéret as closely related to the Ungulates, and even constituting a family of the Perissodactyla; by Cope as an Unguiculate. The discovery of *Artionyx* has important bearings upon these different opinions, as well as upon the hypothesis that *Meniscotherium* is an ancestor of this group. These bearings will be discussed later.

In the present Bulletin we will give (1) a systematic description of the type, comparing it with other forms; (2) a table of the double parallelism of the Artionychia and Perissonychia; (3) a discussion of the affinities of the Ancylopoda.

I. Systematic Description.

The foot of *Artionyx* seems to establish the validity of the order Ancylopoda Cope. The differences between the hind feet of this genus and of *Chalicotherium* are so fundamental that we have placed them in separate suborders, indicating by the terms proposed the double parallelism with the two great subdivisions of the *Diplarthra*. When the skeletons of these two genera become more fully known it may appear that these genera were more closely related than we now suppose, and represented merely two distinct families: the Chalicotheriidæ and Artionychidæ.

Order ANCYLOPODA *Cope.*

Phalanges of the Unguiculate type, terminating in clawed ungues. Teeth, skull, carpus and tarsus, and skeleton, so far as known, of Ungulate type.

I.—Perissonychia.[1]	II.—Artionychia.[1]
Mesaxonic. Odd number of toes and claws. Tarsus, including astragalus, calcaneum, cuboid and navicular, of Perissodactyl type. Ungues cleft.	Paraxonic. Even number of toes and claws. Tarsus, including astragalus, calcaneum, cuboid, navicular and cuneiforms, of Artiodactyl type. Ungues not cleft.

[1] These subdivisions are new. The Perissonychia is not equivalent to the Chalicotherioidea of Gill, because Gill proposed this term as a *superfamily* of the Artiodactyla, equivalent to the Giraffidæ, Camelidæ, Merycopotamidæ, etc. Arrang. Fam. Mamm., Smith. Misc. Coll., 1872, p. 71.

Suborder ARTIONYCHIA.

Artionyx, gen. nov.

Five complete digits, hallux reduced. Ecto- and meso-cuneiforms coalesced.

Artionyx gaudryi,[1] spec. nov.

The specific distinctions are contained in the following description and measurements of the type.

Materials Described.—The materials upon which this genus is proposed consist of the following pieces, viz.: the heads of both femora, broken away at the neck so as not to display either of the trochanters, the distal end of the left femur, including the lower half of the shaft, the patella of the left side complete, and the distal half of the right tibia and fibula, to which is articulated the pes in an almost perfect state of preservation. The only parts of the pes lacking appear to be the internal cuneiform, the metatarsal and terminal phalanx of the hallux, together with the claw of the second digit.

The specimen was obtained from the Protoceras beds or the uppermost member of the White River Miocene of South Dakota, in practically the same stratum in which our specimens of *Protoceras* were found. It was imbedded in a sandy matrix, the distal ends of the tibia and fibula and the pes being found in position almost normally articulated, so that there can be little or no doubt of the proper association of the bones herein described.

The remains pertain to a young adult in which traces of the epiphyses are still visible, and indicate an animal of the size of a full-grown pig, or perhaps a trifle smaller.

The Femur and Patella.—The head of the femur is quite remarkable for its extreme globular form. It represents somewhat more than the half of a sphere, and is marked by a deep pit for the insertion of the ligamentum teres. The shaft of the distal half of the bone is somewhat crushed, but its form is sufficiently well preserved to enable us to state that it is considerably flat-

[1] This species is named in honor of the celebrated French palæontologist Professor Albert Gaudry.

tened from before backwards, especially in its lower portion. In this respect it differs from both the Artiodactyle and Perissodactyle Ungulates, in which the shaft is almost circular in section, with a marked tendency to become more or less quadrangular in sections in its extreme distal portion.

The femoral condyles, and in fact the whole distal extremity of the bone, partake of the nature of the shaft, and are relatively much flattened from before backwards, in marked contrast with the backwardly projecting condyles of both the Artio- and Perissodactyla. The rotular groove is placed upon the anterior face of the bone rather than under the extremity of the shaft, as in the two orders above mentioned. Its direction is somewhat oblique to the outer side of the shaft, as in the tapir, differing in this respect from the pig, in which it is almost straight.

The condyles have comparatively little backward extension, the extremity of the inner one occupying a slightly lower plane than the outer. The intercondylar notch is correspondingly wide and shallow, and it is not overhung by the internal condyle as in hoofed orders.

The patella is relatively small and more elongated than in either the pig or the tapir, but does not otherwise present any points of especial interest. The whole structure of this part of the knee-joint would seem to indicate that the femur was little bent upon the crus, and that the limb was more like that of the elephant in the matter of its straightness than of either the pig or the tapir.

The Tibia and Fibula.—Unfortunately the proximal ends of these two bones are not preserved, so that their description cannot be given at the present writing. In the lower half of its extent the shaft of the tibia may be said to be more or less trihedral in form, expanding distally somewhat to support the articular extremity which it offers to the astragalus.

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.

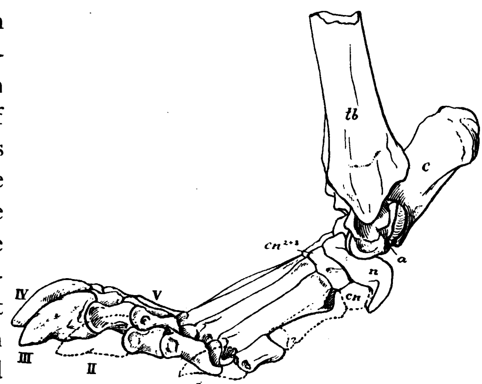

FIG. 3. *Artionyx gaudryi*, inner view of right pes ($\frac{2}{5}$ nat. size).

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 becomes 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.

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 the 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 flattened from behind, and completely overhangs the ectomeso-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 three distinct and widely separated orders, are necessary concomitants, and dependent upon the same or similar causes for their production. (See Appendix.)

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. When the cuneiform and navicular are articulated there is seen a somewhat cup-shaped facet upon the inner side of these two bones, which undoubtedly indicates the existence of an internal cuneiform, although this bone is not preserved.

The Metatarsus.—The metatarsus consists of five elements, of which three are arranged upon the inner and two upon the outer side of the median axis. The metatarsal of the hallux is not preserved, but the presence of the first phalanx of this digit, together with a facet for a distinct and well-developed internal cuneiform, already mentioned, renders it quite certain that the hallux was present, though small. In the drawing its length has been estimated from the length of the phalanx.

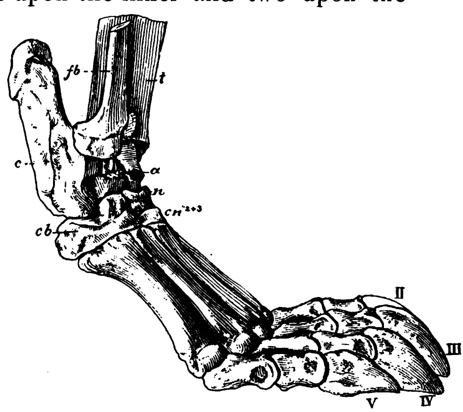

FIG. 4. *Artionyx gaudryi*, outer view of right pes (2/5 nat. size).

Of the remaining 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.

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* (Fig. 5, *A*). 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

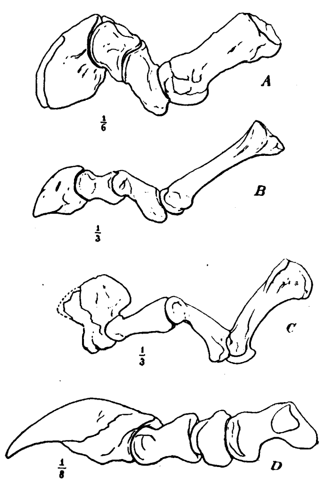

FIG. 5. Median digits of, *A*, *Chalicotherium sansaniense* Gaudry. *B*, *Artionyx gaudryi*. *C*, *Hoplophoneus occidentalis*. *D*, *Megalonyx jeffersonii* (after Leidy).

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 (Fig. 5, *C*). 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*.

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 a median cleft developed.

SUMMARY.—The principal characters of the genus described above may be summarized as follows: (1) Extreme globular form of the *caput femoris*. (2) The slight backward extension of the femoral condyles. (3) The great development of the internal malleolus, and the excavation upon the inner side of the astragalus. (4) The articulation of fibula with calcaneum. (5) The articulation of astragalus with cuboid and navicular, and the formation of a distal ginglymus. (6) The slight extension backwards of the cuboidal facet on the astragalus and its continuity with the sustentacular facet. (7) The great backward extension of the navicular facet, and the obliquity of the sustentacular facet. (8) The weak development of *sustentaculum tali*. (9) The marked depression of the cuboid, navicular, and cuneiforms. (10) The presence of a tuberculum upon the inner border of navicular. (11) The presence of a prominent navicular hook. (12) Coössification of ecto- and meso-cuneiform. (13) Presence of internal cuneiform and hallux. (14) The foot of the paraxonic type. (15) The metatarsals are not displaced upon the tarsals.

(16) The distal keels of metapodials confined to plantar surface. (17) The ungues large, much compressed, and little hooked. (18) Presence of a groove upon the end of the tuber of the calcaneum.

In the table on page 14 we give a list of the principal characters exhibiting the double parallelism of the Ancylopoda to the Diplarthra.

III.—AFFINITIES OF *Chalicotherium* AND *Artionyx*.

Prior to this discovery, four views were advanced as to the affinities of the Chalicotheridæ. First, that the Chalicotheridæ were a specially modified family of Perissodactyla; first based upon the teeth, then upon the teeth and podials by Osborn (5[1]); then upon the entire structure by Depéret (2). Second, that this group bridges the gap between the Ungulates and Edentates, suggested by Filhol, at the time of his discovery (3). Third, that the family belonged to a distant order (Ancylopoda) of the Unguiculata, suggested by Cope (1). Fourth, that it was derived from the Condylarthra (Meniscotheriidæ) or primitive Ungulata, as suggested by Osborn (5).

Edentate Hypothesis.—The main points advanced by Filhol in favor of his hypothesis are the loss of the cutting teeth and the peculiar modifications of the limbs. But the molar type is fundamentally different from that in the Edentata, and the loss of the cutting teeth is not significant. Gaudry and Gervais have shown that the modification of the phalanges is fundamentally unlike that in the Edentates. And Depéret in his thorough discussion of the entire skeleton has finally disposed of this hypothesis by proving first that the skeleton is mainly Ungulate in type, and second that the modifications of the arm and leg are independent parallel adaptations, the Edentate likeness being merely superficial. The cleft terminal claw, which suggested to Cuvier the term "Pangolin gigantesque," we may add, is not exhibited in *Artionyx*.

Unguiculate Hypothesis (Cope).—In a purely descriptive sense both *Chalicotherium* and *Artionyx* are "unguiculate," but in a phyletic sense the problem is whether in their entire structure these animals stood near the Unguiculata. The truth is, the

[1] The numbers in this paragraph refer to the Bibliography at the end of the paper.

ARTIONYCHIA.	ARTIODACTYLA.	PERISSONYCHIA.	PERISSODACTYLA.
(1) Fibula articulating with calcaneum.	(1) Same.	(1) Fibula not articulating with calcaneum.	(1) Same.
(2) Tarsus with double ginglymus.	(2) Same.	(2) Tarsus with single ginglymus.	(2) Same (except in *Litopterna*).
(3) Astragalus narrow, sustentaculum small.	(3) Same.	(3) Astragalus broad, sustentaculum large.	(3) Same.
(4) Navicular with strong posterior hook.	(4) Same.	(4) Navicular without posterior hook.	(4) Same.
(5) Foot of the paraxonic type. Axis between mts. III and IV.	(5) Same.	(5) Foot of the mesaxonic type. Axis through mt. III.	(5) Same.
(6) Metatarsals not displaced on tarsals.	(6) Same.	(6) Metatarsals displaced on tarsals.	(6) Same.
(7) Terminal phalanges unguiculate, uncleft.	(7) Terminal phalanges ungulate.	(7) Terminal phalanges unguiculate, cleft.	(7) Terminal phalanges ungulate.

unguiculate characters, so far as we know at present, are confined to the phalanges. All the other characters are Ungulate. This is as true of the foot of *Artionyx* as it is of the limbs, skull and teeth of *Chalicotherium*. Is it not more probable that the phalanges secondarily acquired an unguiculate structure, rather than that all the remainder of the skeleton passed from an Unguiculate into a pronounced Ungulate type?

Perissodactyl Hypothesis.—Depéret's view that the Chalicotheridæ are modified Perissodactyla is not supported by a detailed comparison of the skull of *Chalicotherium* with that of the older Perissodactyls, for this skull is of a much less modified type, and is distinctly non-perissodactyl in the several features enumerated below, in which it does resemble the skulls of the ancient Condylarthra. Moreover the discovery of *Artionyx* indirectly strengthens Cope's view that *Chalicotherium* belongs to a distinct order. Let us therefore look at the broader question of its relationships to the primitive Ungulata.

Primitive Ungulate Hypothesis.—Exhibiting the affinity of *Chalicotherium* to the Ungulates in general are many features in the limbs, specified by Depéret in support of his Perissodactyl view. The dentition especially bears a most detailed resemblance to that of *Meniscotherium*, which we know to be a Condylarth. The skull is very suggestive of the type seen in *Periptychus*, *Phenacodus* and *Meniscotherium*, in its low, broad occiput, small cranium, well-arched sagittal crest, high maxillary bones, widely open external auditory meatus. It has also the Ungulate conformation of the posterior region of the jaw, the elevated condyle and deep angles, also seen in the oldest Condylarthra.

Mingled with these ancient characters we see many secondary modifications adapted to the peculiar semi-arboreal habits of the animal, probably associated with a long tongue and highly flexible upper lip. Such are the loss of the upper incisors, semi-procumbent position of the lower incisors, the deep recession of the anterior nares, the reduction of the premaxillaries and of the anterior portion of the lower jaw, paralleled by similar modifications among the sloths. One secondary feature of the skull is, so far as we know, unique, that is the large curved cylindrical tympanic bullæ.

Artionyx strengthens the Ungulate hypothesis by its foot structure, but raises a fresh difficulty in the wide differences which it exhibits from *Chalicotherium*. Is it possible, as Scott has suggested to us, that *Artionyx* represents a primitive offshoot of the Artiodactyla, as *Chalicotherium* may be of the Perissodactyla? In such a case we must suppose that these two series independently acquired claws. The main difficulty, of course, with the Ungulate hypothesis is the retrogression from hoofs to claws which it at first sight requires. But we may suppose that the divergence took place before the ungues were hoofed, while they were still subungulate or nailed as in *Meniscotherium*.

Affinities of Meniscotherium.—We have already spoken of the likeness between the *Meniscotherium* and *Chalicotherium* dentition. This question is fully discussed by Osborn in another paper. *Meniscotherium*, like *Chalicotherium*, has the central digit enlarged; this would remove it from the ancestry of *Artionyx*. On the other hand, *Meniscotherium* has the fibulo-calcaneal facet, and deep pit upon the astragalus for the internal malleolus of the tibia which we observe in *Artionyx*. The terminal phalanges of *Meniscotherium* are subungulate, as in the Primates. Thus the feet of *Meniscotherium* bear resemblances to those of both *Chalicotherium* and *Artionyx*, but not of sufficient closeness to enable us to consider it at present as an ancestral type.

Conclusions.—The general conclusion is that the suggested affinity of the Chalicotheridæ to the Meniscotheriidæ is in some degree supported by the discovery of *Artionyx*, although it is somewhat hazardous to place too much reliance upon this hypothesis until we procure the teeth and other portions of the skeleton of this genus. Taking together the condylarthrous character of the skull and the predominant ungulate facies of the skeleton, and our knowledge of these affinities to *Meniscotherium*, we have a presumption in favor of the idea that the Ancylopoda issued from the Ungulata after the ungulate direction had been given to their evolution, but before they had fully acquired the distinctively ungulate phalanges. The double parallelism, so marked in each case, between the Artionychia and Perissonychia and the respective divisions of the Diplarthra is still a very difficult fact to account for, and we trust that additional remains of both these types may soon be discovered.

Appendix.

THE MECHANICS OF THE ARTIODACTYL TARSUS.

A careful study of the anatomy and movements of the ankle joint in a dissection of the hind foot of a deer, in comparison with the pig and hippopotamus, reveals the following important facts, viz: (1) the movement of the tibia and fibula upon the astragalus is comparatively limited, the proximal ends of these bones passing through an arc of only 90° in extreme flexion and extension. An additional 90° of arc is secured by the movement of the astragalus upon the calcaneum and navicular, so that by these combined movements the complete flexion of 180° of the pes upon the crus is possible. Now the articular facet upon the posterior facet of the astragalus is quite oblique, so that its movement upon the calcaneum causes a decided torsion or lateral movement of the calcaneum. (2) This torsion is from within outwards, and in order to prevent displacement of the calcaneum, a strong ligament is developed, stretching from the entire under or plantar surface of the calcaneum to the posterior border or hook of the navicular. Powerful extension of the pes upon the crus, as must necessarily occur in the act of leaping, causes this ligament to become very tense. Both the torsion and the navicular hook are absent in the Perissodactyla. (3) Another marked feature of the Artiodactyle calcaneum is the groove developed upon the top of the tuber, through which the tendon of the *plantaris* glides, as it passes into the sole of the foot to become the perforated tendon. This groove is present in all the Artiodactyla, in *Artionyx*, and the Lagomorpha, but is absent in the Perissodactyla. Its presence seems to indicate a more specialized condition of the *plantaris* in these forms than in the Perissodactyla, but it is difficult to see in what manner it is associated with the foot structure. It is merely mentioned in this connection because of its constant occurrence. (4) In the Perissodactyla there is little or no movement between calcaneum and astragalus, and the strong calcaneo-navicular ligament is wanting. In the Lagomorpha, on the other hand, there is extensive movement between the calcaneum and astragalus, and both the navicular hook and the ligament are present. The marked resemblances of the pes of the rabbit to that of the Artiodactyla have been noted elsewhere. It would thus appear, if we attempt to explain the presence of the navicular hook upon a mechanical basis, that in proportion as there was greater and greater mobility developed between astragalus and calcaneum, increasing torsion of the calcaneum followed as a result of the oblique facets between these bones. This in turn gave rise to special stress or strain upon that portion of the plantar fascia which invests this region of the foot, resulting in the production of the specialized calcaneo-navicular ligament. The hook or process of the navicular has been developed to give greater surface of attachment for this important ligament.

(5) Another interesting fact connected with the mechanics of the tarsal joint is found in the peculiar rotation which the foot makes when the calcaneum is fixed and the tibia is flexed or extended upon the pes. In this case the torsion movement of the calcaneum is transferred to the foot, and it is seen to be distinctly rotated outwards when the metatarsals are approximated to the anterior surface of the tibia as in extreme flexion. Now it is in this outwardly rotated position that the foot strikes the ground in the act of running, so that there would be, therefore, a constant tendency to throw a considerable part of the weight upon the fourth digit. It is conceivable that it is to this cause that we can attribute the shifting of the median axis of the pes from the center of the third digit (mesaxonic) to a line between the third and fourth digits (paraxonic), as well as the selection of the fourth to pair with the third in the cloven foot. This, of course, is assuming that the mesaxonic type of foot is the primitive one for the Ungulate series.

We are as yet unacquainted with a five-toed Artiodactyle pes, but so far as the number of digits is concerned, we have in *Artionyx* a primitive condition. It is thus especially interesting to note the great advance in the perfection of the tarsal articulations over the digital reduction. It would appear therefore, and it will doubtless eventually be found, that the first important step, and as I am inclined to believe the primary cause, in the modifications which have led up to the production of the Artiodactyle pattern of foot, has been the increased mobility of the astragalus upon the calcaneum, cuboid and navicular, associated with the obliquity of the astragalo-calcaneal joint.—J. L. W.

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