

THE HABITAT OF THE SAUROPOD DINOSAURS

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INTRODUCTORY

In the study of the sauropod dinosaurs which has been carried on by the writer for a number of years under the direction of Professor H. F. Osborn in connection with the preparation of the latter's monograph on these reptiles, some problems have presented themselves upon which a study of the habitat, or immediate environment, has a bearing.

The course, or trend, of evolution in a group of organisms is limited, or controlled, by two things: (1) the heritage or assemblage of characters inherited from the ancestors; and (2) the environment. The environment offers the organism opportunities for developing along a limited number of lines. What these lines will be depends upon the general character of the environment. For instance, upon inland plains advanced aquatic adaptations, such as are characteristic of marine organisms, will be barred out, and under strictly marine conditions the development of cursorial locomotor apparatus is impossible. This is true no matter what may be the heritage of the organism under discussion. Within certain limits, however, the environment offers the possibilities or opportunities for evolution along a number of lines. The heritage furnishes the material or instruments by which, or by a modification of which, the organism may evolve along one or more of these lines.

In working out adaptations and habits in a group of animals such as the Sauropoda, morphology, together with comparison with living forms, will be the most important guide. Morphological structures have meanings, and if these meanings can be interpreted the habits of the animals possessing the given structures can be determined to a certain extent. A study of the environment of

the group in question may aid in interpreting the structures and may guide us in determining the habits of fossil animals, because certain types of environment definitely exclude certain modes of life, as has been noted above. The habits of the animals must have conformed to the environment which actually surrounded them when they lived.

The present discussion is concerned with the environment of the Sauropoda. The environment of a group of organisms is divisible into two components: first, the physical, and second, the biotic. These are related to each other in a complex manner, but with regard to their relation to a given group they may be considered separately. The first is concerned with such things as climate, with mountain, plain, delta, lake, or marine conditions, with the geographic extent of a given type of physical condition, with means of communication and barriers preventing communication or intermingling, with the rate of sedimentation and erosion, with the presence or absence of volcanic phenomena, etc. The second is concerned with food supply, with competition, and with enemies. If in a given case the various factors of each of these components may be determined, a comprehensive idea may be had of the habitat, or immediate environment, of the group of animals involved.

PHYSICAL ENVIRONMENT

The physical environment of the Sauropoda is concerned with the geology of the Morrison, Arundel, Wealden, and corresponding Indian, African, Patagonian, and Malagasy formations. The American Morrison may be considered in this connection as an example of sauropod-bearing deposits.

The physical characters of the Morrison, its relations to other formations, considered in connection with the general Mesozoic history of Western North America, indicate certain definite things regarding the geography, topography, climate, and dominant physical processes of the time and region in which the Western American Sauropoda lived. An extension of this study to include world-wide conditions would give a fair idea of the physical environment in general.

The characters of the Morrison may be discussed under the following heads: (1) distribution, present and probable past; (2) lithology; (3) internal structures; (4) stratigraphic relations; (5) conclusions regarding conditions of deposition, physical processes dominant during the period of deposition, and middle Mesozoic history.

1. The present distribution of the Morrison is indicated on a map compiled by the writer.¹ The formation outcrops along the eastern and western borders of the Rocky Mountains in Wyoming, Colorado, and New Mexico; in the rim of the Black Hills; in canyons in southeastern Colorado and northeastern New Mexico; around the borders of the Bighorn and Owl Creek mountains in Montana and Wyoming; in isolated uplifts in Wyoming; in canyons and mesa scarps in northwestern New Mexico, western Colorado, and eastern Utah; and in various other occurrences in the states mentioned. The outcrops are usually not extensive, the formation never being the country rock over a wide area. The total area in which Morrison outcrops occur is, however, very large. There are vast areas where the Morrison must unquestionably underlie younger formations. The areas in which the Morrison was formerly present, but from which it has been removed by erosion, are also very large, their exact size not being known at the present time. The total area which was formerly covered by Morrison sediments must have been extremely large, very likely exceeding a million square miles in extent. As remains of sauropods are now found at practically every region of Morrison outcrops, it follows that the distribution of the Sauropoda in North America was also very wide.

2. Lithologically the Morrison is composed of a variety of rock types. The formation is frequently described as a series of "joint clays," fine-grained sediments which appear to be fairly well consolidated when dry, but which crumble or break readily when wet. These are red, brown, gray, or maroon in color. Petrographically they are fine grits composed mostly of quartz, with some argillaceous interstitial material which may or may not be

¹ Charles C. Mook, "A Study of the Morrison Formation," *Annals of the New York Academy of Sciences*, XXVII (1916), 39-191, Pl. VI.

stained red by hematite, as the case may be. These grits, especially the red ones, are frequently most abundant in the upper levels of the formation; it is in these upper levels that calcareous material is more scarce. Beds of sandstone, sometimes of considerable thickness, occur at various levels; these sandstones are made up principally of quartz, which is often well rounded; feldspar grains, either fresh or more or less altered, occur along with the quartz; in some beds grains of volcanic ash, both fresh and altered, are found; and in a few instances beds of coarse sand several feet thick are made up of volcanic ash. Limestone beds, usually not over a foot or two in thickness, are frequently found in a section; these are sometimes composed largely of the shells of small gastropods. They are more common near the base of the formation than in the upper members. The lower beds are often arkosic, considerable quantities of feldspar being present, often cemented to the accompanying quartz and to each other by a calcite matrix. Thin beds of agate are found in some sections.

Very coarse material is not found in the Morrison. Sandstones of a moderate degree of coarseness are common throughout the entire area of Morrison outcrops. Such sandstones are, however, on the whole thicker and more common in the western exposures than in the eastern.

3. The Morrison contains internal structures of considerable interest. In the first place the various strata often appear to the eye to extend over considerable distances, but when detailed sections are made, even a few miles apart, and compared with each other, it is noticeable that the details of the sections vary considerably. A gradual thinning out of beds of one kind of material, and their replacement by another kind, is the rule in this formation. For all of this variation the general aspect of the formation in one locality is very much like that in another. This type of thing has been aptly described by Dr. Lee as "uniformly variable." In some cases the thinning out of beds is sudden, as in the case of the old stream channel exposed at the site of the old Marsh-Hatcher dinosaur quarry near Cañon City.

The variation and at the same time the uniformity of the thickness of the formation are of special interest. The greatest recorded

thickness is about 900 feet, and it is possible, if not probable, that beds are included in this measurement which are older than the Morrison. The range in thickness is usually from 700 feet in the western sections to less than 100 feet in the Black Hills region. This thickness is exceedingly slight for a formation of such vast geographic extent as the Morrison. In general, the western sections are thicker than the eastern, but this will not hold as an invariable rule. Sections of 400 feet or less sometimes occur in the western areas, and sections fully 400 feet thick exist in eastern New Mexico. No section of more than 500 feet is known from the eastern areas, however, and the western sections frequently reach that or a greater thickness. The Morrison sediments might perhaps be described from the point of view of thickness as a thin mantle of sandstones and clays extending over a vast area, thickest in the west and thinning out definitely, but irregularly, to the east.

Cross-bedding is abundant in the beds of the Morrison, especially in the sandstones. It is represented by the type described by Walther and others as typical of desert deposits, and also by the type usually assigned to stream deposition.

4. The stratigraphic relations of the formation are in a broad way disconformable with regard to the underlying terranes. The deposits rest upon older formations of various ages, from the Unkpapa sandstone of uppermost Jurassic or earliest Comanchean age in the Black Hills region to Archean crystallines in the Rocky Mountain region. The relation of the Morrison to the overlying sediments appears to be a conformable one. The fact that the Morrison appears to be closely related to the succeeding formations has been pointed out by Lee.¹ For further description of the Morrison formation the reader is referred to the above-mentioned article on the Morrison by the writer and to the bibliography contained therein.

Taken together, the physical characters of the Morrison indicate a history something like the following: After an extensive period of erosion, during Jurassic and perhaps late Triassic time, Western North America was invaded from the north by the sea, and the

¹ W. T. Lee, "Reasons for Regarding the Morrison an Introductory Cretaceous Formation," *Bull. Geol. Soc. Amer.*, XXVI (1915), 303-14.

sediments of the Sundance formation were laid down; following this the sea retreated, the retreat taking place along with final Jurassic folding in the Sierra Nevada region. Over the plain exposed by the retreat of the Sundance sea the Morrison sediments were spread out in the form of a very broad, very flat alluvial fan from west to east. This fan must have been crossed by many large streams, dotted with lakes, large and small, and characterized by an interlacing type of drainage, much after the manner of the great alluvial plains of Eastern China at the present time. The plain must have been low, and the streams crossing it must have been characterized, for the most part, by a low gradient. Locally, especially in the western areas, there may, in fact must, have been some deposition in relatively swift currents, as indicated by the cross-bedded sandstones. These sandstones being rather fine-grained for the most part and never conglomeratic, true torrential conditions were probably not present in any part of the Morrison area so far studied. The round sand grains, associated with aeolian type of cross-bedding and sudden variations in thickness, indicate that wind deposition was also a factor in the gradual building up of the Morrison sediments. The presence of unaltered or little altered volcanic ash indicates that volcanic activity must have been going on somewhere in the region. Over a plain as broad and flat as this one must have been material could not have been transported rapidly from the original source to the outer limits of the area of sedimentation. The sluggish streams of the plain must have deposited material and later picked it up again and carried it farther very many times before a selected lot of sediment could have reached the outer margins. This will account for the greater relative abundance of finer clays in the eastern areas. The interlacing stream, lake, and swamp conditions on such a plain would readily admit of rapid shifting of the courses of streams, areas which were at one time stream beds constantly changing to inter-stream areas, and the reverse. This would result in the slow, gradual shifting of material outward. The end result would be the product of alternate deposition and erosion, erosion and deposition, for a long period of time, the material being very slowly worked eastward. In some such manner as this the relatively thin sheet of

Morrison sediments may have been spread out over a vast area. In this area of deposition, and living while it was in progress, were the Sauropoda and their contemporaries.

BIOTIC ENVIRONMENT

I. VERTEBRATES

The known vertebrate fauna of the Morrison is large and varied. The unknown fauna must have also been larger; perhaps, in fact quite likely, larger still. Of the mountain fauna of Morrison time nothing can be said, but the mountain fauna was not part of the sauropod habitat.

1. *Mammalia*.—Between twenty and thirty species of mammals have been reported from Morrison beds. These were small triconodonts, trituberculates, and multituberculates. They are known only from teeth and fragmentary jaws, so that their structure and adaptations cannot be made out. It has been suggested that they were arboreal. They might serve very well for arboreal members of the Morrison fauna. These small mammals could scarcely have competed with the Sauropoda for food; they certainly could not have constituted food for the Sauropoda in themselves; nor could they have been directly formidable as enemies. It has been suggested, however, that they may have fed, in part at least, upon reptilian eggs. If they did, and if they existed in large numbers, they may have been very troublesome companions for the sauropods.

2. *Aves*.—Only one species of bird is known from the Morrison. Undoubtedly more were present in Morrison time, but there is no direct evidence of their existence. It is not likely that the birds had any important effect upon the lives of the sauropods, although they may have had something to do with the distribution of species of plants which perhaps composed part of the sauropod diet.

3. *Reptilia*.—The reptilia of the Morrison were many and varied. They all represented degrees of organization and stages of evolution which were comparable to the degree of organization and stage of evolution of the member of the fauna under discussion—the Sauropoda. Undoubtedly there was competition of several sorts between the Sauropoda and their reptilian contemporaries.

The reptilian fauna of the Morrison suggests the following analysis:

a) Rhynchocephalia. The only modern representative of this group is non-marine, and there is nothing in the structure of the single Morrison representative of the order to suggest that it was anything different. It may perhaps have been amphibious, or fluviatile, or terrestrial. It is not probable that there was any direct competition between the members of this group and the sauropods.

b) Crocodilia. Several species of mesosuchian crocodiles are known to have existed in Morrison time along with the Sauropoda. The modern crocodiles are amphibious creatures, either fluviatile or lacustrine, not marine, and the Morrison forms probably lived in a similar manner. They were good-sized, active, carnivorous, relatively intelligent animals, which may easily have preyed upon the young of the Sauropoda.

c) Pterosauria. The pterodactyls were aërial forms. One species is known from the American Morrison. It is hardly to be expected that sauropod dinosaurs and pterosaurs would enter into any direct conflict or competition with each other.

d) Squamata. Lizards, snakes, and mosasaurs are entirely unknown from the Morrison. Some of them must have been living somewhere at the time, for lizards are known to have existed since the Triassic, and mosasaurs appear well developed early in the Cretaceous. Consider in this connection the fact that the mosasaurs were marine animals.

e) Chelonia. Turtles at the present time are marine, fluviatile, lacustrine, or terrestrial. Only one species in this group is known from the Morrison, and it is probable that the chelonian element in the Morrison fauna was not very important. The turtles could hardly have come into severe competition with the Sauropoda.

f) Sauropterygia and Ichthyopterygia. The plesiosaurs and ichthyosaurs were entirely marine. No trace of them has been found in Morrison rocks, though they must have been living in the sea during Morrison time. They are found in marine rocks both younger and older than the Morrison.

g) "Dinosauria." The two great orders of reptiles collectively known as "Dinosauria" were represented in the Morrison by a variety of forms. These were all terrestrial or amphibious, perhaps some forms being largely fluviatile or lacustrine. Of the saurischians there were present, besides the sauropods, several types of carnivorous forms. Some of these were small, active, and not very formidable. *Ornitholestes* may be considered as a typical example of this group. Probably these small dinosaurs had little importance, so far as the Sauropoda were concerned, unless, perhaps, they ate sauropod eggs. They were too small and weak to attack the sauropods, and by their activity and carnivorous structure could obtain food that would not be available for gigantic, largely herbivorous swamp dwellers. The larger carnivorous dinosaurs, such as *Allosaurus*, *Creosaurus*, and *Ceratosaurus* undoubtedly played a very important part in sauropod economy. The association of carnivore teeth and grooved sauropod bones is in perfect accordance with the idea that the sauropods were prey for the large carnivores. The large carnivores were unquestionably land-living forms. It is not at all likely that they entered the water except under unusual circumstances or along the margins. The gigantic sauropods, therefore, were less likely to be attacked in the water than on land. This may have tended to keep the sauropods in the water, and may have had considerable control over the evolution of the group. The ornithischian dinosaurs must also have had an effect upon the Sauropoda, but as competitors rather than as direct enemies. The stegosaurs and the iguanodonts, both large and small, existed along with the sauropods. These forms, especially the stegosaurs, were probably land animals. They were herbivorous beyond all doubt. If the sauropods spent a considerable part of their time on land they must have come into competition with the predentates in the matter of getting food. Perhaps such a competition took place early in the history of the Sauropoda, and may have been instrumental in forcing the latter to take to the streams, and finally to develop some aquatic adaptations and spend the greater part of their time in the water. The predentates may have aided the sauropods in their struggle for existence by furnishing a considerable amount of food for the carnivores. If the predentates

and carnivores were almost exclusively terrestrial and the sauropods largely aquatic in habit, the latter might escape the carnivores much more frequently than if the predentates were not present.

4. *Amphibia*.—The known amphibian fauna of the Morrison consists of one frog or toad. A fauna of this nature could scarcely have had any effect upon the lives or development of the Sauropoda.

5. *Pisces*.—The only fishes known to have existed along with the American Sauropoda were a few species of *Ceratodus*. These could hardly have furnished food for the sauropods, or have had any direct effect upon the security of the latter.

II. INVERTEBRATES

The known invertebrate fauna of the Morrison is neither very large nor varied. It consists of a number of fresh-water pelecypods and gastropods, together with a few ostracods. None of these were large enough nor abundant enough to have served as an essential part of the diet of the sauropods, but they may have served as accessories, to a very small extent, to the normal sauropod diet.

III. FLORA

The known flora consisted almost entirely of cycads. These might also have comprised an accessory portion of the sauropod diet, but probably not much more. The remainder of the Morrison flora is very little known. Silicified wood is found occasionally, and rarely some imperfect reeds. The Kootenie formation contains leaves of deciduous trees, but few if any sauropods. The Arundel formation of Maryland contains both sauropod bones and deciduous leaves. The latter also might have formed an accessory part of the food of the sauropods, but could scarcely have been abundant enough to have sustained their huge bulk. In a region such as the one described above there might have been a considerable amount of soft vegetation which would not be easily preserved. In the interstream areas, especially where considerable amounts of windblown sands were being deposited, little vegetation may have been present, certain areas being semiarid. Other areas were probably well covered with vegetation. The character of the known flora suggests a rather warm climate, and the physical

conditions point more to an abundance of rainfall than to a widespread lack of it. We may therefore conclude, provisionally at least, that the climate was warm and moist.

INTERPRETATION OF HABITAT

From the evidence of the physical characters of the Morrison formation and from the nature of its flora and fauna it may be possible to work out, to a certain degree at least, the environment which surrounded our American Sauropoda. In the first place, there was a vast plain in the Western United States, possibly extending northward into Canada; this plain was low throughout its entire extent, but slightly higher in the west than in the east; it was bordered on the west by mountainous country. From this mountainous area streams issued, bringing sediment and depositing it along the western border of the plain. The streams, upon leaving the mountains, became sluggish and split up into a large number of distributaries. As in the great plains of China, streams would be split up into distributaries and united again. Between the streams, and more or less connected with them, were lakes. A considerable amount of vegetation was present, especially along the stream and lake banks. In this respect the plain would resemble the interior of Florida, which has often been suggested as the type of habitat possible for sauropod dinosaurs. Our Morrison plain would differ from Florida, however, in its extent, the central Florida swamps being relatively small and the Morrison plain being a million square miles or more in area. In some of the interstream areas, especially in the west, vegetation may have been more scarce. Active volcanoes were present somewhere, either in the mountains or on the plain. Somewhere to the southeast was the sea, but its exact border is not known, especially with regard to the earlier part of Morrison time. On this plain lived an extensive terrestrial, amphibious, fluvial, or lacustrine fauna. Little, primitive mammals climbed the trees or scurried over the ground; here and there some birds flew through the air; along the shores of the lakes and rivers lived some *Sphenodon*-like rhynchocephalians; pterosaurs flew through the air; some turtles swam about in the water; crocodiles inhabited the stream and lake banks, and infested the

waters themselves. On land, large and small carnivorous dinosaurs roamed about, seeking what they might devour; stegosaurus and camptosaurus endeavored to escape their voracious contemporaries; some frogs inhabited the swamps. In the rivers and lakes lung fish swam about. Fresh-water mollusks and crustaceans lined the river and lake bottoms in places or swam about freely in the water. Cycads grew in abundance, and soft swamp vegetation probably furnished the food supply for hungry reptiles. In some such environment as this, or at any rate in one very much like it, lived the American sauropod dinosaurs. So far as is indicated by evidence now directly available, conditions of practically the same sort prevailed in other parts of the world inhabited by Sauropoda.