THE POSE OF SAUROPODOUS DINOSAURS

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THE POSE OF SAUROPODOUS DINOSAURS[1]

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THESE four articles discuss a question of considerable general interest. Did the huge Sauropodous dinosaurs, *Diplodocus, Brontosaurus* and their allies, walk like elephants, or crawl like crocodiles? The skeletons and casts in the larger museums of America and Europe have all been mounted straight limbed, with the body well clear of the ground. But the evidence for giving them this pose, so different from that of the generality of reptiles, although well known to those who are responsible for it, has not until recently been published. Hence it is not surprising that these reconstructions have been criticized more or less seriously, especially in Germany, and that two writers of high scientific standing—Dr. Tornier in Berlin, and Dr. Hay in Washington—have contended that these animals could not have walked upright, but must have dragged the belly on the ground as crocodiles and lizards normally do. Both writers have attempted and discussed at length the re-articulation of the skeleton in the crocodilian pose.

Dr. Tornier's argument is, briefly, that reptiles crawl

[1] "Die Rekonstruktion des Diplodocus," von O. Abel, *Abh. k. k. Zoöl.-Bot. Gesellschaft in Wien*, Vol. V., 1909–10, pp. 1–60 of separata, three plates and text figures; March 24, 1910.

"Review of some Recent Criticisms of the Restorations of Sauropod Dinosaurs Existing in the Museums of the United States, with Special Reference to that of *Diplodocus Carnegiei* in the Carnegie Museum," by Dr. W. J. Holland, AMERICAN NATURALIST, 1910, Vol. XLIV., pp. 259–283, plate I. and text figures, May, 1910.

"On the Manner of Locomotion of the Dinosaurs, Especially *Diplodocus*, with Remarks on the Origin of the Birds," by Oliver P. Hay, *Proc. Washington Acad. Sci.*, 1910, Vol. XII., pp. 1–25, pl. 1, text figs. 1–7, February 15, 1910.

"Wie war der *Diplodocus carnegii* wirklich gebaut?" von Gustav Tornier, *Sitz.-ber. Gesell. Naturf. Freunde zu Berlin*, 1909, pp. 193–209, pl. II. and 6 text figures.

while mammals walk; that *Diplodocus* is a reptile and resembles the lizards and crocodiles far more closely than it does any mammals in the details of construction of the shoulder- and hip-girdles, limbs and feet. Therefore, it should be posed like one of the larger lizards, except for the long neck, which he compares to the long-necked birds and poses in accordance. A sketch restoration and a number of diagrammatic drawings illustrate his views. The subject appears, frankly, to be somewhat outside the range of his studies, and his comparisons are not broad or thorough enough to be at all convincing.

His criticisms are very effectively and completely answered by Dr. Abel and Dr. Holland. These authors point out that while the dinosaurs were reptiles and as such their bones were constructed upon the reptilian plan, yet they form a group apart, differing from other reptiles and in many respects resembling the struthious birds; that these resemblances, especially as regards the construction of pelvis and hind limbs, leave no reasonable doubt that the typical dinosaurs walked pretty much as do the great ground birds; that the limbs of *Diplodocus* and its allies differ from the normal dinosaur type in a marked superficial and adaptive resemblance to the elephant, indicating a quadrupedal "rectigrade" mode of motion; that the skeleton articulates satisfactorily in this pose and that the attempt to articulate it in the pose of a crocodile or lizard involves either a demonstrably false interpretation of parts, or a disarticulation of the joints which proves such a position to be highly abnormal if not utterly impossible for the creature to assume.

Dr. Hay's contributions to the discussion—the article cited and an earlier one in the American Naturalist—are worthy of more careful consideration. Hay is a high authority on fossil vertebrata, especially upon Chelonia and fishes, and has recently devoted considerable study to the dinosaurs. He recognizes the fact that the dinosaurs, while pertaining to the class Reptilia, form a group apart, with many analogies to the birds; that many dinosaurs did walk with the body clear of the ground, and that many lizards walk or run in this way at times. He does not deny that even the Sauropoda may have done so at times, but regards them as too massive and heavy for this to have been their normal mode of progress. But his chief protest is against the placing of the knee and elbow joints in sagittal planes (*i. e.,* bending parallel with the middle line of the body) as in mammals, instead of bending outward as in all modern reptiles. In certain points of his argument he makes out a convincing case in the reviewer's opinion; other points may be satisfactorily answered.

Dr. Hay misstates the supposed significance of the peculiar type of femur seen in *Diplodocus.* He observes:

> If the mammal-like gait of *Diplodocus* be insisted upon on the ground of straightness of the femur, it may be pointed out . . . 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.

But no one, so far as the reviewer knows, has asserted that the straightness of the shaft of the femur of *Diplodocus,* considered alone, proved that the animal walked like a mammal. For among mammals there are both straight and curved femora, and a wide variety of gaits.

The argument that Dr. Hay presumably has in mind is this: That in the elephants and several other types of gigantic mammals the femur is relatively long, straight-shafted, with its articulations terminal rather than lateral, the feet short, rounded, heavily padded and capable of but limited motion, the whole limb being pillar-like and normally held straight under the body. All gigantic mammals show some degree of approach towards this type of limb; and in the Sauropoda the resemblance in form and proportions is very marked. The same type is seen in *Coryphodon, Uintatherium, Titanotherium, Arsinoitherium, Pyrotherium, Astrapotherium, Dipro-*

todon, gigantic mammals of widely diverse stocks, in *Stegosaurus* and *Triceratops* among the dinosaurs, and an approach towards it in various other groups. The modern horses, rhinoceroses, cattle and other large animals, and most of the very large extinct mammals show a distinct approach toward these proportions as compared with their smaller and more agile ancestors; so too do the gigantic *Trachodon* and *Tyrannosaurus* as compared with their smaller and more agile ancestors or relatives, *Laosaurus, Camptosaurus,* and *Allosaurus.*

On the other hand, a glance at a lizard femur shows that the straight shaft is associated here with a wholly different position of the proximal and distal articulations and of the trochanters by which the limb is moved. The distal articulations for the tibia and fibula are on the back of the femur, not on its end; the great trochanter for the hip muscles projects outwards from the shaft instead of upwards in line with it; the feet are long and the toes relatively elongate; there is very little padding.

The shaft of the femur is nearly straight in the aquatic turtles and the articulation for the lower limb is quite distal in position; but the trochanter projects upward, the limb is carried outward from the body and more or less straight. In the land turtles and in the crocodiles the femur has a strongly curved shaft, bent downward at the distal end, the limb still projecting outward from the body but flexed sharply downward at the knee. Here then are two distinct methods by which a swimming limb may be converted into a crawling limb.

The straight-shafted femur does not *per se* prove that *Diplodocus* walked in any of the various ways that mammals walk. But taken in connection with the numerous other adaptive resemblances in form and proportions of the bones of the hind limb, feet and pelvis, to the elephants and other gigantic mammals and reptiles cited, it does afford a very strong argument for asserting that *Diplodocus* walked like an elephant as to its hind limbs.

Dr. Hay's next point appears to be a strong one. He observes that if we compare the femora of such dinosaurs as *Allosaurus, Tyrannosaurus, Trachodon* or *Camptosaurus,* admittedly erect-walking bipedal forms, with the femora of the Sauropoda, we find a great difference in the quality of the bone and the finish of the articulations.

The shaft of the former appears to be more elaborately modelled, and to consist of finer and harder bone; all the articular surfaces are smooth and they carry the 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; [it would be more accurate to state that the great trochanter is not a separate process but a rugose area marginal to the head of the femur] and the head lacks much of filling the acetabulum. In its [*sic*] low stage of differentiation the femora of the sauropods resemble greatly those of the crocodiles and are hardly above those of the lizards.

It is not clear what lizards Dr. Hay had here in mind. The larger land lizards have a much more "differentiated" femur. Even in the crocodiles the resemblance is not very close. But a much closer and more striking resemblance in the characters cited may be found if we compare the femora of large *aquatic* reptiles, ichthyosaurs, mosasaurs or plesiosaurs, or large *aquatic* mammals such as the Cetacea, with the femora of the Sauropoda. The reviewer would agree entirely with Dr. Hay that the lack of differentiation and finish in the limb bones of Sauropoda is a strong argument that they were not adapted to the habitual support of the whole weight of the body. But the evidence cited accords exactly with the theory of Owen and Cope that they were wading animals, and the limbs were designed for the support of the body in the water, with most of its weight buoyed up thereby.

Dr. Hay believes that the position of the great trochanter in the Sauropoda was well down on the shaft, as it is in the Triassic Theropoda; but he fails to give any good reason for rejecting Osborn's view that the very clearly marked rugosity around the proximal-external angle of the head is the area of attachment of the gluteal muscles.

The character of this rugosity is certainly that of an attachment for powerful muscles; its position is substantially that of the distinct process in the larger bipedal dinosaurs; while the surface where Dr. Hay would locate the attachment is a surface of smooth bone. On the other hand, the view of Marsh and Hatcher, apparently shared by Holland, that the entire proximal-external angle, including part of the rugose surface of the proximal end, similar in character to the rest of the anatomical head or articulating surface, is the great trochanter, appears to be indefensible, and Dr. Hay's arguments conclusive as against it. This view seems to have been founded on the analogy with the proboscidean femur, carried further than the facts warrant. But Dr. Hay's conclusion that the femur of the Sauropoda represents a very early stage in progressive adaptation of the limb from the primitive swimming to the walking type, is not warranted if Osborn's view as to the position of the trochanter be correct, for as Hay rightly observes, in the progressive stages of adaptation to upright carriage this attachment moves up towards the head of the bone. But the only semblance of argument that Dr. Hay offers against this view seems to be the assumption that *Diplodocus* was more primitive than its Triassic predecessors. The truth seems to be that the Sauropoda were highly specialized as regards the adaptations for upright walking, but degenerate as regards the adaptations for bearing great weight on the limbs.

As to the aquatic habitat of the Sauropoda, Dr. Hay's statement of the evidence can hardly be regarded as a fair one, although he seems to be of the opinion that the larger forms, at any rate, were secondarily aquatic.

> The ability of any large animal to walk about 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 used 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, 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.

In a brief description of the *Brontosaurus* skeleton[2] which Dr. Hay consistently ignores, although he can hardly fail to be acquainted with it, the reviewer pointed out that there was a very marked difference in the massiveness of the upper and lower parts of the skeleton in the Sauropoda. All the bones above a line passing through the acetabulum and glenoid cavity of the scapula are very lightly constructed, and thus far Dr. Hay's statement is correct. All the bones below this line are, on the other hand, very massive, and solid or nearly so. So far as the reviewer can judge from comparison of a large series of bones, they are quite as dense and massive as the corresponding bones in the hippopotamus; and they certainly are not hollow in the sense that the bones of *Allosaurus* are hollow. All of them are cancellous towards the center, and in the femur there is an open cavity of proportionately small size in the shaft. But they are certainly far more dense than in the elephant, and wholly lack the devices for lightening the weight that are so conspicuous in the skull, cervical and dorsal vertebræ, the first few caudals, the ilium and the proximal ends of the ribs. The median and distal caudals, the ischia, pubes and limbs, the shoulder-girdle, except for the blade of the scapula, and especially the feet, must be wholly excepted from Dr. Hay's statement in regard to the lightening of the skeleton; they are certainly unusually massive in form; and while the precise degree of density of the petrified bone is not very easily compared with modern bone, yet in the reviewer's opinion they compare most nearly with the bones of aquatic animals, such as plesiosaurs and mosasaurs among the reptiles, cetaceans, pinnipeds, sirenians and hippopotami among the mammals, and are materially exceeded in density only by the sirenians.

Dr. Hay's observations in regard to the pose of bipedal dinosaurs form an interesting corollary to his views in

[2] Amer. Mus. Guide Leaflet No. —, 1905.

regard to the Sauropoda. For although admitting that they were in general bipedal and walked with the body clear of the ground, he finds himself compelled, in the logical development of his theories, to assign them a widely straddling walk. This compels him to explain the observed tracks of *Iguanodon,* which are not straddling, as being an unusual mode of progression associated with slow walking, but that if the animal had been running it would have had a wider trackway. So far as the reviewer's observations extend, the faster an animal is walking or running the more it is inclined to plant the feet close to the median line of its trackway, and the less likely to waddle—this is assuredly true of our own gait, and probably holds good with any bipedal animal. The stronger evidence derived from the numberless tracks of the Connecticut Valley Triassic, Dr. Hay would explain by supposing that these tracks were made, not by dinosaurs which we know existed, but by birds of whose existence at that time we have no evidence.

But Lull has shown that not only do many of these tracks correspond precisely and in detail with the reconstructed hind feet of carnivorous dinosaurs, but the occasional impressions of the fore feet, the pubes and the tail, correspond equally well. A disputed hypothesis in regard to the amount of straddling in their gait is hardly sufficient ground to question the accepted view that these tracks were made by dinosaurs.

It is indeed quite reasonable to suppose that ancestors of the birds, more or less closely related to the dinosaurs, were living during the Triassic. But the extreme rarity of bird remains during the whole Mesozoic, and the fact that, with the exception of *Archæopteryx,* the better known forms are highly specialized aberrant types, gives ground for supposing that the normal habitat of Mesozoic birds was such that their remains were not buried in the areas of sedimentation. They were presumably confined to the higher and drier uplands, remote from the river-deltas and coastal swamps which were the normal habitat of the heavy and bulky dinosaurs, and which the lighter and smaller dinosaurs of the upland visited to a greater or less degree.

Dr. Hay makes considerable use in his discussion of Marsh's restoration of *Anchisaurus,* as in this reconstruction the limbs appear relatively shorter and the proportions more lizard-like than in most Theropoda. But while this is true to some extent of *Anchisaurus* and apparently of most Triassic Theropoda, it is exaggerated in Marsh's reconstruction by insertion of several additional dorsal vertebræ which are probably not warranted.[3] The restoration is a composite from two or three partial skeletons; the number of vertebræ is really uncertain. If the body be shortened to the proportions of the more completely known dinosaurs, there is less difficulty in supposing the animal to have been habitually bipedal, and bird-like in gait. The general contention that the dinosaurs evolved from a crawling lizard-like gait to a bipedal bird-like gait without passing through a quadrupedal walking mammal-like gait appears probable enough. But the Sauropoda seem to be most easily explained by the hypothesis that they acquired secondarily a quadrupedal elephantine gait, that they were at first more or less amphibious and finally exclusively aquatic waders.

Whether we state, as does von Huene, that the Sauropoda are derived from Theropoda, or, as Dr. Hay will have it, that the Theropoda are derived from Sauropoda seems to be largely a question of terms and definitions. Both are derivable from a common ancestral group, but the Sauropoda have specialized fully as much in one direction as the Theropoda in another. In fact, in the present writer's opinion, the Sauropoda are decidedly more specialized, although their specialization is in part degenerative and a re-adaptation to the aquatic environment of the remote ancestors of the Reptilia.

[3] Marsh has inserted additional dorsal vertebræ in most of his dinosaur restorations, as may be seen by comparison with the more complete skeletons which have since been mounted and described in several American museums. There are three too many in *Brontosaurus* (Riggs), five too many in *Camptosaurus* and six too many in *Triceratops* (Gilmore) and so on probably throughout. His general concept of the analogy of the group seems to have been too much lizard-like and not enough bird-like.

Dr. Holland's article is a brilliant, well-illustrated and cruelly convincing polemic in support of the accepted pose of the *Diplodocus* skeleton, but in the reviewer's opinion he does not at all do justice to the real weight of some of the arguments advanced by Hay and Tornier, especially the former. Serious exception might be taken to the positiveness of some of his assumptions, as well as to the ridicule of his opponents' views.

Holland shows by aid of a series of photographs and carefully finished drawings that the pose advocated by Dr. Tornier could not have been assumed without an entire dislocation of the important limb joints; that the pelvis of the sauropods is like "the pelves of the dinosauria in general, distinctly ornithic in type, not lacertilian nor crocodilian," that the body is deep, narrow and short as in birds, while in the crawling reptiles it is broad flattened and more elongated; that the scapula and fore-limb differ in important features from those of crocodiles and lizards, and the fore limb can not be articulated in a crawling pose; that the long heavy tail affords no argument for a crawling posture; that the feet are digitigrade and not plantigrade as asserted by Tornier; that the general form and proportions of the limbs point to an elephantine pose, and that the single known footprint of a Jurassic Sauropod supports the same interpretation. (It is worthy of note that Dr. Lull has carefully examined this footprint and come to the conclusion that it was probably made under water rather than on land.) The whole article is very readable and clearly written, and would seem to close the case so far as the possibility of Tornier's reconstruction is concerned.

Dr. Abel's contribution is a careful, thorough and fair-minded consideration of the problem by a high authority upon fossil vertebrates, who has devoted a great deal of time and thought to paleontologic reconstructions. He reviews the principles governing such work, the relationships of *Diplodocus* and the data for the reconstruction, the opinions that have been held in regard to the pose and habits of the Sauropoda, and cites Tornier's arguments in some detail. He then gives a careful and critical presentation of the evidence afforded by the form and relations of the different parts of the skeleton. He concludes that the generally accepted poses, as shown in the several skeletons of Sauropoda that have been mounted, and in the published restorations by Marsh, Hatcher, Holland and Osborn, are in the main correct, except that the scapula should be somewhat more vertical, the elbow directed more outward, and fore and hind foot completely digitigrade. He finds no warrant for the radical changes in pose recommended by Tornier and Hay. The evidence can not well be condensed within the limits of a review. The marked analogy to the elephants, especially in the proportions and relations of both fore and hind feet, and in the limb bones the relationship to the bipedal dinosaurs, much closer than to the crawling reptiles, the mechanical requirements for the support of a body of the size and proportions of a Sauropod dinosaur, are the chief criteria used to interpret the direct indications from the bones of the *Diplodocus* skeleton.

Dr. Abel's conclusions may be condensed from his summary as follows:

1. The animal did not crawl, but walked, with the body well clear from the ground, the knee bending forward, the elbow outward and backward, the feet digitigrade as in the elephant. In a standing position the angle at the knee was slight (15°), while the bend at the elbow was more considerable (60°). The fore feet were longer and more completely digitigrade than the hind feet; both fore and hind feet were exaxonic, the weight of the body resting chiefly on the outer digits, which were heavily padded, with rudimentary toes, while the innermost toe of the fore foot and the inner three toes of the hind foot bore large blunt claws.

2. The body was deep and narrow, strongly arched from front to back, the neck long and flexible, normally carried forward, with the head continued in the same direction.

3. There were twelve thoracic vertebræ, of which the

first is unknown; and sixteen cervicals, of which the first (pro-atlas) is unknown. The problematic bone identified by Holland as clavicle, by Nopsca as os penis, by Tornier as episternum, is the first rib.

Some of the points cited may be questioned or disproved,[1] but the main contention, that the Sauropoda were walking, not crawling animals appears to be abundantly proved.

Nevertheless, there is a great deal yet to be said on the pose and habitat of the Sauropoda, and there are certain lines of evidence which none of the authors cited have considered adequately.

In the first place, the nature and cause of the parallelism between sauropod dinosaurs and elephants has not been very clearly pointed out. The type of limb and foot structure which they show in common was first clearly defined, so far as the reviewer is aware, by the late Professor Gaudry, under the name of "rectigradism." It is a specialization directly associated with gigantic size, the limb becoming straight and pillar-like, the foot short, round, heavily padded, with toes reduced or vestigial. The movements of the limb are chiefly at the upper joints, the foot serving chiefly as pad or cushion to absorb the shock in locomotion. This is very different from the typical "digitigradism" of the dog or cat; it may be observed with modifications, in large plantigrade and unguligrade animals as well as in digitigrade forms, and a progressive approach towards it may be observed in all races of land vertebrates as they approach gigantic size. The proximal segments of the limbs tend to become longer and straighter, their articulations more terminal, the distal segments shorter, their range of movement decreasing, the toes become much shortened and vestigial, buried in an elastic pad, or, as in ungulates, with a broad horny hoof, which absorbs shock less completely but gives a firmer footing.

[1] The insertion of two additional dorsal vertebræ is certainly erroneous, and with this falls to the ground the interpretation of the "clavicle" as a rib. Positive evidence from other partially articulated skeletons is likewise available, I believe, to determine the number of cervical vertebræ.

Obviously a specialization of this kind will occur only in an animal which habitually rests its weight on the limbs, and it is necessary with increased weight, because the increase of weight varies as the mass (cube of the linear dimensions) while the increase in strength varies as the cross section (square of the linear dimensions).

This last circumstance will very clearly set a limit to the size that an animal may attain as a practical working mechanism. And here we are brought to face an unanswerable difficulty if we consider the Sauropoda as land animals. How is it that with their less perfect reptilian organization of limbs and feet they were able to attain so much larger size than has since been attained by the land mammals with their more perfected organization. Throughout the Cenozoic we see race after race of gigantic land mammals successively culminating and disappearing, each a little larger than its predecessor, each assuming the rectigrade limb as it approaches its maximum size, the Proboscideans, the latest and largest of all, and, so far as can be judged, the most perfect in mechanical organization. But the Sauropoda, away back in the Jurassic, far surpassed the largest elephants in size; and yet their joints are rough, imperfect, cartilage covered, their muscular attachments imperfectly differentiated. If the elephant is the largest size that the perfected mammalian organization permits, how is it possible that the relatively imperfect dinosaur organization could so far exceed it? And if it is not, why have none of the numerous gigantic Tertiary mammals exceeded this size?

If, indeed, we regard the Sauropoda as aquatic animals, adapted to wading, we solve this difficulty readily enough, and find also an explanation for various peculiarities in their construction which remain unexplained if they are considered as land animals. A wading animal has the greater part of its weight buoyed up by the water, and might attain a much larger size without transcending its mechanical limitations, just as the whales and some true fishes attain a much larger size than any land animal.

A second point that does not seem to have been brought out in the discussion is that the dinosaurs are distinguished from other reptiles by the relatively large size of the legs as compared with the body. In this respect they have the proportions of mammals and birds. The significance of this would seem obvious. A crocodile, turtle or lizard crawls habitually, because his legs are not large enough to carry the weight of his body. In dinosaurs, as in mammals and birds, the legs are large enough to carry the body comfortably clear of the ground and presumably served that purpose.

The nearest approach to the dinosaur proportions is seen in some of the lizards, and it is just among these that we find a tendency to lift the body from the ground, especially during running.

Another general consideration lies in the question of the primary adaptation of the dinosaurs. Dr. Hay very justly remarks that it is by no means necessary to suppose that the bird-like (bipedal) dinosaurs had passed through a mammal-like (quadrupedal) stage of evolution. Indeed, if we regard the lizard as illustrating early stages of a similar adaptation, the evidence would be just the other way; the bipedal stage in dinosaurs came first, the quadrupedal stage was a secondary adaptation. This is generally admitted as regards the quadrupedal dinosaurs of the Predentate group; the reviewer believes that it is also true of the Sauropoda, although the indications of former bipedalism are less apparent in this group. The hypothesis would serve, however, to explain several odd features in their construction—*e. g.*, the combination of everted elbow with straight knee—and would connect them more definitely with the Theropoda of the Triassic, to which they are structurally traceable, as von Huene has demonstrated.