

RECONSTRUCTION OF *DIPLODOCUS* (SAUROPOD) BODY SHAPE AND GAIT WITH KINESIOLOGICAL METHOD

Norihisa INUZUKA

Palaeo-Vertebrate Laboratory
Saiwai-cho 45-25-303, Itabashi-ku, Tokyo 174-0034, JAPAN

ABSTRACT

Sauropods are among the largest of all dinosaurs. They have been restored to various body shapes, but the reason for their unique body shape with long necks and tails has not been clarified. Here, we focus on *Diplodocus*, known as the longest dinosaur, and attempt to consider it based on comparative osteology, functional morphology, biomechanics, syndesmology, ichnology, and kinesiology. The unique features of sauropod fossils are the abnormally long neck and tail, the relatively short trunk, the V-shaped spinous processes of the cervical and dorsal vertebrae, and anterior caudal vertebrae, the tallest spinous process of the sacral vertebrae, and the forefoot prints that are significantly smaller than the hind foot prints. It would be desirable to have a theory that can explain all these observed facts with a single body shape and gait. In conclusion, it is speculated that diplodocoids had a bow-shaped body shape, that was balanced by the head, trunk and tail, with the hips as the fulcrum, and that they walked at a very slow trot and substantially bipedally, aided by the recoil of the spine, which was supported by long supraspinous ligaments containing elastic fibers.

Key words: biomechanics, comparative osteology, gait, ichnology, kinesiology, sauropod, reconstruction, restoration

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竜脚類は恐竜のなかでも最大級のものである。これまでに様々な体形で復元されてきたが、首と尾の長い独特の体形の理由は解明されていない。ここでは、最長の恐竜として知られるディプロドクスを中心に、比較骨学、機能形態学、生体力学、靭帯学、足跡学に運動学の法則を加えて考察を試みた。竜脚類独特の化石の特徴は、異常に長い首と尾、相対的に短い体幹、頸椎、胸腰椎や前位尾椎のV字形の棘突起、仙椎で最も高い棘突起、後足印に比べて著しく小さい前足印である。これらの多くの観察事実を単一の体形と歩容で説明できる説が望ましい。結論としてディプロドクス上科は腰を支点にして頭胴部と尾でバランスをとる弓形の体形で、弾性線維をふくむ長大な棘上靭帯で支えられた脊柱の反動の助けを借りて、very slow trot で実質的に二足性で歩いたものと推測した。

INTRODUCTION

Sauropods are the largest of all dinosaurs. They have long been restored in a variety of postures, with differences in the direction of the limbs, the shape and angle of the neck, and the elevation of the tail. In addition, in relation to their large size, there have been differing theories about their habitat and the amount of fleshiness in the restored living body. It is already accepted that they had inferior-type limbs, a slim body, did not drag their tails, and were not aquatic animals, but there is a debate about the posture of the spine, gait, and the reason for the long neck and tail. Abel (1925), the founder of paleobiology, argued that it is necessary to restore locomotion before reconstructing the skeletal form. I therefore reconstructed

the gait from the fossil evidence of *Diplodocus*, known as the longest dinosaur, and considered the appropriate body shape. The large size and enormous number of vertebrae derive the longest body length. The length and thickness of the limb bones derive a short trunk from biomechanics. The deep V-shaped groove at the end of the spinous process of the cervical vertebrae suggests the development of a nuchal ligament rich in elastic fibers. The sacral spinous process is the largest, and the fact that the V-shaped spinous processes extend to the dorsal and anterior caudal vertebrae suggests that the entire spinal column was elastic. The length connecting the midpoints of the left and right fore and hind footprints indicates the glenoacetabular length. The ratio of the area of a sauropod's fore and hind footprints reflects the ratio of loads on the forelimbs and hind limbs, and indicates the position of the body's center of gravity. From the arrangement of the footprints, the gait can be determined by overlaying the position of the center of gravity on the support triangle formed by the supporting legs. Dinosaur gait can be

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E-mail: ashoroa@yahoo.co.jp

Tel & Fax : 03-5926-7183

estimated by substituting fossil data into African elephant gait data and kinematic formulas. Walking in a slow trot, with diagonal feet touching the ground at the same time, most efficiently reflects the elasticity of the spine in locomotion.

HISTORY OF RESTORATION AND PROBLEMS

The earliest sauropod whose skeleton was reconstructed is *Brontosaurus* by Marsh (1896). Although the anatomical basis for the restored posture has not been shown, it was estimated that the body length was about 60 feet and the weight was more than 20 tons, making bipedal walking almost impossible. Marsh (1896) also pointed out the possibility that because of its huge body, it had more or less amphibious habits, and its food was probably aquatic plants or other succulent vegetation.

Subsequently, *Diplodocus*, the best-preserved and longest dinosaur, was reconstructed in various postures. Inuzuka (1997) described the morphological characteristics as follows, based on several representative skeletal reconstruction drawings (Fig. 1), although the basis for the posture of the skeletal reconstructions is not shown for most of them.

The skeleton of Hatcher (1901) (Fig. 1a) is low hill-shaped as a whole, with a lower neck and a dragging tip of the tail. The lumbar part is higher than the shoulder in the trunk. The ribs extend parallel ventrally, reflecting the straight spine. The forelimbs and hind limbs extend under the trunk but are slightly bent at the elbows and knees. The skeleton of Tornier has a perfectly lateral-type limb posture like a lizard, with horizontal humeri and femurs, and elbows and knees that protrude laterally and are bent at right angles (Fig. 1b). The spine is higher at the shoulders than at the lumbar parts, and the neck is S-shaped like a swan. Hay (1908) published a life restoration drawing of this posture. In Abel's skeleton, the hind limbs are almost straight, the lumbar part is the highest, and the spinal column descends smoothly fore-and-aft from there (Fig. 1c). The shoulder girdle is on the side of the thorax, and the elbows are bent deeper than the knees so as not to block the flow from the dorsal vertebrae to the cervical vertebrae. Compared to Hatcher's or Tornier's postures, the position of the shoulder girdle is moved backward to narrow the space between the fore- and hind limbs, and the posture changed from plantigrade to digitigrade. It is true that such a posture is anticipating 80 years later. There is no doubt that Norman (1989)'s skeletal drawing is also based on Hatcher's. The improvement is in the posture of the tail. Due to the influence of the "Dinosaur Renaissance" by Bakker (1986) and others, the fact that sauropods do not drag their tails has finally become widespread. The most distinctive feature of the skeleton of Czerkas and Czerkas (1990) is the position of the shoulder girdle (Fig. 1d). It is clearly more caudal than the conventional one, and the rear end of the shoulder blade reaches near the center of the thorax. As a result, the distance between the fore- and hind limbs narrowed relative to the body length. It is also positioned lower, which compensates for the length of the forelimbs, which are about 30% shorter than the hind limbs, bringing the shoulder height closer to the lumbar height and

keeping the back horizontal. Paul's skeletal drawing is a modern reconstruction common with Czerkas's one, having a short trunk, straight legs, and a horizontal tail, but it shows that there are differences in the details (Fig. 1e).

In view of the above description, the following points are the main problems in the reconstruction of *Diplodocus*.

1) Orientation of the limbs. Following the limb posture of the *Brontosaurus* by Marsh (1896), Hatcher (1901) adopted the inferior-type, but Tornier changed to the lateral-type.

"According to Hay, the undoubtedly very great body weight is the main reason why sauropods in general, and therefore also *Diplodocus* could not walk and stand with upright legs, but rather that the great body weight literally pressed the body to the ground and forced the legs into a position such as we know from crocodiles (Abel, 1925)." On the other hand, Abel (1925) did not adopt the lateral-type, but basically adopted the inferior-type limb posture. However, no anatomical basis has been shown.

Bakker (1986) presented a schematic cross-sectional view of the body of a sauropod, supporting the inferior-type limb posture because herbivores with a huge belly would result in dragging the belly in the lateral-type limb posture.

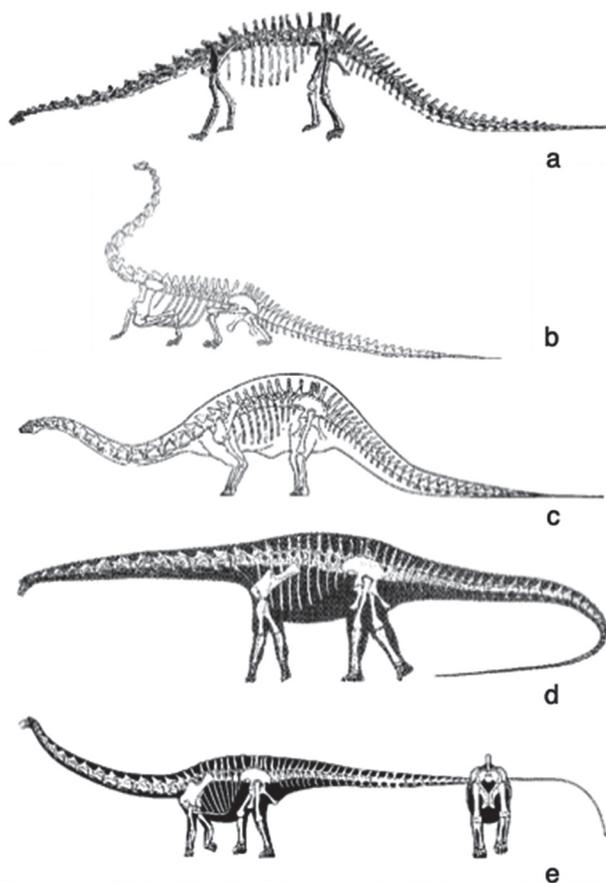


FIGURE 1. Various skeletal reconstructions of *Diplodocus*. a. Hatcher (1901), b. Tornier's skeletal reconstruction with lateral-type limbs and swan-shaped neck (Abel, 1925), c. Abel (1925), d. Czerkas & Czerkas (1990), e. Paul (1996). After Inuzuka (1997).

2) Posture and function of the neck. The posture of the neck of sauropods differs from horizontal to lower, higher, or near vertical. There are linear and S-shaped. Upchurch (2000), Stevens and Parish (2005), and Taylor et al. (2009) considered the reconstruction of the cervical spine from the shape of the articular surface of each vertebra. This is a reconstruction using the joint method, which Inuzuka (1984b) named, and has the disadvantage that it is not possible to determine the range of motion of each joint and its position in the basic posture, making it impossible to achieve uniformity as a whole. The long necks of sauropods are thought to be for feeding purposes, with those with their necks upright eating the leaves of tall trees and those with their necks lying down eating undergrowth. In addition, there is a theory that *Mamenchisaurus*, with a long neck, swings its neck from side to side while walking to feed over a wide area (Yamazaki, 1995). Any organ of any animal is undoubtedly useful for feeding, since animals must move in order to obtain nourishment. For example, the whale's neck is short because it has a body shape that is convenient for eating a large amount of food while swimming. Recently, Woodruff (2017) has considered the function of the neck in relation to feeding. However, the neck-feeding theory cannot explain the reason for the long tail. When considering the basic posture of extinct animals, it is not necessary to stick to the feeding theory. It is known that the basic posture was first determined in the evolution of the Order Desmostylia, and later it was differentiated into each genus according to diet (Inuzuka, 1987).

3) Posture and function of the tail. In the past, the tails of sauropods were drawn dragging on the ground. However, Gilmore (1936) has already examined the shape of the articular surface of the sacrum and the base of the first caudal vertebra in detail, and clarified that the tails of sauropods were initially raised from the base. After the so-called dinosaur renaissance, the posture of lifting the tail became common, but there are few opinions about why this posture was adopted. "That *Diplodocus* was able to defend itself successfully by striking with its whip-like, elongated tail is evident from healed injuries that can be seen on various tail vertebrae of *Diplodocus* (Abel, 1925)." There is also the theory that the tail is used as a whip in this way, but this is an analogy with living monitor lizards, etc., and is actually unlikely. In lizards with the lateral-type limbs, the caudofemoralis longus muscle is well developed as the retractor muscle of the hind limbs. When walking, the muscle is contracted alternately to the left and right to move forward. Since the right and left legs are grounded at rest, the tail can be swung to the contracted side of this muscle (Figure 2). However, because the limb posture of dinosaurs was the inferior-type, the femur extended below the hip joint, and the caudofemoralis longus would have pulled the tail ventrally rather than laterally.

BODY SHAPE, HABITAT, AND MODE OF LOCOMOTION

A model method that assumes a specific model is erroneous in the reconstruction of extinct animals for which no relatives exist. For example, *Desmostylus* was reconstructed by Takumi Nagao

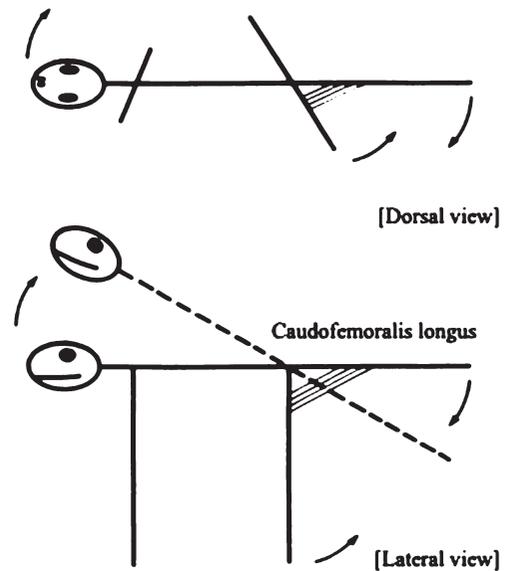


FIGURE 2. Schematic diagram of the action of the caudofemoralis longus (Inuzuka, 1993).

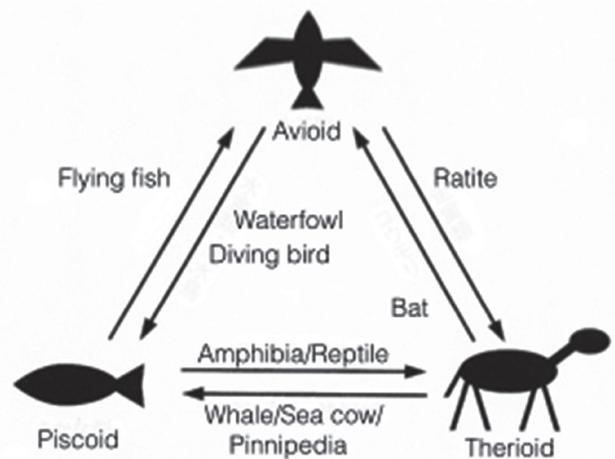


FIGURE 3. Triangular diagram of body shape and locomotion (Inuzuka, 2006).

of Hokkaido University using a hippopotamus as a model, and by Tadao Kamei of Kyoto University using a rhinoceros as a model (Inuzuka, 1984a). Desmostylians are extinct animals that are not closely related to extant Artiodactyla or Perissodactyla, and their bone shapes are different. As a result, both reconstructions contain unnatural features such as dislocations and separation of the forelimb bones from the thorax. This is because we cannot prove the relationship between extinct species and arbitrarily selected models based on partial morphological similarities. Dinosaurs are different from modern reptiles and mammals, but they are clearly vertebrates, so five modern Classes from fish to mammals are compared. It is necessary to find correlations between morphology, function, and ecology that are common among these kinds, and to apply those laws to fossils.

The body shape of vertebrates is determined by the habitat

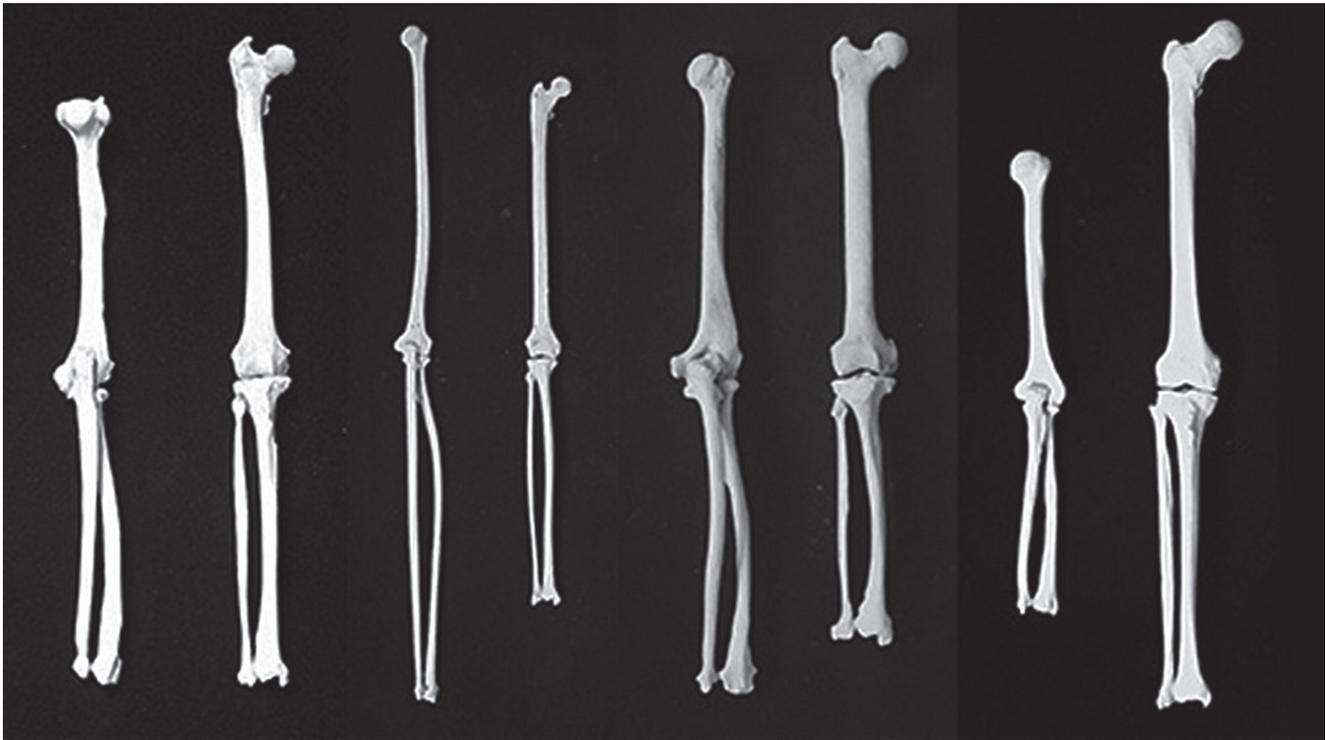


FIGURE 4. Comparison of forelimb and hind limb bone relative lengths in primates (Inuzuka, 2010). From left: *Macaca*, *Hylobates*, *Pan*, and *Homo*.

and mode of locomotion there (Figure 3). When the habitat is divided into three types, water, land, and air, the typical designs are the piscoid (fish type), the therioid (beast type), and the avioid (bird type), and the main skeletal organs used are the spinal column, limb bones, and forelimb bones, respectively. The morphology of animals that have changed their habitat secondarily converges to a similar mode of locomotion rather than a phylogeny. Amphibious crocodiles swim with their spines and walk with their limbs. Dinosaurs are terrestrial animals, so basically they are beast-like animals that walk on their feet. Even within the same taxonomic group, the mode of locomotion varies, and the main locomotor system in the body becomes larger. For example, even among the same birds, eagles that fly in the air have large forelimbs that support their wings, and ostriches that run on the ground have large hind limbs. Among primates, in Japanese macaques, which walk on four legs, the lengths of the forelimbs and hind limbs are almost the same, but in the apes, which are brachiators originally, the forelimbs are longer. In gibbons, the length from the clavicle to the manus corresponding to the arm of the pendulum is long. Chimpanzees perform knuckle walking on the ground. In upright humans, the lower limbs are much longer than the upper limbs (Figure 4). Large prosimians, which cling to trees in an upright posture, jump, and move on the ground by leaping on two legs, also have long lower limbs. Therefore, the largest part of the body suggests the main mode of locomotion. Dinosaurs were originally bipedal animals because their hind limbs were larger than their forelimbs.

As mentioned above, according to the comparative anatomical method, sauropods are quadrupedal animals that walk on four limbs, but according to the functional morphological method, it seems that they are peculiar animals that use their long spinal column for locomotion. Sauropods are characterized by their long vertebral columns.

BODY SHAPE AND SIZE

There is the square-cube law (Alexander, 1989) in biomechanics, and no animal can ever be enlarged in exactly the same shape. The body of a quadruped can be compared to a table. If the length is doubled, the weight is eight times greater, and the four times the cross-sectional area cannot support it. For example, among carnivores, a small weasel has a long trunk relative to the length of its legs, but wolves, bears, and other large animals have relatively short trunk lengths, which is the distance between their fore- and hind legs. Among the proboscideans, the progenitor *Moeritherium* is 3 m long and 70 cm tall, while the Asiatic elephant is 3 m tall and the largest mammoth is 4.5 m tall, with the shortest relative trunk length (Figure 5). Therefore, in sauropods even larger than the largest elephants, the relative trunk length should be even shorter. In the reconstruction of the same *Diplodocus*, Paul's (1996) skeletal drawing makes more sense than Czerkas and Czerkas's one (1990) in terms of relative trunk length (Figure 1d, e).

The distance between the forelimbs and hind limbs of giant animals must be relatively short. The actual trunk length of

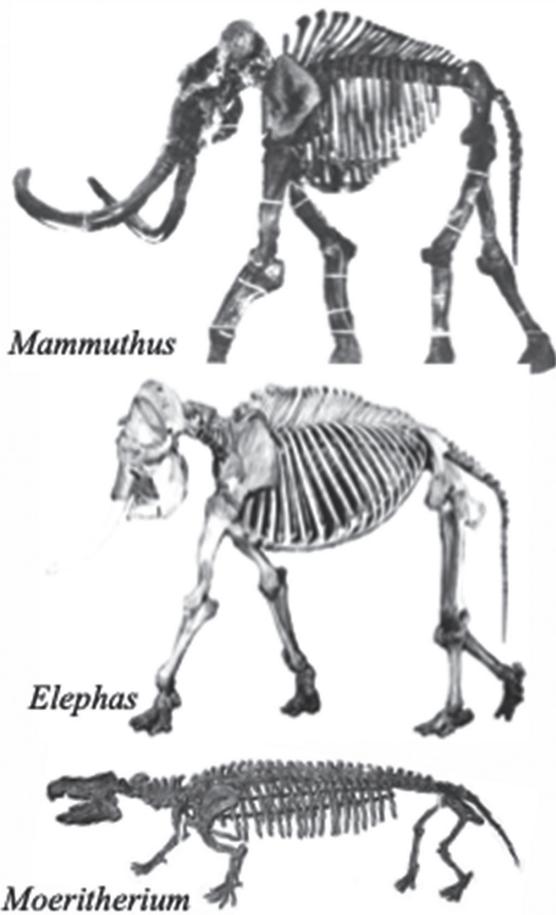


FIGURE 5. Relationship between trunk length and body size in proboscideans.

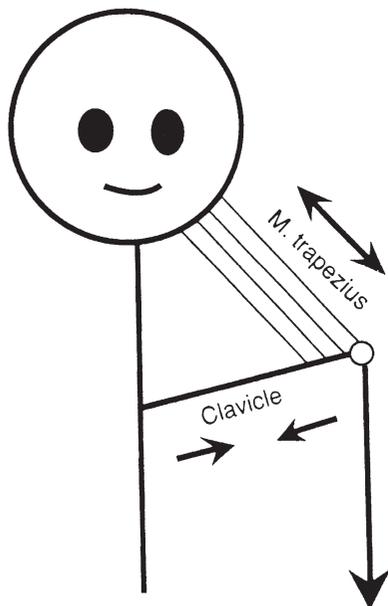


FIGURE 6. Human clavicle as a cantilever (Inuzuka, 1992).

Diplodocus can be approximated by the sum of the vertebral body lengths of the 11 dorsal vertebrae. According to Hatcher (1901), it is about 3.4 m. If the body length is about 27 m, it is about 1/8. The anteroposterior balance of the body of sauropods is similar to that of bipedal dinosaurs. Although sauropods are quadrupedal, the center of gravity of the body is situated near the lumbar part, so the entire head, neck and body should be in balance with the longer tail. The established theory is that the tail of sauropods does not drag, but considering its function as a counterbalance for the entire head and body, it is understandable that it must be kept floating.

Biomechanical methods suggest that the body length of sauropods should be short relative to their height, as proportions change with increasing size.

Abel (1925) noted as follows. "Immediately after the morphological reconstruction, the biological reconstruction must begin, i.e., the investigation of how the animal moved and in what position it rested. This is undoubtedly the most difficult, but also the most important part of the entire reconstruction process. Only after these questions have been resolved will one be able to address the question of in which posture the skeleton should be mounted and what habitus pattern should be assumed." This is an important point for reconstruction. In fact, the author once answered a question in a discussion of skeletal reconstruction of *Desmostylus*, showing that the animal could walk in a lateral-type limb posture by rotating the femur against the hip joint (Halstead, 1985; Inuzuka, 1985). Therefore, we first try to estimate the gait before reconstructing the body shape of the sauropod.

ACTION OF LOCOMOTOR SYSTEM

The locomotor system usually refers to the musculoskeletal system, and the muscular system that contracts by itself is called the active locomotor system, and the skeletal system is called the passive locomotor system. In fact, joints and ligaments that join bones together are also included, and the field dealing with these is called syndesmology. In locomotion, the larger the body, the greater the force that acts on it, so the ligaments are important organs for saving force.

The cervical vertebrae support the neck, and the spinous process (Processus spinae) of each vertebra protrudes dorsally. The tip of the spinous process is bifurcated, and the left and right interspinous muscles act to dorsiflex the neck. The median groove is attached to the nuchal ligament (Lig. nuchae), which extends from the spinous process of the anterior thoracic vertebra to the nuchal crest (Crista nuchae) of the head, and on the median plane dorsoventrally from the spinous process of the cervical vertebrae to the supraspinous ligament.

Biomechanically, the neck can be regarded as a cantilever extending from the trunk. A cantilever is a horizontal bar with one end fixed. Since tension is applied to the upper side of the cantilever and pressure is applied to the lower side, if it is too long and heavy, it will break at the center. In order to support this efficiently, a tension brace is stretched from a distant

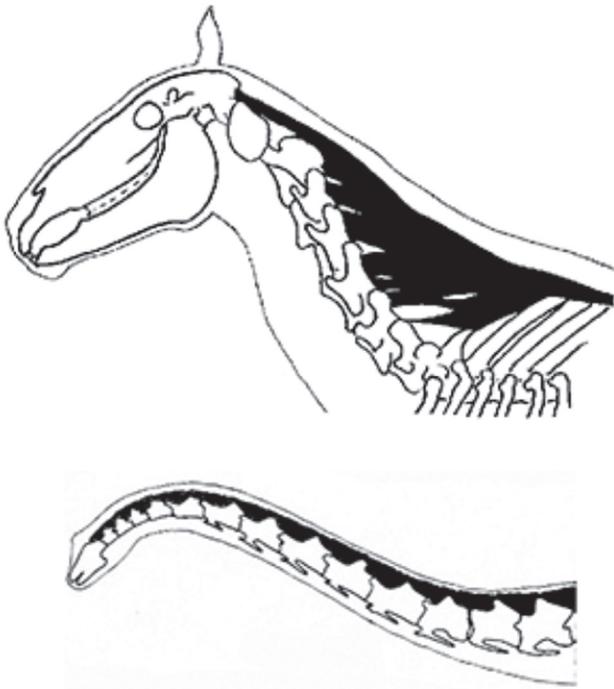


FIGURE 7. Top: Horse cervical vertebrae and nuchal ligament (Modified from Hildebrand, 1974), bottom: Lateral view of the cervical vertebrae of *Diplodocus* (Modified from Alexander, 1989).

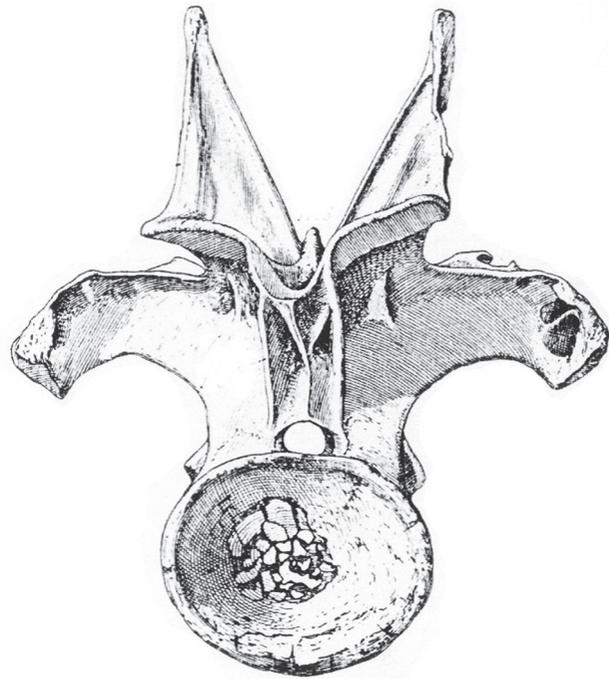


FIGURE 9. Caudal view of spinous process of the third dorsal vertebra of *Diplodocus* (Hatcher, 1901).

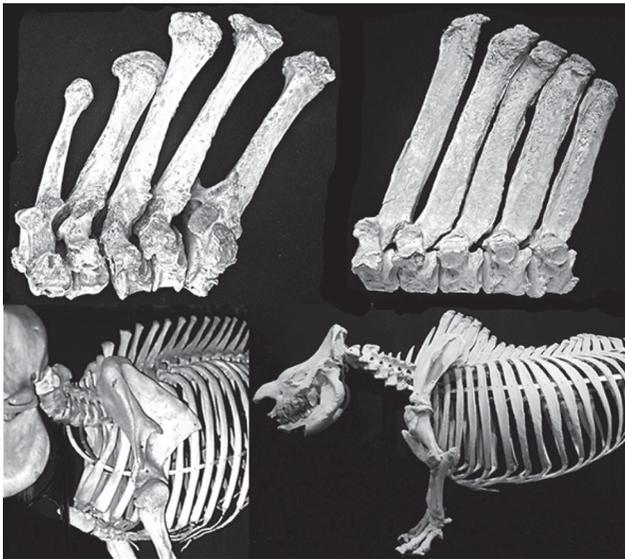


FIGURE 8. Anterior thoracic vertebrae of large animals. Elephant, rhinoceros.

point on the top to the tip. The beam is then evenly stressed, maximizing strength with minimal material. Figure 6 shows an example of the human clavicle as a cantilever beam. The clavicle extends outward from the sternoclavicular joint with the sternum as a fulcrum, and supports the arm at the shoulder joint via the scapula. At this time, the upper muscle bundle of the trapezius muscle, originating from the superior nuchal line of the occipital bone, attaches at the scapular spine and the distal part of the

clavicle, acting as a tension brace. For this reason, when a heavy object is lifted with the arm, the medial muscle of the shoulder swells.

The horse's nuchal ligament originates from the long spinous process of the anterior thoracic vertebrae, runs away from the cervical vertebrae, and inserts at the nuchal pit of the heavy head (Figure 7). Because the nuchal ligament is rich in elastic fibers, it functions as a tension coil spring that normally keeps the head high, lowers the head only when necessary, and returns to the original position when relaxed. In large mammals such as elephants and rhinos that support heavy heads, the spinous processes of the anterior thoracic vertebrae are many times longer than the height of the vertebral bodies, the spinous processes of the cervical vertebrae other than the axis are short, and the nuchal ligament is widely distributed on the median plane (Figure 8).

In contrast, the cervical vertebrae of sauropods are unusually long and tapered, with small heads and bifurcated cervical spinous processes. Figure 7 is a schematic diagram of the cervical spine based on Alexander (1989). However, unlike horses, the ligaments run close to the vertebrae. In sauropods, the spinous processes of the anterior thoracic vertebrae are not as long as in large mammals. On the other hand, in *Diplodocus*, the spinous processes from the 3rd cervical vertebrae to the 6th dorsal vertebrae are bifurcated, and the dorsal vertebrae are V-shaped with a wide space in the median part (Figure 9). I speculate that the supraspinous ligament, which was originally located at the tip of the spinous process, changed into an elastic ligament like the nuchal ligament and ran between the spinous

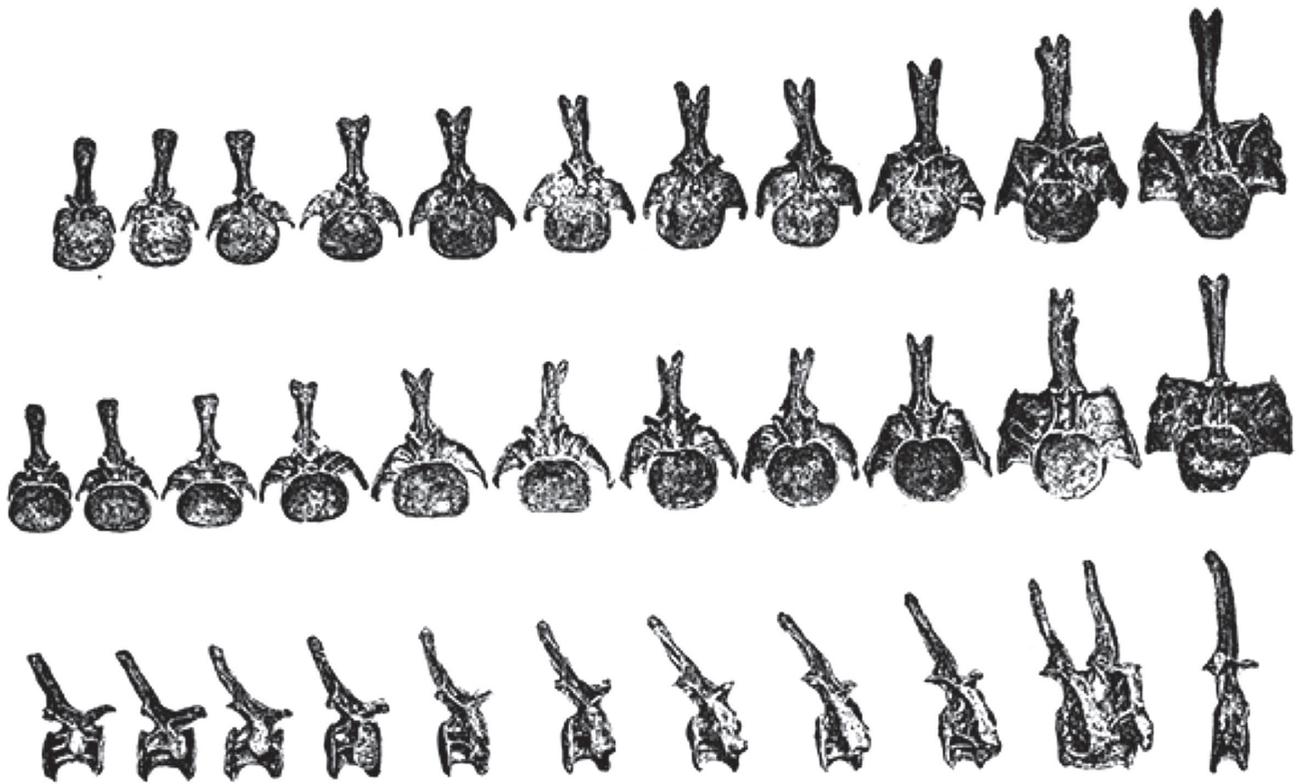


FIGURE 10. *Diplodocus* caudal vertebrae (Hatcher, 1901) Top: posterior, middle: anterior, bottom: right side, From the right, the first caudal vertebra, and the fused second and third caudal vertebrae.

processes. Since the spinous process of the sacral vertebrae is the highest among the vertebrae of the trunk, it is a structure that suspends the spinal column with elastic ligaments using it as a base point.

In addition to the nuchal ligament, ligaments rich in elastic fibers are widely distributed throughout the bodies of vertebrates. In the limb, suspensory or springing ligaments of horses are well known, and absorb the impact when the horse touches the ground, supplementing the kick force. In the trunk, the ligamentum flavum (*Ligg. flava*), which stretches between the vertebral arches, maintains the elasticity of the spinal column and aids dorsoventral movements. In large mammals, the subcutaneous elastic ligaments of the limbs of elephants are also locomotion aids in the limbs (Gambaryan, 1974). Therefore, it would not be surprising if the elastic ligaments stretched from the neck to the trunk as the size and weight increased.

MORPHOLOGY AND FUNCTION OF THE CAUDAL VERTEBRAE

The tips of the spinous processes (*Processus spinosus*) of the caudal vertebrae (*Vertebrae caudales*) of *Diplodocus* are bifurcated from the first to the ninth vertebrae (Hatcher 1901). The chevron bones are Y-shaped and extend long ventrally from between the second and third vertebrae to between the

eleventh and twelfth vertebrae. From the twelfth vertebra, the ventral end extends long anteroposteriorly, forming an inverted T shape when viewed from the side. This shape continues up to the sixteenth vertebra, and from the seventeenth vertebra, the vertical bar of the T shape disappears. The chevron bones remain long anteroposteriorly like skis up to the 28th caudal vertebra, which is the origin of the genus name *Diplodocus*.

From the first to the third caudal vertebrae, the transverse processes (*Processus transversus*) are expanded to make a quadrilateral broader than the surface of the vertebral body transversally. From the fourth onwards, the dorsolateral corners become rounded, and the area gradually decreases. In the lateral view, the tips of the transverse processes are long dorsoventrally and inclined in the same direction as the spinous processes (Figure 10). This type of transverse process is unique and has no other examples. In human anatomy, there is a small muscle called the intertransverse muscle (*Mm. intertransversarii*) in the cervical and lumbar vertebrae between the transverse processes. The quadratus lumborum muscle (*M. quadratus lumborum*) may be attached to the costal processes of the lumbar vertebrae. So, did *Diplodocus* also have the intertransverse and quadratus lumborum muscles? The function of these muscles is to assist in the lateral bending of the spine.

Biomechanically, the long tail extending from the sacrococcygeal joint is a cantilever beam. The supraspinous

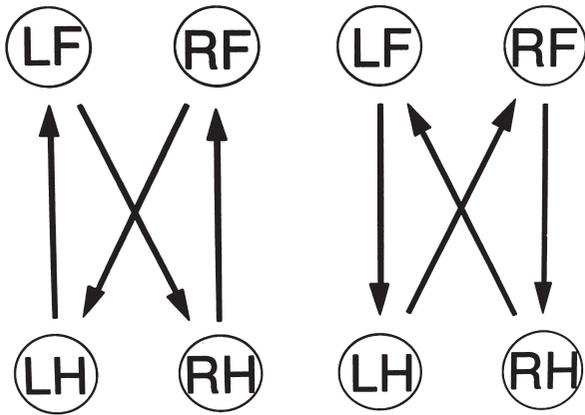


FIGURE 11. Comparison of symmetrical gaits. Left: diagonal sequence, right: lateral sequence. See main text for explanation.

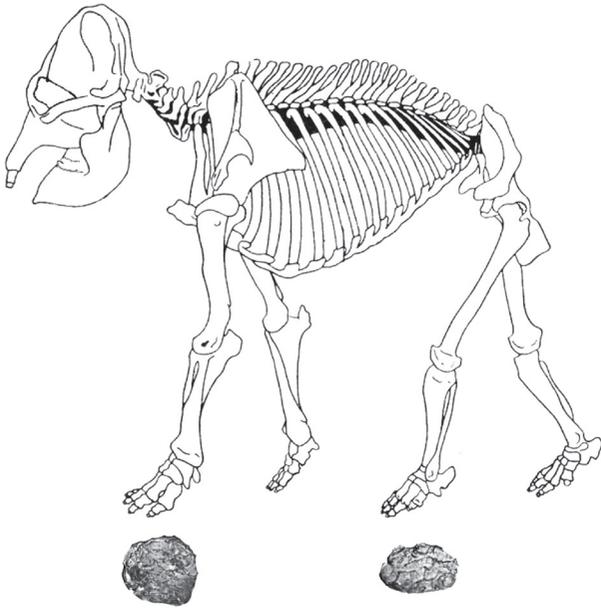


FIGURE 12. Elephant load distribution and sole shape comparison of manus and pes (Gambaryan, 1974 modified).

ligament (Lig. supraspinale), which acts as a tension brace supporting the cantilever beam, passes through a V-shaped groove at the tip of the spinous process. Compared to the spinous processes of the cervical and dorsal vertebrae, the caudal vertebrae are small, and the grooves in the spinous processes are narrow. The size of the spinous processes is smaller in the more posterior ones. The transverse processes are widest at the base of the long tail and become narrower in the more posterior ones. In the lateral view, the inclination of the tip of the transverse process and the direction in which the spinous process extends also match. It originates from a high position at the sacral apex (Apex ossis sacri), and runs caudoventrally and medially, resembling a wire running from the top of a shelf attached to a wall to the edge of the shelf. From the above points, it is thought that an elastic ligament similar to the supraspinous ligament was

stretched between the transverse processes, acting as a tension brace supporting the tail.

The caudal vertebrae of *Apatosaurus*, closely related to *Diplodocus*, are illustrated up to the 82nd vertebra (Gilmore 1936). Each caudal vertebra is long compared to its transverse diameter, contributing to the length of the tail. The neural spines are short compared to the height of the vertebral body, and there are no hemal spines. In general, the tail vertebrae of fish have long neural spines and hemal spines, and the epaxial and hypaxial muscles attached to them swing the tail from side to side to swim. On the other hand, the transverse processes of whales and sea cows extend horizontally, and they swing their tails up and down to swim. The facts seen in the tail vertebrae of living species indicate that the length of the process indicates the amount of muscle, and the type of process indicates the direction of movement. There are no extant species with tail vertebrae as long and slender as *Diplodocus*, but the short spinous processes of *Diplodocus* suggest that they did not move their long tail much. There are no hemal spines on the ventral side of the vertebrae, and the fact that the chevron bones are long anteroposteriorly is similar to the fact that the cervical ribs of the cervical vertebrae extend long in the direction of the cervical vertebrae's longitudinal axis. The thin bones running along the ventral sides of these vertebral bodies along their long axes are thought to be the attachment points of ligaments. Ligaments have a high resistance to tension and often function as a tension brace. The long neck and tail of *Diplodocus* would have flexed with every step, and the ventral longitudinal ligaments would have prevented it from bouncing upwards in recoil. This would suggest that they acted like a bowstring, helping to lift the 20-ton body.

These findings suggest that the supraspinatus ligament, which runs close to the dorsal side of the dorsal vertebrae in sauropods, consisted of elastic fibers as if the nuchal ligament of mammals. Therefore, it is speculated that the vertebral column itself, from the sacral vertebrae through the dorsal vertebrae to the cervical vertebrae and including the caudal vertebrae, was an elastic body.

FOSSIL FOOTPRINTS AND GAIT

Symmetrical gaits of quadrupeds can be broadly divided into two types (Sukhanov, 1974; Gambaryan, 1974). Figure 11 shows the fore, hind, left and right feet viewed from above, with arrows indicating the order of contact. Gambaryan (1974) defines it as follows. "1) symmetrical-diagonal, when movement of a forelimb is followed by that of the contralateral hind limb; 2) symmetrical-lateral, when movement of a forelimb is followed by that of the ipsilateral hind limb." Sukhanov (1974) similarly states as follows. "For example, in the tables presented by Muybridge, an elephant can be found using a *symmetrical-diagonal* sequence, a baboon using a *symmetrical-lateral*."

In many quadrupedal mammals, the forelimbs support the fore half of the body and head, and the hind limbs support the hind half of the body and tail, so the load on the forelimbs is

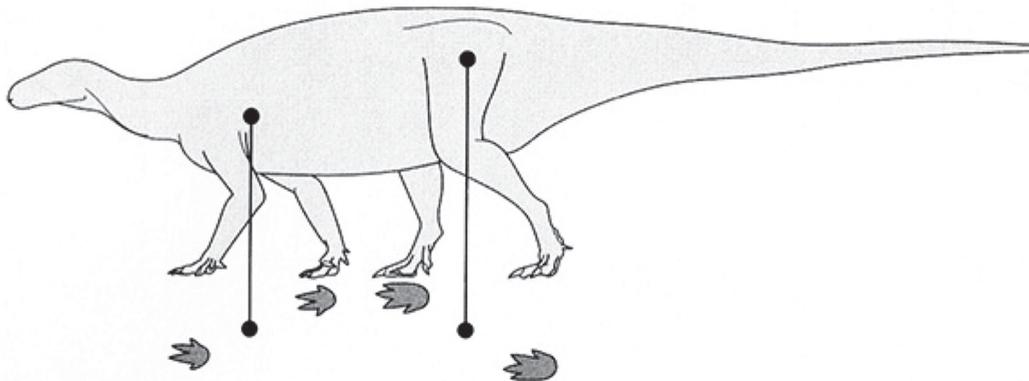


FIGURE 13. Estimation of trunk length (glenoacetabular length) from footprint fossils of quadrupedal dinosaurs (Inuzuka, 2006).

greater and the legs are thicker. In the case of elephants, the ratio is approximately 6:4 (Figure 12). The shape of the sole of the elephant's foot is narrow and elliptical, and the area is narrower than that of the palm, while the palm is almost circular. Therefore, the plantar area can be regarded as corresponding to the load distribution. The anterior-posterior load distribution of *Diplodocus* has been calculated as 22:78 (Alexander, 1989).

On the other hand, in the quadrupedal dinosaurs, the trunk length can be estimated from the fossil footprints (Figure 13). The midpoint of the line connecting the left and right fore footprints is regarded as the position of the glenoid fossa of the scapula, which is the fulcrum of the pendulum of the forelimb. Similarly, the midpoint of the line connecting the hind footprints is regarded as the position of the acetabulum of the hip joint. So, the line segment connecting is the glenoacetabular length, which approximates the trunk length. If the trunk length is proportionally divided by the load distribution of the fore and hind legs, the approximate position of the center of gravity of the body can be obtained.

"Throughout the great group of mammals, we find there are two main classes of animals: those where the centre of gravity is nearer to the forefeet, and those where it is nearer to the hind feet. The horse is an example of the first type (Gray, 1953)." "...the center of gravity of Mammals is originally located substantially at the level of the central region or anticline of the spine, from where, for dynamic reasons, it tends to move forward in runners, for example Ungulates or Canids, with a predominant foreleg, and backward on the contrary in jumpers, arboreal animals, bipeds (Lessertisseur and Saban, 1967)."

When walking by moving one leg at a time, the triangle formed by the grounding points of the three supporting legs is called the support triangle (Figure 14; Gray, 1953). If the center of gravity of the body is inside the triangle, it will be stable, otherwise it will fall down outside. The lizard in Fig. 14 can tell whether it is a diagonal sequence or a lateral sequence, depending on which side of hind leg it puts out after the right fore leg. In the lateral sequence of right side, the centroid is behind the support triangle, so the right hind leg cannot be lifted and cannot advance. Figure 15 shows a trackway of sauropods

(Lockley & Gillette, 1989) superimposed with support triangles. As mentioned above, the glenoacetabular length was obtained, and the position of the center of gravity was set to around the posterior 1/5 based on the weight distribution of *Diplodocus*. After grounding of the right hind foot, and then the left or right fore foot touches the ground next, which determines the diagonal sequence or the lateral sequence. In the lateral sequence on the right, the position of the center of gravity is just on the anterior margin of the support triangle, so we can see that it is about to fall forward and that it can walk with the help of this gravity. That is to say, it is possible that most sauropods had their center of gravity near the hind limbs and walked in a lateral sequence, just like primates.

ESTIMATION OF GAIT

In order to estimate the gait of extinct animals, it is necessary to decipher the direct evidence, fossil footprints, making full use of the rules of ichnology and kinesiology based on living animals. The gaits of CG sauropods seen in television and movies appear to have already been restored using the largest terrestrial mammals, especially the Asiatic elephant, as a model. However, the above consideration indicates that sauropods with the center of gravity on the lumbar part cannot walk in the diagonal sequence.

So, did sauropods, many times heavier than elephants, walk in the lateral sequence in the same way as arboreal primates, whose center of gravity is at the lumbar part? The problem with this gait lies in the fact that the timing of contact with the ground of each foot is different. As mentioned above, the larger the body, the greater the need for gravity help and muscle force saving. In order to walk using the elasticity of the very long spinal column, it must be more efficient to make the number of contact ground two times rather than four times. Among lateral sequence gaits, trot is a gait that the timing of contact ground of diagonally positioned feet coincides.

All symmetrical gaits are determined by the interrelationship between the rhythm of limb work and the rhythm of locomotion (Sukhanov, 1974; Gambaryan, 1974). "The rhythm of limb work

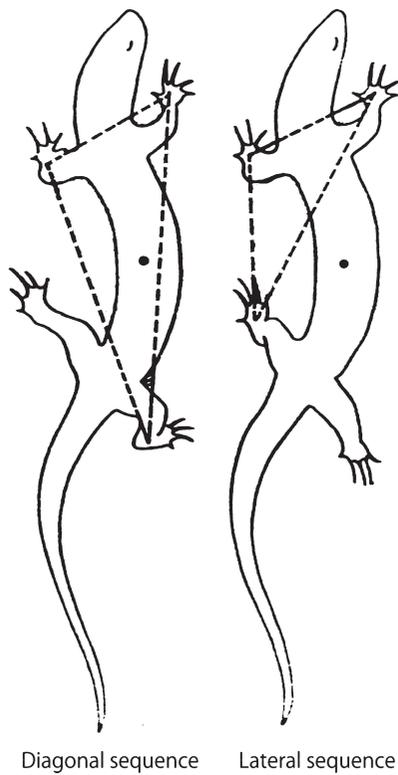


FIGURE 14. Relationship between support triangle and symmetrical gait (Gambaryan, 1974 modified). See main text for explanation.

is defined as the relation between the phase of support and the period of free movement of each limb, in other words, in the graphic form, the ratio between the hatched and nonhatched areas of the bar corresponding to a given limb. The rhythm of locomotion characterizes the temporal relationships in the joint work of all four limbs. It is defined as the ratio of the time intervals between the moments at which the feet land consecutively (Gambaryan, 1974)."

The slowest gait for large animals is when the rhythm of limb work is 7:1 and the rhythm of locomotion is 4:0. In order to estimate the gait pattern of *Desmostylus*, the author has collected gait data of mammals walking in various grounding patterns with a video camera (Inuzuka, 1996). Here, we adopted the gait of an African elephant that satisfies this condition as a model, and created a gait diagram based on this film printed every 1/20th of a second (Figure 16).

This data can be said to be a very slow trot corresponding to 8) in Fig. 9 of Gambaryan (1974). In the slow trot the diagonal feet step at the same time and so it makes the most efficient use of the elasticity of the spine. Since it is the slowest gait, the inverted pendulum model is applicable and the pendulum isochronous formula can be used. This formula is expressed as follows, where T is the period, l is the length of the pendulum, and g is the gravitational acceleration.

$$T \approx 2\pi \sqrt{l/g}$$

In other words, the walking period is proportional to the

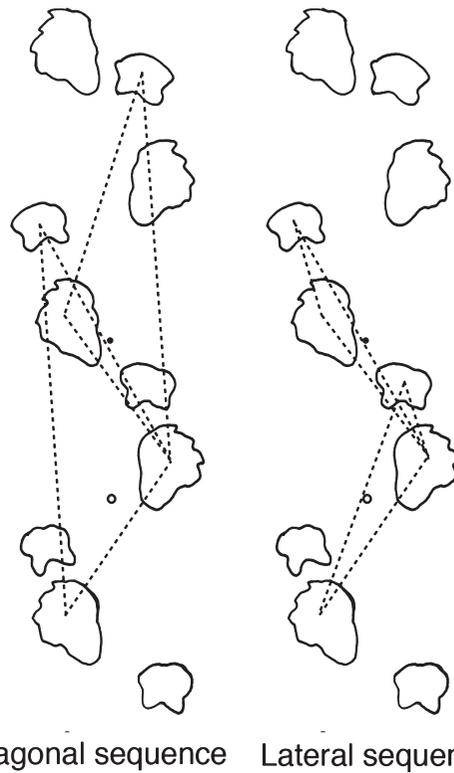


FIGURE 15. Relationship between centroid, support triangle and gaits on the sauropod trackway (Lockley and Gillette, 1989 modified). See main text for explanation.

square root of the pendulum length. Substituting the African elephant's walking cycle of 3.5 seconds into this equation, the length of the pendulum is approximately 3m. Hind limb length of 3 m is included in the range of the African elephants. Assuming that the femur length is 1m, which is the same as that of an Asiatic elephant, the femur length of *Diplodocus* is about 1.5m (Hatcher, 1901), so the hind limb length is about 4.5m. Substituting this value into the above formula gives a walking cycle of about 4.2 seconds (Figure 17).

RECONSTRUCTION AND EVOLUTION OF SAUROPODS

Hallett's life restoration of *Mamenchisaurus* (Czerkas and Olson 1987) depicts the tail as Abel had proposed, with the tip hanging down softly as if it were used as a whip. However, when balancing the heavy head and torso, the length of the tail is essential for the moment, so a stiffer tail that is less likely to deform is required. Gilmore (1936) suggested that the base of the tail would rise up once, based on the wedge-shaped opening between the sacrum and caudal vertebrae. However, the lumbosacral joint between the lumbar vertebrae and the sacrum in humans has a wedge-shaped intervertebral disc that opens forward, so the surfaces of the head (Caput vertebrae) of the first caudal vertebra and the vertebral socket (Fovea vertebrae) of the sacrum are not necessarily parallel.

The intervertebral disks between the sacrococcygeal joints

were probably replaced by thick elastic ligaments that helped to keep the entire caudal vertebrae in a high position, just like the entire presacral vertebrae. The dorsal and ventral surfaces of the caudal vertebrae were stretched by strong anterior (Lig. longitudinale ventrale) and posterior longitudinal ligaments (Lig. longitudinale dorsale), making them less flexible and more elastic, like a pole vaulting pole. The long transverse crests on the anterior and posterior sides of the chevron bones are also thought to have developed as attachment points for these ligaments (Figure 18).

The morphology of animals with the above mode of locomotion can be considered as follows. First, it must stand stably when stationary. Due to the increased size, the trunk length between the fore and hind limbs was relatively narrow, and the head and trunk were in balance with the longer tail with the lumbar part as the fulcrum. This explains why amphibians and mammals do not have sauropod-like body shapes, why the fore footprints are much smaller than the hind footprints, and why the tails were always suspended in the air rather than dragging. Also, in order to support a weight of 20 tons, the limbs should have been of inferior-type and the joints of the elbows and knees should have been fully extended to reduce the load on the muscles.

Locomotion is the movement of the center of gravity of the body (Inuzuka, 2022). Dinosaurs and mammals with inferior-type limbs have a relatively high centroid and excellent mobility compared to other reptiles with lateral-type limbs. When walking, with a trunk that is relatively short fore-and-aft, the long neck increases the moment, and this downward rotational force should help the forward movement. Considering the head and neck as a cantilever beam, the head must be small for the convenience of support, and the neck must be long due to the moment of force.

When walking, the center of gravity of the body must be positioned in front of the support triangle. In order to utilize most efficiently the elasticity of the supraspinatus ligament, which runs longitudinally throughout the dorsal side of the spine, the slow trot gait which requires only two contact ground per cycle is suitable. In slow trot, diagonal feet ground at the same time, so the support triangle is a diagonal line connecting the contact points of the feet. If the body's centroid is in front of this line, the body will fall forward with the help of gravity, and it will be able to move forward. Also, taking a step forward, the hip joint lowers slightly from its highest position. This drop would bend the elastic spine, and the repulsive force would lift the body more or less to help the next step.

In this way, a body that is extraordinarily long fore-and-aft, a relatively short trunk, and that balances craniocaudally at the lumbar position can be considered. Since a strong elastic ligament runs throughout the dorsal side of the vertebral column, there should be no significant bending of the dorsoventral or bilateral direction in the basic posture, and the dorsoventral vibration should have been limited to the gait cycle.

Consequently, the evolution of the body shape and gait of sauropods can be estimated as follows. Originally, bipedal

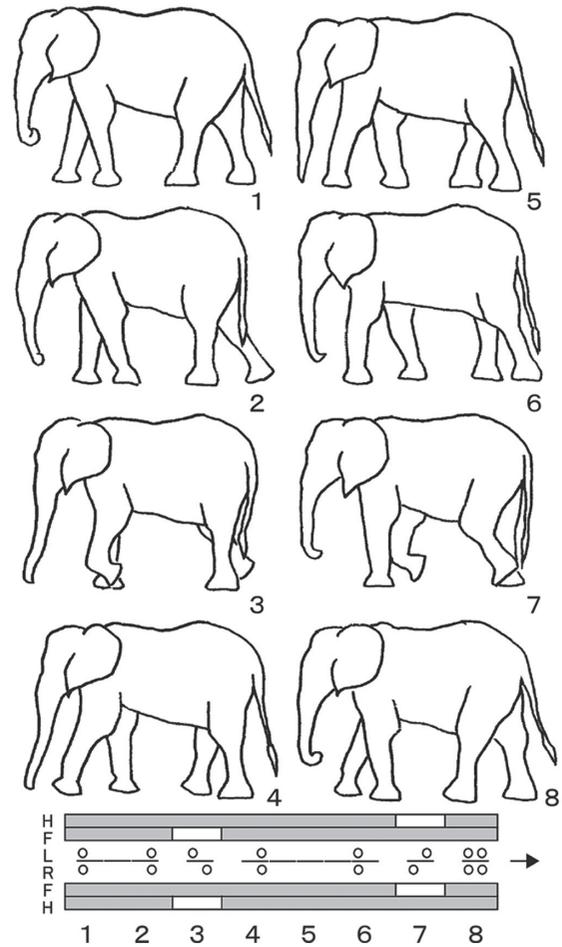


FIGURE 16. Very slow trot gait chart of an African elephant.

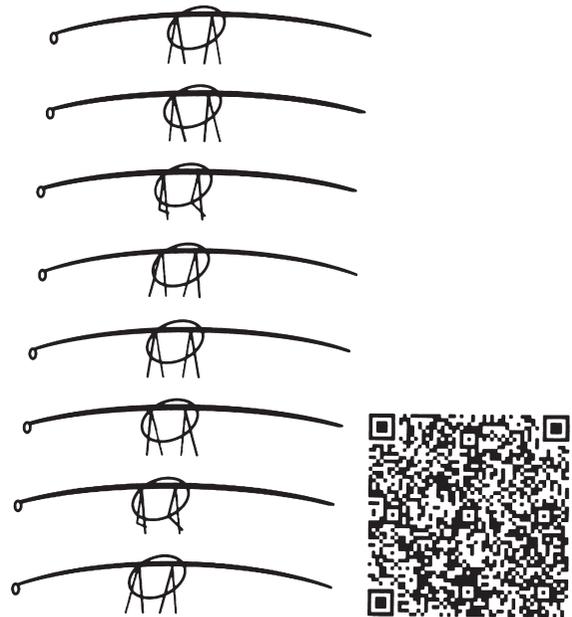


FIGURE 17. QR code for animation of *Diplodocus* slow trot (Inuzuka, 2024).



FIGURE 18. Reconstructed skeleton of *Diplodocus* (modified from Inuzuka and Hirono, 2023).

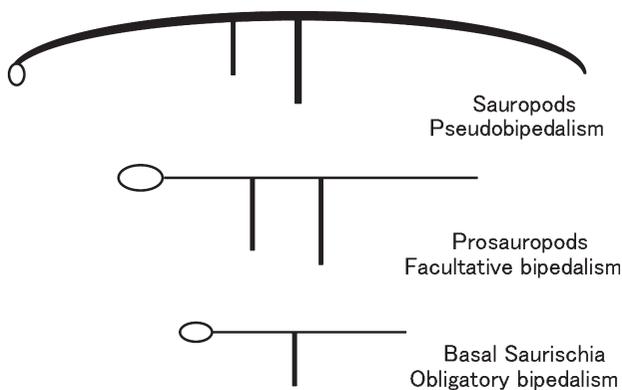


FIGURE 19. Evolutionary diagram of sauropod body shape and mode of locomotion.

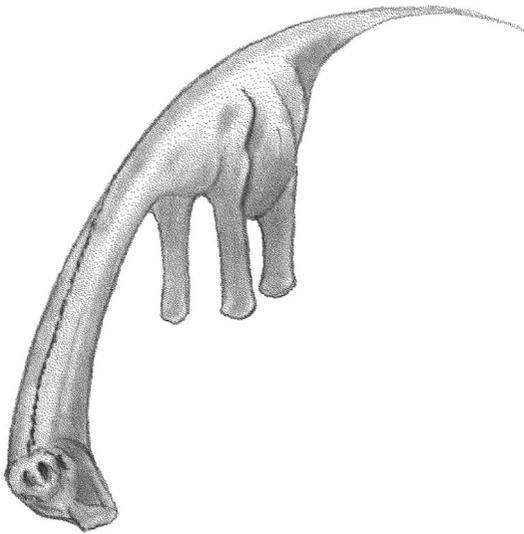


FIGURE 20. Life restoration of *Diplodocus* (modified from Inuzuka and Hirono, 2023).

dinosaurs had their center of gravity on their lumbar part and balanced on their head, trunk and caudal part. Secondary quadrupedal prosauropods walked facultative bipedally. As the size increases, the trunk length becomes relatively shorter. In sauropod fossil footprints, the hind footprints are four times larger than the fore ones, so the body's centroid is close to the lumbar, and it must not have been able to walk in a diagonal

sequence like an ordinary mammal. Sauropods, on the other hand, would have had unusually long necks and tails relative to their bodies, with thick elastic ligaments running along the dorsal side of the spine. The largest organ in the body must have been the main locomotor system. After all, although sauropods are quadrupedal, they can be said to have been peculiar, substantially bipedal, pseudobipedal animals that used a far longer vertebral column as their main locomotor system (Figure 19).

Sauropods evolved a variety of body shapes from the elongated basic type like *Diplodocus*. *Brachiosaurus*, which grew large by erecting its neck like a giraffe, was exceptional among dinosaurs in that its forelimbs were longer than its hind limbs, and its center of gravity would have been in the chest like most large mammals (Henderson, 2006). Therefore, a long tail to provide balance was unnecessary, and it would have been shorter than its ancestors. Elevating the head by about 10 m would have required high blood pressure (Fastovsky and Weishampel, 1996), but the skin on the limbs would have been tight like a supporter, and the blood vessels in the head would have had a more efficient wonder net than those of a giraffe. Its gait is thought to have been diagonal sequence like that of many mammals.

Furthermore, in Macronaria (Benton, 2015) including *Brachiosaurus*, the large external nostrils at the end of the neck that extended upward like a chimney would have allowed breath air that was warmer than the outside temperature to be expelled due to pseudohomeothermy. Reptiles, which do not have a muscular diaphragm, would have needed an alternative ventilation system. *Camarasaurus*, known for its buried posture with its neck tilted back, is a member of the same Macronaria as *Brachiosaurus*. If *Brachiosaurus* is likened to a giraffe, then it may have been similar to an okapi. If so, it may have held its neck upright in life.

On the other hand, in the skull of *Diplodocus*, the narial opening (Apertura nasi ossea) is located as far back as the orbits (Figure 20). If the normal posture of tilting the long neck was correct, it would not be surprising if the breathed air, which is warmer than the outside air, was pushed back so that it could be expelled from a slightly higher position. Also, if the head had been shaken up and down with each step, this would have helped with ventilation. Some ecological restorations of sauropods show them standing on their hind legs with their manus claws dug into tree trunks. Since the body's center of gravity is at the

hips, this is mechanically possible, but in reality, it is unlikely to happen. If it were easy to lift the head, there would have been no need to move the narial opening back to eye position.

The position and size of the orbits in the skull of *Diplodocus* are also unique. The orbits are situated posterior to the lower temporal fenestra. This is the same reason why horses have long faces, as their eyes are positioned higher than the grass to keep watch for predators while they are feeding. The skull is small relative to the body, but the orbits are large and round compared to those of other dinosaurs. Elephants are the largest land mammals, and even a 2-ton Asiatic elephant will eat 100kg of grass in 18 hours a day. As dinosaurs are reptiles, their metabolic rate is thought to be around 10% of that of mammals, but with a weight of 20 tonnes, they would still have been eating after twilight. The size of the orbits suggests that they needed to keep watch for predators even at twilight.

Titanosauria, which grew even larger, had a small stride and wide-gauge limbs with wide contact points on both sides (Wilson and Carrano, 1999). Lateral limb-type giant tortoises and monitor lizards are stable and slow-footed. Inferior limb-type mammals and dinosaurs have a high center of gravity, which makes them more mobile at the cost of being more prone to tipping over. In fact, it could be said that they moved with the help of gravity. When I first saw the inwardly curved femur of a "*Titanosaurus*", I couldn't believe it, but despite being an inferior limb-type, it appears that it was designed for lateral stability. It's like when a large crane and ladder trucks extend support legs from the four corners of the vehicle when in use. Although their stride was short and they could not walk fast, they must have gained lateral stability. They must have been able to swing their long necks from side to side to eat leaves from a wide range of trees. It follows that sauropods had to wait until the appearance of the titanosaur body shape before they could completely utilize their long necks for feeding.

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