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ON THE MANNER OF LOCOMOTION OF THE DINOSAURS ESPECIALLY DIPLODOCUS, WITH REMARKS ON THE ORIGIN OF THE BIRDS.

By Oliver P. Hay.

In a paper published some months ago (Amer. Naturalist, vol. xliii, 1908, pp. 672–681) the writer advanced the proposition that the sauropodous dinosaurs, especially *Diplodocus*, did not walk, as the elephants do, with the body high up from the ground and with the legs straight or nearly so, and moving in approximately perpendicular planes, but rather as do the crocodiles, with the body low down, and with the thighs standing well out from the animal's sides. While I was further considering the subject I received from my friend Dr. O. Abel, of Vienna, a paper[1] in which, while endorsing my views regarding the nature of the food of *Diplodocus* and the manner of taking it, he endeavors to show that I am in error as to the bodily pose and the manner of locomotion of the sauropods. Dr. Abel maintains that the accepted views of the way in which these animals walked is the correct one and he finds support for this view in the structure of the feet. He accepts Hatcher's opinion that *Diplodocus* and *Brontosaurus* were digitigrade and argues that therefore they walked as represented in Hatcher's restoration of the reptile. The evidences that they were digitigrade are found in the belief, probably correct, that the upper ends of the metatarsals and metacarpals were not arranged in a straight line, but

[1] Verhandl-zool.-botan. Gessellsch. Wien, 1909, pp. 117–123.

in an arc of a circle; further, that the feet were entaxonic, that is, had the inner digits more strongly developed than the outer ones.

Now, it is the writer's opinion that these evidences of digitigrady will hardly stand a test. The hinder feet of the bear are certainly plantigrade and yet the metatarsals are arranged very distinctly in an arc of a circle. On the other hand, the tiger and the hyæna are digitigrade, but their metatarsals are almost in a plane. Various animals will, I think, be found to transgress Dr. Abel's rule, as one may see by looking through a collection of skeletons. Furthermore, if it is desired to see an entaxonic foot in which the metatarsals are arranged in an arc of a circle and which is nevertheless plantigrade one has only to examine the foot of the human skeleton.

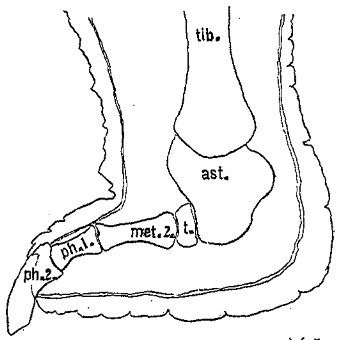


FIG. 1 SECTION THROUGH HIND FOOT OF TESTUDO. × 1. *ast.*, ASTRAGALUS; *met. 2*, METATARSUS OF SECOND DIGIT; *ph. 1*, *ph. 2*, FIRST AND SECOND PHALANGES; *t.*, TARSAL OF SECOND ROW; *tib.*, TIBIA.

The writer is not disposed to deny that *Diplodocus* and its relatives were more or less digitigrade; but this digitigrady, through perhaps equal to that of the hinder foot of the elephant, does not prove that these reptiles walked like the elephant. The land tortoises of the genus *Testudo* have the feet constructed much like those of the elephant, being provided with a thick pad of skin, muscles, tendons, and connective tissue under the astragalus and the metatarsals and applying only the ungual phalanges to the ground. Nevertheless the legs of these reptiles stand out from the sides of the body as I have supposed that those of *Diplodocus* did. A figure (Fig. 1) is here presented showing a section made through the hind foot of *T. tabulata*. Unfortunately I have not been able to find or make a similar section through

the hind foot of the elephant; but, to judge from various mounted skeletons and from good figures of others, one can hardly suppose that the heel of the elephant is lifted farther from the ground relatively than that of the tortoise.

I grant that Dr. Abel's efforts are along a line where they are needed. Those who believe in the mammal-like gait of *Diplodocus* ought to give their reasons therefor. I do not assert that reasonable arguments for their view cannot be produced, but hitherto the correctness of this view has been assumed. The subject is a difficult one and needs to be studied from various points of view and by all who have the opportunity. And in studying the movements of animals one soon learns that they can assume so many positions that one may be at loss, in the case of an extinct creature, to determine which positions were the usual ones.

In the primitive condition the limbs of the Tetrapoda stand out at right angles with the body,[2] and in approximately this position they are found in most Amphibia and Reptilia. When these animals are walking, the humerus and the femur move backward and forward mostly in horizontal planes. In most mammals, on the contrary, the humerus is turned backward against the thorax and the femur forward against the flank. The hand, which otherwise would be directed backward, is turned forward by the crossing of the bones of the lower arm. The movements of arm and leg are then mostly in sagittal planes. In the duckbill and the echidnas the limbs have retained the position found in most reptiles.

Now, among all the reptiles that live today there are none, except perhaps the chameleons, that have attained even an approach to the condition found among the mammals.

It is evident that before the close of the Jurassic there existed both carnivorous and herbivorous dinosaurs that went about habitually on only their hinder legs; but it is by no means necessary to believe that the immediate ancestors of these bipeds walked first like mammals and afterwards like birds. It is well known that certain lizards can run swiftly on their hind legs, the fore legs and the tail being held free from the ground. Furthermore, as may be seen from W. Saville-

[2] Huxley, Anat. Vert. Animals, 1872, p. 33; Flower's Osteology of the Mammalia, 1885, p. 362.

Kent's figures[3] the hinder limbs are not carried backward and forward in sagittal planes like those of mammals.

It seems not difficult to understand the history of the attainment of the bipedal habit among lizards and dinosaurs. When the fore-legs of a quadrupedal reptile are of nearly the same length and have the same structure as the hind legs there seems to be no good reason why the animal cannot run as fast on four legs as on two. However, the hinder limbs, being nearer the center of gravity of the animal, receiving more of the weight, and being more devoted to propulsion of the body, are likely to become larger and more powerful, while the fore legs may become more or less reduced, with or without special modification for other purposes. If now a reptile whose fore legs have become relatively much shorter than the hinder ones has occassion to run with the greatest possible speed, it is likely to find that the fore legs cannot take as long steps as the hinder ones; and naturally it endeavors to get them out of the way by lifting them up in the air.

This practice would be of great advantage and would tend to become fixed. The reduced limbs might then become modified for other purposes or undergo further reduction. In the beginning, the femora would stand out from the body, giving the animal a wide tread. In time, however, the knees might be drawn closer to the flanks, the tread would become narrower and the pace more rapid. At no stage, however, would the reptile walk like a quadrupedal mammal; and no argument in favor of such a gait for *Diplodocus* can be deduced from bipedalism in lizards.

If the mammal-like gait of *Diplodocus* be insisted upon on the ground of straightness of the femur it may be pointed out, as I did in the article in the American Naturalist, that the femora of sphenodon and of lizards, animals that creep, are straight. If it be contended that it is in the heavy-bodied animals that a straight femur is correlated with a lifting of the body from the ground during locomotion, it may be permitted to recall that the femora of *Allosaurus* and *Tyrannosaurus*, great carnivorous dinosaurs, are distinctly bent. The femora of *Trachodon* are straight, while those of *Camptosaurus* and *Laosaurus* are curved. Curvature of the femur seems, therefore, to have no relation to size of body or erectness of pose. The femora of

[3] Nature, vol. 53, 1895, pp. 396–397.

crocodiles, little and great, are curved; as were too those of their predecessors, *Aetosaurus*, of the Triassic, and of *Alligatorellus*, of the Jurassic, the former with femora hardly four inches long, the latter with these bones about an inch in length.

Diplodocus has been erected on column-like legs partly because it has been supposed that the great weight of its body required this. However, the legs of animals are not straight in proportion to the the weight of their bodies. The legs of the largest camels seem not to be straighter than the legs of the llamas. Some rhinoceroses and some oxen have very heavy bodies; nevertheless, their femora lack much of being in line with their tibia and these much of being in line with the metapodials. Certainly it is not because of the immense weight of the body that the legs of a man are straight.

There must, of course, be a limit to the size of an animal that can move itself about on land, in whatever position; but it may be suggested that a reptile that could not walk about as crocodiles do, resting at least now and then, its body on the ground, could not well have erected itself when once it had lain down. That the largest crocodiles are far from the limit of active movement on the land may be judged from the following extract taken from W. Saville-Kent.[4]

> The celerity with which a huge 25-footer, as witnessed by the writer in the Norman River, North Queensland, will make tracks for and hurl itself into the water, if disturbed during its midday siesta by the near impact of a rifle bullet, is a revelation.

It must be further taken into consideration that the weight of a crocodile 25 feet long, with short, thick neck, large head, long body, and heavy tail, would be much greater than that of a sauropod of the same length, in which most of the length is composed of slender neck and comparatively slender tail.

It is generally conceded that such carnivorous dinosaurs as *Allosaurus*, *Dryptosaurus*, and *Tyrannosaurus*, and such herbivorous forms as *Trachodon* and *Camptosaurus* walked bipedally erect. If now comparison be made of the femora of any of these with those of the sauropods great differences will be noted. The shaft of the former appears to be more elaborately modeled and to consist of finer and harder bone; all the articular surfaces are smooth and they carry the

[4] Living Animals of the World, p. 547.

conviction that the original surfaces, barring a thin layer of cartilage, are preserved; there is a definite head, separated from the shaft by a distinct neck and nearly filling the acetabulum; and there is a definitely formed trochanter major. In the *Sauropoda*, on the contrary, the shaft seems to be composed of coarser bone; the articular surfaces are rough and show that they were covered by a thick layer of cartilage; the head merges imperceptibly into the supposed great trochanter and into the shaft; and the head lacks much of filling the acetabulum. In its low stage of differentiation the femora of the sauropods resemble greatly those of the crocodiles and are hardly above those of the lizards. They furnish no warrant for the belief that their possessors walked in mammalian fashion.

The structure of the foot of *Diplodocus* indicates that this reptile walked in a way very different from that in which the bipedal dinosaurs walked. In the latter the foot had the third toe most strongly developed (mesaxonic); in the sauropods the two inner toes were the strongest, the third somewhat weaker, while the other two were greatly reduced. This difference of structure must have had its history and its meaning. That the feet of *Diplodocus* were shortened and more or less digitigrade indicates that they were employed for walking, not at all for swimming. The feet of the crocodiles are to be regarded as entaxonic, the inner digits being of stouter build, although slightly shorter than the third; but here the digits are elongated and webbed to assist in swimming. When the animal is walking, the pressure comes against principally the inner side of the foot. The trionychid turtles have the three inner digits most strongly developed and clawed; the others are slender and unarmed. The clawed digits are, of course, the ones employed for excavating hiding places in the sand and mud and getting foothold in walking and running; and these turtles are, for moderate distances, rapid and powerful runners on the land and on the bottoms of streams.

It is true that the foot of man is entaxonic and is directed nearly forward, but its history is wholly different from that of the sauropod foot. It is certain that the ancestors of man were climbing animals, with hallux strongly developed and opposable to the other digits. Being later employed for locomotion on the ground, the foot underwent a transformation to its present form. The form assumed at any time by an organ must depend greatly on the form previously possessed. Doubtless the Sauropoda and the Theropoda started out with the same pedal outfit, and there seems to be no reason for supposing that the former passed through an arboreal stage and back into an ambulatory stage.

The position of the trochanter major of the sauropods is open to question and there are differences of opinion. Marsh[5] regards as this trochanter the outer upper angle of the femur, including a part of the rough surface forming the proximal end of the bone. Hatcher's view (Mem. Carnegie Mus., I. p. 46) appears to be the same. Osborn[6] has identified as the trochanter the rough surface which descends for some distance below the upper end of the femur on the fibular border. Neither of these views seems to the writer satisfactory. If the femora of the Triassic dinosaurs described by v. Huene in his monograph, *Die Dinosaurier der europäischen Triasformation,* be examined it will be found that the trochanter in question is placed at a considerable distance below the head of the bone, on the dorsal surface, and near the fibular border. In the more highly specialized dinosaurs of the Jurassic the trochanter is a distinct process arising from the position described and ascending nearly to the level of the head. In such dinosaurs as *Trachodon* and *Triceratops* the trochanter has reached the outer upper angle of the femur, and is well separated from the head by a distinct neck. The writer believes that in the sauropods the trochanter occupied the same primitive position that it has in the Triassic Theropoda. It is not essential that it should be represented by a process or even by any unusual roughness, as is shown by the femur of the crocodile.

This being the case, what explanation is to be made of the outer portion of the rough surface on the proximal end of the femur? The writer believes that it forms a part of the head of the bone and entered into the acetabulum. The matter will be discussed. In order to illustrate a possible position of the femur in the acetabulum a figure is here presented (Fig. 2). This has been obtained by placing a section of the proximal end of the femur, taken from Hatcher's figure in Memoirs of the Carnegie Museum, vol. I, p. 46, in the acetabulum as shown in the same writer's figure in the second volume of the same

[5] Dinosaurs N. A., Pl. XVI, fig. 3, t.
[6] Mem. Amer. Mus. Nat. Hist., i, p. 211, fig. 14.

Memoirs, plate IV, fig. 2. The so-called head of the femur is toward the left, against the pubic process. According to this figure, there was room in the acetabulum for the femur, standing at right angles with the pelvis, so that it could rotate on its longer axis and could swing backward and forward. Such movements would be required in case the reptile walked as does the crocodile. In the execution of these movements it would probably happen, as it does in the lizards, that some part of the head would at times be outside of the acetabulum. in order to show the resemblance of this joint in the lizards to the one

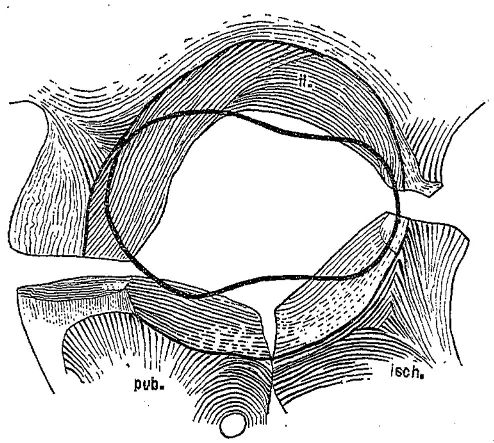


FIG. 2 LEFT ACETABULUM, CONTAINING SECTION OF PROXIMAL END OF FEMUR; THIS SECTION SHOWN BY HEAVY LINE. $\times \frac{1}{10}$; *il.*, ILIUM; *isch.*, ISCHIUM; *pub.*, PUBIS.

depicted, a drawing (Fig. 3) is shown of the acetabulum and head of the femur of *Metapoceros*.

However, the articulation at the hip was probably not effected in just this way. It appears that in some cases the proximal end of the femur is wider than the acetabulum. Dr. E. S. Riggs informs me that in *Apatosaurus* (*Brontosaurus*) and *Brachiosaurus* the upper end of the femur is about 23 inches wide, exceeding the fore-and-aft diameter of the acetabulum by 3 or 4 inches. I do not regard this fact as wholly irreconcilable with the view illustrated by figure 2, the head of the femur having sometimes a greater diameter than the acetabulum, as in the land tortoises. Nevertheless, I will not argue the matter. A somewhat different arrangement at the articulation is more probable.

Certain principles must be regarded as indisputable. One of these is that primitively, in the common ancestor of the dinosaurs, the crocodiles, and the lizards, probably in the early dinosaurs themselves, the whole proximal end of the femur constituted the anatomical head. Another is that before there could be any such structures and conformations of these as we find at the hip joint of *Allosaurus*, for instance, or of *Trachodon*, every possible stage from the one just described must have been passed through. Through countless generations the thigh must gradually have assumed a more and more forward position in habitual locomotion. While muscles and nerves were being trained

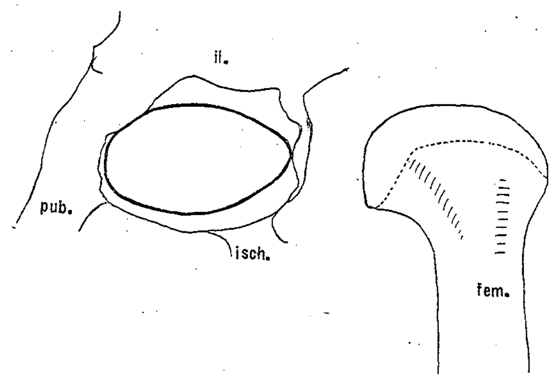


FIG. 3 ACETABULUM OF LIZARD METAPOCEROS, CONTAINING SECTION OF HEAD OF FEMUR. $\times$ 2. SECTION OF FEMUR SHOWN BY HEAVY LINE. ALSO SIDE VIEW OF FEMUR $\times$ 2. *Fem.*, FEMUR; *il.*, ILIUM; *isch.*, ISCHIUM; *pub.*, PUBIS.

to this end the femur must have been developing a projecting head, that part of the proximal end on the fibular side was being excluded from the acetabulum, and the rotation of the proximal end of the femur around a perpendicular axis was being changed to rotation around a horizontal axis, which in mammals would pass through both femoral heads. Now, as regards the hinder leg and the hip joint, at what stage in the long journey indicated above, do we find *Diplodocus?* Obviously those who believe that this animal ought to be set up on its legs in the way seen in drawings, plaster restorations, mounts of the actual bones, and the plaster facsimiles of the skeleton that are being distributed over the world, must hold that *Diplodocus* had reached practically the ultimate, or mammalian stage. The writer believes that it had attained only the first station in the journey.

A study of the femora of the sauropods shows that the proximal end varies somewhat in shape. Usually it is more or less truncated or it is slightly concave toward the fibular side and convex toward the tibial side. Figure 4 represents in outline a side view of the proximal half of the bone, as represented by Hatcher. As already stated, the

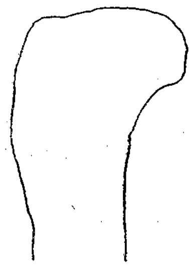


FIG. 4 OUTLINE OF SIDE VIEW OF PROXIMAL END OF FEMUR OF DIPLODOCUS. $\times \frac{1}{16}$.

proximal border is very rough, as shown by figure (Fig. 5) also taken from Hatcher. Undoubtedly this was covered by a thick layer of cartilage. Cope (Amer. Naturalist, xii, 1878, p. 84) says that if the layer of cartilage were ossified it would be an epiphysis, like that of the mammals. Figure 6 presents the same outline as does figure 4,

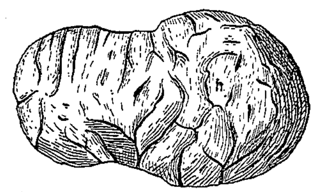


FIG. 5 PROXIMAL END OF FEMUR OF DIPLODOCUS. *h*, THE SO-CALLED HEAD

but to it there has been added a dotted line which is intended to indicate the writer's view of the form of the upper end of the femur when the cap of cartilage was present. The stage of development reached by the animal was that at which a femoral head was being developed on the tibial side of the bone and the fibular border was being freed from the articular cup. Although the whole proximal end may, in some genera, have been too broad to enter the cavity

the greater part did so enter. Doubtless, when the leg was extended forward, a considerable part of the cartilage-covered surface on the fibular border was out of the cup, and when the leg was directed backward the rounded anterior part of the head was out. This is exactly what happens in the lizard and, for that matter, in most animals. The head of the femur of *Diplodocus*, compared with that of the crocodile, differed in having its long axis coincident with the plane through both condyles; while in the crocodile the head is twisted from the plane mentioned about 75°. Figure 7 represents the same humerus as figure 6, but lines are drawn across the head to show the varying relations of the bone to the acetabulum. The line *aa* may

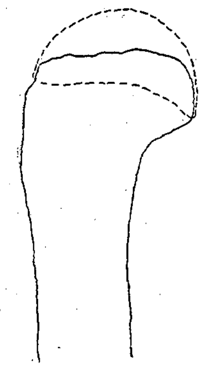


FIG. 6 PROXIMAL END OF FEMUR OF DIPLODOCUS. $\times \frac{1}{16}$. THE DOTTED LINE SHOW THE LIMITS OF THE CARTILAGE.

be regarded as a section through the acetabulum when the leg is thrown far forward; *bb*, when the leg is at right angles with the body; *cc*, when the leg is thrown well backward. Of course, as the leg is swung from front to rear, the femur will turn also on its long axis.

As is well known, the acetabulum of the Sauropoda is widely open in the skeleton. I am not aware that any one has discussed the way in which in life this opening was filled. It seems improbable that it was shut simply by membrane, for this would have been too yielding to the pressure of the head of the femur, if inserted as generally supposed. It seems most probable that the opening was occupied by a mass of cartilage, an unossified portion of that common cartilage from which were developed the ilium, the pubis, and the ischium. This would have formed a firm concave bed on which the convex head of the femur could rotate. If the femur was inserted as the writer supposes it was, its pressure would have been exerted mostly against the bony side-walls of the acetabulum and but little against the tissue filling the inner opening.

In his splendid monograph on *Die Dinosaurier der europäischen Triasformation* Dr. v. Huene has presented numerous restorations of the Triassic carnivorous dinosaurs (Pls. IC-CX). In order to show the author's conception of their modes of progression, three species, *Plateosaurus reinigeri, Thecodontosaurus antiquus* and *Anchisaurus colurus* are restored each in two positions, walking on all fours and on their hinder extremities only. Dr. v. Huene has the following to say (p. 291) regarding the position of the hinder limbs:

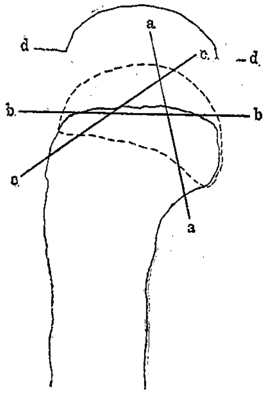


FIG. 7 PROXIMAL END OF RIGHT FEMUR, WITH ITS CAP OF CARTILAGE, AND HORIZONTAL SECTION THROUGH ACETABULUM. *dd*, SECTION OF ACETABULUM; *aa*, LINE CORRESPONDING TO *dd* WHEN LEG IS THROWN FORWARD; *bb*, LINE CORRESPONDING TO *dd* WHEN LEG IS AT RIGHT ANGLES WITH BODY; *cc*. LINE CORRESPONDING TO *dd* WHEN LEG IS THROWN BACKWARD.

> Das Femur passt in der Weise in den Acetabularschnitt, dass das verbreiterte medial abstehende Proximalende nicht transversal unter dem Ileum liegt, sondern schräg nach vorn und medial gerichtet ist (daher wendet sich auch das Knie etwas auswärts).

Notwithstanding this explanation, one is struck by the very mammal-like position of the body and the limbs of these reptiles in the quadrupedal pose. Elbows and knees are drawn well towards the sides and the digits are directed straight forward. At least, the pose of these restorations is quite different from that of any living reptiles.

One of these species, *Anchisaurus colurus* was described by Marsh from the Triassic of the Connecticut Valley, and he published a restoration of the skeleton in his work The Dinosaurs of North America, Pl. IV. Dr. R. S. Lull[7] has identified this dinosaur as the maker of the tracks known as *Anchisauripus dananus* (Hitch.) This identification is extremely interesting, in case it can be substantiated. The bones of the hind foot of *Anchisaurus colurus* fit accurately in the tracks named. These tracks are placed close to or on the line along which the animal was moving, the "line of direction" (Beckles), and there are, in the several specimens known, no indication of impressions of either the fore feet or the tail.

A study of the various printed restorations of this species reveals an animal of elongated body, with limbs not greatly unlike those of a crocodile, the hinder legs being a little longer in proportion to the length of the body than in the crocodile, while the fore legs are about three-fourths the length of the hinder ones. In the crocodile the fore limb is little more than two-thirds as long as the hinder.[8] As compared with the hind foot of the crocodile that of *Anchisaurus* is a little longer. Now, with this view of the creature, what is there in it to lead one to suppose that it erected itself on its hinder limbs, unless it were on rare occasions; and on such occasions would it not have borne itself as did the running lizard figured by Saville-Kent? What one is asked to believe is that it bore itself so loftily that it is never found to have put its hands on the ground or to have dragged its tail in the mud. Furthermore, this reptile walked with all the skill and the circumspection of the heron and the barn-yard fowl; for each foot was brought forward and placed very near or on the line of direction and thus immediately under the center of gravity. This is very different from the way in which Saville-Kent's lizard ran; for when a foot was advanced it was placed far from the line of direction and at the same time the tail was jerked violently toward the same side, in order to bring the center of gravity over the advanced foot. The dinosaur in question seems to have had no other use for its tail than to serve as a counterpoise to the weight of the head and trunk.

Omitting the feet, the legs of most birds consist of three long segments, viz: the femur, the tibia, and the tarsometatarsus. The

[7] Mem. Bost. Soc., Nat. Hist., v. p. 487.
[8] Dollo, Bull. Mus. roy. d'Hist. nat. Belgique, ii, 1883, p. 107.

relatively short femora diverge downward so that the knees are almost always farther apart than are the great trochanters, sometimes much farther. Nevertheless the feet in walking are generally placed on the line of direction, a result brought about through the convergence of the elongated middle and lower segments of the two legs. If they are not brought close to this line, as in the short-legged ducks and geese, the walk becomes a waddle.

The femur of *Allosaurus*, of the Upper Jurassic, possesses a head that projects strongly inward; and this was provided with a well-defined smooth articular surface, which is elongated transversely to the animal and convex from front backward. The surface of the ilium against which this head fitted is also smooth. Now the conformation of the head of the femur and the ilium is such that the femur must have diverged considerably from its fellow, thus widely separating the knees. The tibia is shorter than the femur, and the inner condyle appears to stand lower than the outer. The metatarsus is relatively short. I see no way, therefore, for the feet to be brought, except with unusual effort, near the line of direction in walking or near each other in standing. The limbs of *Allosaurus* may be compared to those of the penguins, although in *Allosaurus* the femora may not have been directed so strongly forward and the feet may have been more digitigrade. It would probably be very difficult for the penguin to plant its feet one in front of the other in walking. I believe therefore that *Allosaurus* had a wide trackway and that when it walked and ran it preserved its equilibrium by whisking its tail from side to side.

Examination of a femur, accompanied by the tibia and the fibula, in the U. S. National Museum, apparently that of *Tyrannosaurus*, shows the same form of the head of the femur that is found in *Allosaurus*, thus making it probable that this dinosaur also had a straddling gait. Professor Osborn (Bull. Amer. Mus. Nat. Hist., xxii, p. 293) presents a figure of the femur of *Tyrannosaurus*. He says that the plane of the head makes an angle of 45° with the axis of the vertebral column, and that therefore the distal ends of the femora are approximated. Whether the angle is in front of or behind the head of the femur is not stated. In *Allosaurus* the head is directed inward and forward. The effect of this would certainly be to throw the knees outward and to plant the foot farther away from the line of direction.

The convergence of the femora is rare even among the mammals. If Professor Osborn is right the hind legs of *Tyrannosaurus* had attained the human stage in the respect mentioned.

Another potent reason for believing that the dinosaurs just named, together with *Iguanodon* and *Trachodon*, walked with a wide tread is found in the form of the body. In mammals the abdomen is usually contracted posteriorly, so that between the thighs it is shallow, permitting the femora to remain parallel with each other or even to converge. Therefore, in walking, the feet are placed near or on the line of direction. In the birds the baggy abdomen descends between the thighs and spreads these, thus requiring the convergence of the long lower segments to bring the feet together. The kangaroos have the abdomen much like that of the birds; and in them the thighs are found to diverge toward the knees, but the long tibiæ permit the feet to be placed close to each other in standing and leaping. In *Allosaurus* and *Iguanodon* the belly came down nearly to the knees and passed backward between the thighs into the tremendous tail. It must be that the knees were much farther apart than the upper ends of the femora were and that the tread was wide. The writer is further of the opinion that in the bipedal dinosaurs the femora were directed more strongly forward than they are usually placed in restorations, although not so much so as in birds. This position would tend to reduce the height of the reptiles and would make the thighs more divergent.

In a paper published by Mr. William H. Ballou (Century Mag., lv, 1897, pp. 15–23), but the facts and suggestions of which were furnished by Professor E. D. Cope, there is a figure representing two individuals of *Hadrosaurus* (*Trachodon*) *mirabilis*. One of these is on the shore, resting on its hind legs and haunches, the other is standing and feeding in the water. By examining these restorations, made by Mr. Charles R. Knight, one may judge regarding the probability that these reptiles could leave a straight row of tracks behind them.

Mr. S. H. Beckles[9] has described and figured some series of large footprints found in the Wealden near Hastings, England. These have been identified by Dollo (Bull. Mus. roy. d'Hist. nat. Belgique,

[9] Quart. Jour. Geol. Soc., x, 1854, 456, pl. xix.

ii, 1883, p. 117, pl. iii, fig. 8) as the tracks of *Iguanodon mantelli*. A study of these footprints shows that in the case of the series designated by *cc* the length of the step was close to 5 feet while the width of the trackway was about 2 feet 2 inches. The tips of the inner toes came, however, pretty close to the line of direction. It must be observed that in all of these tracks the toes are turned inward so much that the axis of the middle toe prolonged passes through the next imprint in front, made by the opposite foot. Now, I find no reason for supposing that in life the toes were so directed inward. None of the figures of *Iguanodon* so represent them; nor are the toes thus placed in any of the restorations of *Trachodon*. The explanation of the matter seems to be that the reptile, if reptile it was, was lounging leisurely along, with short steps, and, to keep its equilibrium, was swinging its body around a perpendicular axis passing through the pelvis, the tail being thrown in one direction, the trunk in the opposite. In this way the feet would be planted not far from the line of direction and pointing toward it. Had the animal been running, the feet would have been planted farther from the line of direction and with toes directed forward.

Now, if these conclusions regarding the gait of the Upper Jurassic and Upper Cretaceous carnivorous dinosaurs are justified, is it probable that the Triassic *Anchisaurus colurus*, with an equally heavy abdomen and with less elongated and more primitive limbs, had the ability to walk, just as a bird does, accurately placing one foot directly in front of the other and under the center of gravity? It seems to the writer that we need more proof of it. If it could so walk, one might inquire what was the use of all the modifications undergone by the dinosaurs up to the end of the Cretaceous. It seems most probable that *Anchisaurus* walked usually in crocodilian or lacertilian style, with, however, the femora drawn somewhat more closely to the sides. Now and then, when in great haste and for short distances, it was probably able to progress bipedally in an awkward fashion. In the same category may be placed some of the European dinosaurs figured by Dr. v. Huene, such as *Thecodontosaurus antiquus* and the species of *Plateosaurus*. Others, as *Pachysaurus ajax* and *Massosaurus carinatus*, probably walked more or less habitually on their hinder limbs, but with a wide trackway and with much swinging of the tail from side to side.

Dr. v. Huene's statement of his view of the manner of insertion of the femur has been quoted above. To the writer it seems probable that the whole proximal end of the bone constituted the head and was inserted into the acetabulum, as in lizards and crocodiles, and that the thigh was directed outward still more than Dr. v. Huene has supposed.

What then made those bird-like tracks that are so abundant in the sandstones of the Connecticut River valley? Why not birds, indeed? Although remains of birds have not yet been found in Triassic rocks there can be little doubt that these animals had already freed themselves from the dinosaurs. Already long before the close of the Jurassic the hinder limbs of birds had, as we learn from *Archæopteryx* taken on its present form, with doubtless ability to plant its footsteps on the line of direction. This limb was at that early time far in advance of the hind leg of the dinosaurs of even the Upper Cretaceous; and it was doubtless even in the Triassic far in advance of the limb of the dinosaurs of that time. No bird remains have been found where those famous tracks occur, it is true. It is also true that nearly 100 kinds of tracks have been distinguished, while only 8 or 10 species of dinosaurs have been discovered in the North American Triassic; and of these only one has had its tracks identified. Therefore, it seems to the writer entirely reasonable to suppose that those bird-like tracks, even some of them that show the presence of fore feet and tail, were really made by birds. For if the birds diverged from the dinosaurs early in the Triassic their wings were as yet probably unfitted for continuous flight in the air. Many of them were probably running animals and some of them may still have retained a tendency to grow to a large size. Success in flying necessitated in later times a reduction in size of body. In the Trias the hands had not yet become reduced and transformed through the development of great pinion feathers, and they may have been at times applied to the ground in walking and resting. The tail was yet long, little befeathered, and might drag on the ground and leave a trail. And it must not be regarded as wholly certain that the tracks of large bipedal animals of later times were made by dinosaurs. There may have been in the Jurassic and the Cretaceous, as well as in the Tertiary, running birds of even greater size than the largest moa, whose foot was hardly inferior in size to that of many dinosaurs. On the other hand, such dinosaurs as *Compsognathus* and *Hallopus* may have walked like birds, but the remains of such are found in the Triassic no more than those of birds.

If now such Theropoda as *Anchisaurus colurus*, more advanced probably in every respect than the Sauropoda ever were, did not walk habitually erect, like mammals, on either two or four legs, but progressed either in more or less crocodilian manner on all fours or in a straddling way on the hind legs, is it probable that the sauropods ever walked high up on four legs in the jaunty manner in which they have been represented? It is to be considered that these great herbivorous reptiles possessed a huge abdomen, deep and probably broad, which extended backward and merged into the tail, necessitating the divergence of the relatively long femora. The outer surfaces of the pubic and ischiadic bones were clothed with great masses of muscles, as were too the insides of the femora. Assuming that the legs were as straight as they have been represented, the feet could have been hardly closer together than the knees, probably considerably farther apart. A bulky animal walking thus could preserve its equilibrium only by either swaying the body from side to side, to throw it over the advanced foot, or throwing the tail toward that side. In the case of the fore foot the long neck might be used to preserve the balance. One might amuse and instruct himself by working out the movements of the animal according as it was walking, trotting, pacing, or perchance galloping.

The writer is not willing to assert that *Diplodocus* and its relatives never straightened out their legs, thus lifting themselves well above the ground, and never walked thus. Even the crocodiles have been known to do this, as a rare occurrence.[10] In the U. S. National Museum there is a specimen of the Florida crocodile mounted in this position. The femora are directed forward and outward, the tibiæ downward. The feet are widely separated as a mechanical necessity. What is disputed by the present writer, is that this was the customary attitude of the sauropods; and their great bulk makes it doubtful if it was ever assumed.

The writer is of the opinion that the feet of the primitive dinosaurs had the inner digits somewhat more strongly developed than the median and outer ones; that is, they were entaxonic, not mesaxonic,

[10] Hornaday, Two Years in the Jungle, pp. 55, 266.

resembling in this respect the feet of the crocodiles. A reason for this conclusion is found in the fact that all the feet of the sauropods are entaxonic and also the fore feet of the earliest known theropods. It is therefore more probable that the hinder feet of the latter reptiles became mesaxonic from an entaxonic condition than that their fore feet and both fore and hind feet of the sauropods should be transformed. That the manus of the theropods was entaxonic may be seen from Marsh's figure of the fore foot of *Anchisaurus colurus* and *A. polyzelus* (Dinosaurs N. A., pls. ii, iii) and from Dr. v. Huene's figures. Furthermore, the hinder feet of the early theropods present plain indications of a former entaxonic arrangement. The foot of *Ammosaurus*[11] shows a very stout first digit, not greatly shorter than the others, while the second does not fall behind the third and fourth in diameter of the bones, little in length. The superiority of the second to the third seems to have been retained in *Allosaurus*. When the hind leg began to be drawn forward against the side and the weight of the body was thrown to a greater extent on the median digits a stimulus appears to have been given to the development of the third digit, while the first, relieved to some extent of its former duty, became reduced and turned backward.

In the later theropods the manus also became mesaxonic. This is seen in Marsh's restoration of the skeleton of *Ceratosaurus* (op. cit., pl. xiv). Mr. C. W. Gilmore, who has recently mounted this skeleton has shown me the remains of the one hand preserved. Most of the phalanges are missing. There are present four metacarpals, and there are no traces of the fifth in the rock. The first is considerably reduced, the second is the largest. Thus, there is evidence that all the feet of the carnivorous dinosaurs became transformed from the entaxonic to the mesaxonic condition. It further appears that the sauropods retained the primitive condition of the feet, fore and hinder, more persistently than did the other groups of the order.

For reptiles that progress by creeping, having the humerus and the femur at right angles with the body in the middle of the step, the entaxonic condition seems most effective. It is found in the crocodiles and the turtles, being especially well displayed in the trionychids and the land tortoises. In reptiles the first digit is usually

[11] Marsh, op. cit. pl. iii, fig. 6.

retained long after the disappearance of the fifth. In the lizards, however, the fifth is often larger than the first, a condition dependent perhaps on their habit of climbing about on rocks and trees. In the mammals, on the other hand, it is the first digit that earliest suffers reduction.

An attempt has already been made on a previous page to account for the origin of the bipedal habit in reptiles. Evidences are present, it is believed, which show that bipedalism in the dinosaurs was not due to specialization of the anterior limbs. If an examination be made as to the relative lengths of the fore and the hinder limbs in the carnivorous dinosaurs, it will be found that in *Anchisaurus colurus* the fore limb is about three-fourths as long as the hinder; in *Plateosaurus quenstedti* about two-thirds; in *Pachysaurus ajax*, about one-half. These are Triassic dinosaurs. In *Ceratosaurus*, of the Upper Jurassic, the fore limb is only about two-fifths as long as the hinder. In *Tyrannosaurus*, of the Upper Cretaceous, the fore limb is diminutive, in case the humerus found with the specimen really belonged to it.[12] As we have seen, the great pollex of the late Triassic forms had become much reduced in the Upper Jurassic species. Therefore, in place of specialization, the whole limb suffered degeneration. If now it be asserted that bipedalism in the theropods was occasioned by specialization of the fore limb for other purposes than locomotion, we shall have the case presented of an organ which, as soon as it was free to continue its specialization, began to degenerate. Without doubt however, the fore limb continued to be used for various purposes, just as the ostrich continues to use its diminutive wings.

Various opinions have been expressed regarding the origin of the Sauropoda. Marsh[13] expressed the opinion that the group included the most primitive forms of dinosaurs. Baur[14] held that the Sauropoda had no close relationships to the other reptiles usually classed with them as dinosaurs. Osborn[15] believes that it is possible to derive the sauropod type from a primitive quadrupedal theropod type. In his work already so often quoted, Dr. v. Huene expresses

[12] Osborn. Bull. Amer. Mus. Nat. Hist., xxii, pl. xxxix.
[13] Dinosaurs N. A., p. 164.
[14] Amer. Naturalist, xxv, p. 450.
[15] Nature, vol. 73, 1906, p. 284.

his view that the sauropods were derived from the carnivorous dinosaurs. He sums up his conclusion as follows (p. 351):

> Die Sauropoden ein frühes Theropoden-Stadium festhalten and fixiren und so eine gleichartige und relativ wenig weiterbildungsfähige Masse bilden, die sich wohl nur infolge des Riesenwuches bis zum Schluss der Kreidezeit behaupten konnte.

Regarding the time of origin of the Sauropoda Dr. v. Huene has the following to say (p. 351):

> In der Zeit zwischen dem Schluss der Trias und dem Auftreten von Dystrophæus im älteren Jura ist die erste Umprägung zum Sauropoden-Typus erfolgt.

Dr. v. Huene calls attention to the numerous characters common to the Theropoda and the Sauropoda, and he believes that the latter inherited these common characters from the former suborder. Such a derivation would, the present writer holds, require extremely important modifications in the structure of the early Theropoda. The hind foot had, at the end of the Trias, become decidedly mesaxonic, with the hallux greatly reduced and probably somewhat turned backward. To create the foot of *Diplodocus*, for example, the hallux and the second digit must have been stimulated to increased growth; that is, the foot must have been made entaxonic; whereas, the upright gait that is usually attributed to *Diplodocus* ought to have increased the size of the middle digits and further reduced the hallux. The metatarsals that had become lengthened had to be shortened. The fore limb, that in the late Triassic theropods had become reduced in length, sometimes greatly so, must have taken on renewed vigor and increased size. All the modifications that had been attained and all the tendencies established that looked toward making bipeds out of these theropods had to be reversed.

Probably little or no importance can be attached to the fact that no remains of sauropods have yet been encountered in the Triassic deposits. It is certain that but a small proportion of the animals that made those Connecticut Valley tracks have left us other traces of their existence. Then, it is extremely probable that comparatively few of the residents of that region were accustomed to parade on those desolate and dangerous tidal flats. The sauropods especially, being slow-footed plant-eaters, would naturally have sought localities where there were fewer long-legged enemies and where the grazing was more satisfying.

To the writer, therefore, it appears most reasonable to suppose that the Sauropoda were a more primitive stock than the Theropoda and that the latter were derived from the early Triassic representatives of the former. Those primitive sauropods were no doubt far smaller than any of the group that are known to us. They probably had shorter necks, although with no fewer vertebræ; the vertebræ were less complexly constructed than those of their Jurassic descendants, and fewer of these had coösified to form the sacrum. The digits, too, were probably longer and the outer ones were less reduced. We can hardly doubt that they crawled on their bellies.

The conviction has been expressed that bipedalism in the dinosaurs was caused by the relative reduction of the fore limbs. On the other hand, the writer believes that bipedalism among the birds was the result of specialization of the fore limbs. These different tendencies gave the signal for the parting of the dinosaurs and the birds. The birds were the gainers by the separation. They secured all that the dinosaurs got and far more besides. The two groups separated at an early period, early in the Triassic, possibly even in the Permian. It was undoubtedly at a time when the members of neither the one group nor the other had begun to walk on the hinder legs only. The feet, fore and hinder, were yet entaxonic. The hinder fifth digit was probably somewhat reduced, while the hallux was large and directed forward. Not until after the divergence of the two groups did the legs of the birds begin to be turned against the flanks and the body to be lifted from the ground. As greater and greater pressure began to be thrown on the middle digits the hallux began to be dwarfed and to be relegated to the hinder part of the foot. *Archæopteryx* shows that the hand had been entaxonic, for in it the two outer digits had wholly disappeared; while the pollex, though somewhat reduced, was yet large and functional.

It seems quite certain that the differentiation of the fore limb was initiated by the appearance of incipient feathers in the form, perhaps, of enlarged scales, which stood out from the ulnar side of the arms. The presence of these feathers, or scales, led to the flapping of the wings in the air, not conversely. Perhaps the individuals on which these rudimentary feathers first appeared were accustomed to clamber about over rocks and shrubs and the limbs of trees. Possibly the primitive birds, although not more than many lizards, strictly arboreal, often found safety and repose amid the branches and leaves of the Triassic ferns, calamites, and conifers. Possessing a fringe of feathers on their arms, they soon found these of advantage when they were running or making leaps to catch their prey or to escape capture by their enemies. When once they had made this discovery, the race entered on the conquest of the realms of the air.

It will be observed that the writer, in opposition to Dr. Francis Nopcsa[16] holds that the primitive birds became bipedal while they were learning to fly and because of it, instead of becoming so long before the flying habit was initiated. It will be observed that the fore limbs of Dr. Nopcsa's "Pro-avis" are already greatly reduced, and it might be questioned whether such limbs could be rejuvenated. It is certain that the ostriches have for untold generations been flapping their wings, to aid in running, but these limbs have steadily degenerated.

As believed by Dr. v. Huene, the Orthopoda probably took their origin from the Theropoda. If the views expressed by the present writer are true or approach truth, birds came on the arena before either of the suborders of dinosaurs just named; and hence most of the characters which have suggested relationship between the birds and the dinosaurs, which characters have been so clearly presented by Dollo and Nopcsa in the papers already quoted, have all arisen independently in the two groups as a result of their starting from the same goal and speeding in nearly the same direction. On the other hand, the sauropods are nearest the stock from which sprang the birds, and it is in their skeletons that we must seek for the primitive common characters.

To the writer it seems probable that the avidinosaurs were not amphibious animals, but dwellers on the land. It is not likely that wings were developed on animals that lived much in the water. The Theropoda and the Orthopoda continued to inhabit the land, although this did not prevent them from seeking their food in swamps or from refreshing themselves in the water. After the sauropods had attained such bulk that locomotion on the land became troublesome they

[16] Proc. Zoöl. Soc. London, 1907, p. 234.

betook themselves to the streams, in order to enjoy the advantages of easier transportation; and then they became still more massive. Had they originally been aquatic and had they continued so, their feet would have remained more like those of crocodiles, less digitigrade and less shortened than they were in *Diplodocus*.

In his paper on the relationships of the birds and the dinosaurs[17] Professor Osborn says:

> Thus tridactylism is correlated with rapid bipedal progression, the inner and outer digits suffering reduction.

In formulating this apparently important generalization Professor Osborn did not qualify it with the statement that most of the so-called tridactyl animals are really tetradactyl, the hallux being present and usually functional. Nor could he have had before him the skeleton of any of the sloths, animals that are strictly tridactyl behind, but which are neither bipedal nor endowed with great speed. Tridactylism prevailed among the extinct horse-like perissodactyls and is a characteristic of modern tapirs. On the other hand, there may exist swift bipedal progression independently of tridactylism. The ostrich makes rapid headway with only two toes, one might almost say, with a toe and a half. The kangaroos are wonderful bipedal leapers, whose functional digits are reduced to two, the fourth and the fifth. Man may be justly counted among the swift runners, trained individuals making their mile in four and a quarter minutes, and he possesses a pentadactyl entaxonic foot. No bipedal artiodactyl is recalled, but, as illustrating a possibility, one must not forget to mention Pan, the shepherd god of old Arcady. From which considerations it may be concluded that the bipedal rapid runners have adopted no standard form of foot.

Accompanying the present paper is a drawing (Pl. I) which is intended to represent the habits of *Diplodocus*, especially as regards its habitual pose of body and its manner of locomotion, as conceived by the writer. This drawing was executed by Miss Mary Mason Mitchell, after consultation with the author of the paper. Two individuals are in the foreground. One is collecting food from the surface of the water; the other has the head high in air and is jealously

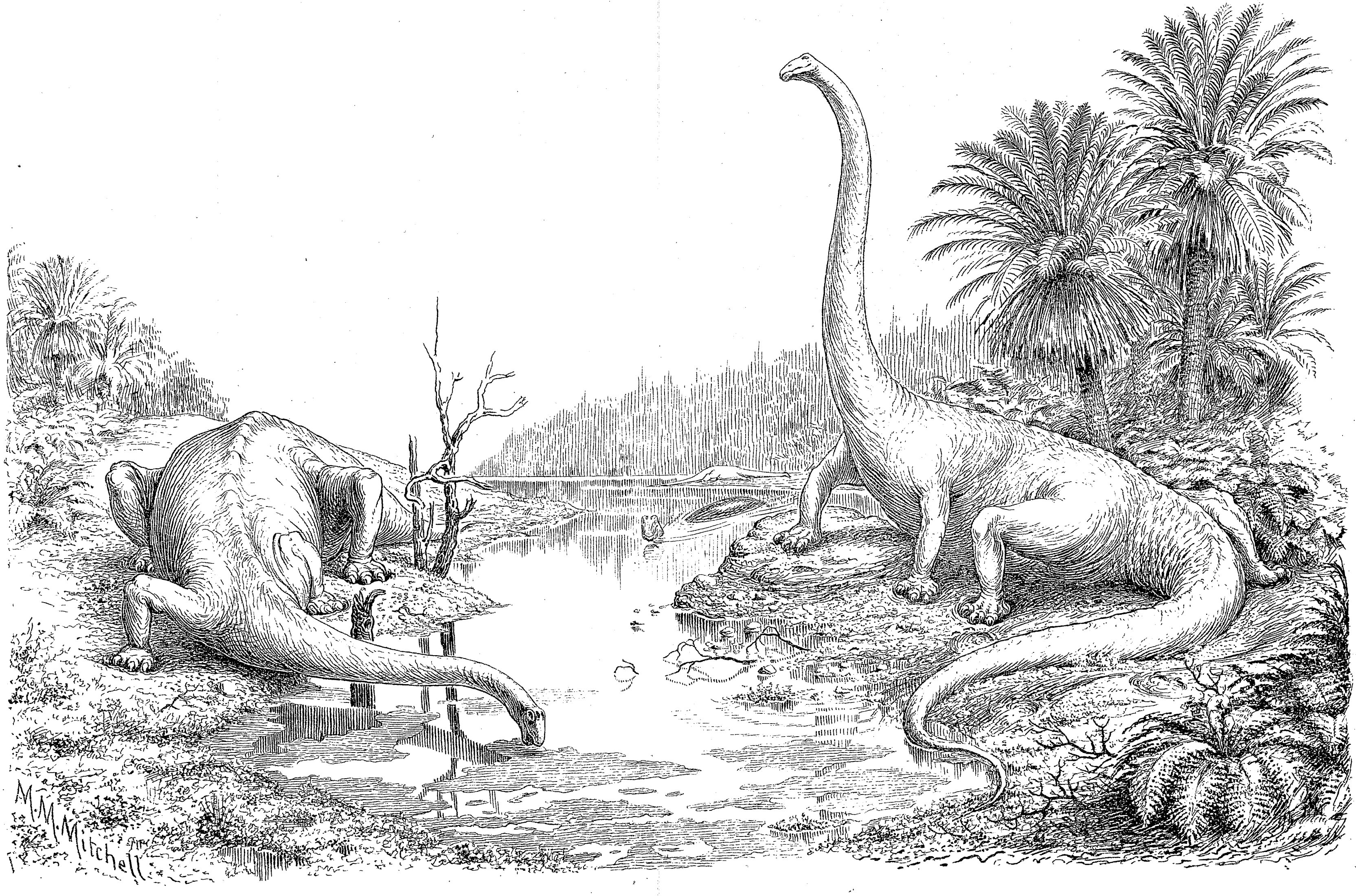
[17] Amer. Naturalist, xxxiv, 1900, p. 796.

regarding the approach of another, which is swimming. In the far distance is a fourth specimen lying stretched out at full length on the bank.

In the paper published by Mr. Ballou, referred to on page 15, there is a figure which represents a group of four individuals of *Amphicœlias latus*, a dinosaur closely related to *Brontosaurus* and attaining a length of from 60 to 80 feet. These animals are shown as walking about on the bottom of a river, feeding on the vegetation there and rising on their hind legs to reach the air. The idea here suggested is adopted by Professor Osborn[18] as correct. Mr. Knight, under Professor Osborn's direction, has made a restoration of Brontosaurus[19] in which the same idea regarding the habits of the sauropods is inculcated. In this restoration a number of individuals, otherwise invisible, are sticking their heads out of the water. The ability of any large animal to walk thus submerged must depend on its having a massive skeleton, as have the hippopotamus and the manatee. In *Diplodocus*, on the contrary, almost every conceivable device has been employed to reduce the weight of the skeleton. The great vertebræ contain large and small internal cavities, while externally the processes are carved into thin plates and buttresses and the centra are deeply excavated on each side. Moreover, as has been shown by Hatcher,[20] the limb bones are hollow. It would seem to have been hardly more possible for *Diplodocus* to walk about immersed in water than it would be for a man to do the same. Even if the reptile could have remained sunken, any pressure by the feet in the effort to walk would have sent it to the surface.

After the text and the drawings of this paper had been completed the writer received the Scientific American of November 6, 1909, in which is printed a popular article on the attitude of *Diplodocus*. In this article mention is made of a paper on this subject recently published by Dr. Gustav Tornier of Berlin, a paper not previously seen by the present writer. Unfortunately too, he has not seen the original papers of Messrs. Drevermann and Boule. No numbers of the Umschau, of Frankfort, for the present year are accessible.

[18] Bull. Amer. Mus. Nat. Hist., x, p. 220.
[19] Amer. Mus. Jour., V. p. 68.
[20] Mem. Carnegie Mus., i, p. 53, fig. 23.



THE FORM AND ATTITUDES OF DIPLODOCUS