

ARMOR OF *STEGOSAURUS STENOPS*, AND THE TAPHONOMIC HISTORY OF A NEW SPECIMEN FROM GARDEN PARK, COLORADO

KENNETH CARPENTER

*Department of Earth Sciences, Denver Museum of Natural History,
2001 Colorado Blvd., Denver, CO 80205, USA*

(Received in final form 4 April 1997)

A new specimen of *Stegosaurus stenops* from Garden Park, Colorado, provides new information about arrangement of plates on the back, and about other body armor. The taphonomic context of this specimen indicates that the animal may have died during a prolonged drought, possibly due to illness caused by infections in the tail. The carcass was eventually buried by crevasse splays following the break of the drought by heavy rains.

The skeleton is mostly articulated and preserves the plates in alternating fashion separated medially by matrix. This evidence is interpreted as indicating that the plates of *Stegosaurus* were in two alternating rows separated from the midline. Throat ossicles were found articulated and show a rosette pattern.

The data obtained from this specimen was incorporated into the remounting of another *Stegosaurus stenops* skeleton found previously about 300 m away. The angle of the articular face of the last sacral and the wedge shaped first caudal indicate that the tail of *Stegosaurus* was carried in the air. This position is maintained without the use of muscles by interspinous and supraspinous ligaments, and the overlap of long segments of vertebrae by the caudal plates. With the tail so high in the air, the terminal spikes could not have projected upwards. A groove on the underside of the spike base and the natural position of the spikes in the new *Stegosaurus* skeleton indicate that the spikes projected posterolaterally.

Keywords: Armor; Plate arrangement; Throat ossicles

INTRODUCTION

The armor plated dinosaur, *Stegosaurus*, was named by O.C. Marsh in 1877 for material collected from the Morrison Formation near the town of Morrison, Colorado. Since then, nine species have been named, but only

three are recognized as valid by Galton (1990), *Stegosaurus armatus*, *S. stenops* and *S. longispinus*. All species of *Stegosaurus* are characterized by plates and spikes on the neck, back and tail. The arrangement of this armor is controversial because so few specimens have been found with armor preserved *in situ*. Much new light on the "plate problem" has been shed in recent years with the discovery of new *Stegosaurus stenops* specimens. These include the Bollan specimen at the Museum of Western Colorado (Bollan, 1991), the Utah Field House Museum of Natural History (UFHMNH; Bilbey, personal communication), and the Small specimen of the Denver Museum of Natural History (DMNH). Of these, the Small specimen is the most complete and provides the most new information about *Stegosaurus*.

The chance discovery of the skeleton occurred when Bryan Small, of the Denver Museum of Natural History, thrust the pick-end of his rock hammer into the bank and a cervical vertebra rolled out. A thin veneer of alluvium and colluvium hid the bones and no trace was seen on the surface or as bone debris on the sloping gully wall (Carpenter, this volume, for locality and biostratigraphic data). Excavation revealed an almost complete *Stegosaurus stenops* skeleton with the plates preserved *in situ*. This skeleton is one of three almost complete *Stegosaurus stenops* skeletons from the Garden Park area. A comparative study of the three specimens, which come from within 10 m stratigraphically each other, is in progress and should provide evidence for the range of variation and sexual dimorphism in this species of *Stegosaurus*.

TAPHONOMY OF THE SMALL STEGOSAURUS

The specimen, DMNH 2818, was found lying on its back, with the skull upside down (Figs. 1 and 2). The tail is on its left side with its plates preserved mostly in their natural position. The throat ossicles are offset to one side of the skull, but retain their position relative to one another. This indicates that the ossicles were still bound by connective tissue at the time of their burial. In fact, the general articulated condition of the skeleton suggests that a considerable amount of ligament still bound the skeleton at the time of burial.

The skeleton lay in a lenticular gray lacustrine mudstone containing a considerable amount of disarticulated vertebrate material (see Carpenter, this volume). The mudstone is carbon rich, some of which is in the form of fusain or charcoal. Some of the fusain is large, 7 cm or more in diameter, and demonstrates that one or more forest fires had swept through the area.

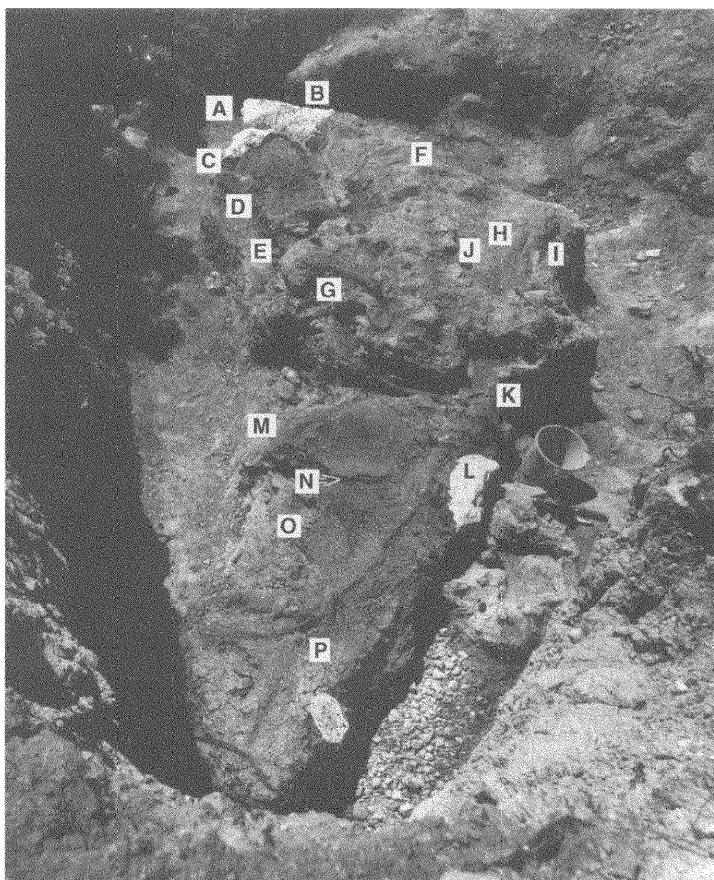


FIGURE 1 The Small *Stegosaurus stenops* (DMNH 2818) from Garden Park, Colorado. A, area where the skull block was removed (skull, axis, anterior cervical plates, and gular ossicles); B, cervicals and point of discovery; C, D, E, dorsal plates; F, dorsal vertebrae (right ribs to the left); G, right ilium; H, left ilium; I, left femur; J, area where possible keeled scutes were seen; K, break in tail (base of large first caudal or sacro-caudal plate visible below letter G); L, caudals (sauropod vertebrae in cluster to lower right); M, second caudal plate; N, third caudal plate separated from plate M by matrix at arrow; O, fourth caudal plate; P, diverging spikes. Photograph courtesy of Photography Department, Denver Museum of Natural History.

The lack of evidence for a nearby volcano suggests that it was not the cause of the fire. Instead, the fire most probably was the result of dry thunderstorms that sometimes accompany droughts today. Evidence for droughts in the Garden Park area during the Late Jurassic has been presented elsewhere (Demko, this volume; Evanoff and Carpenter, this volume).

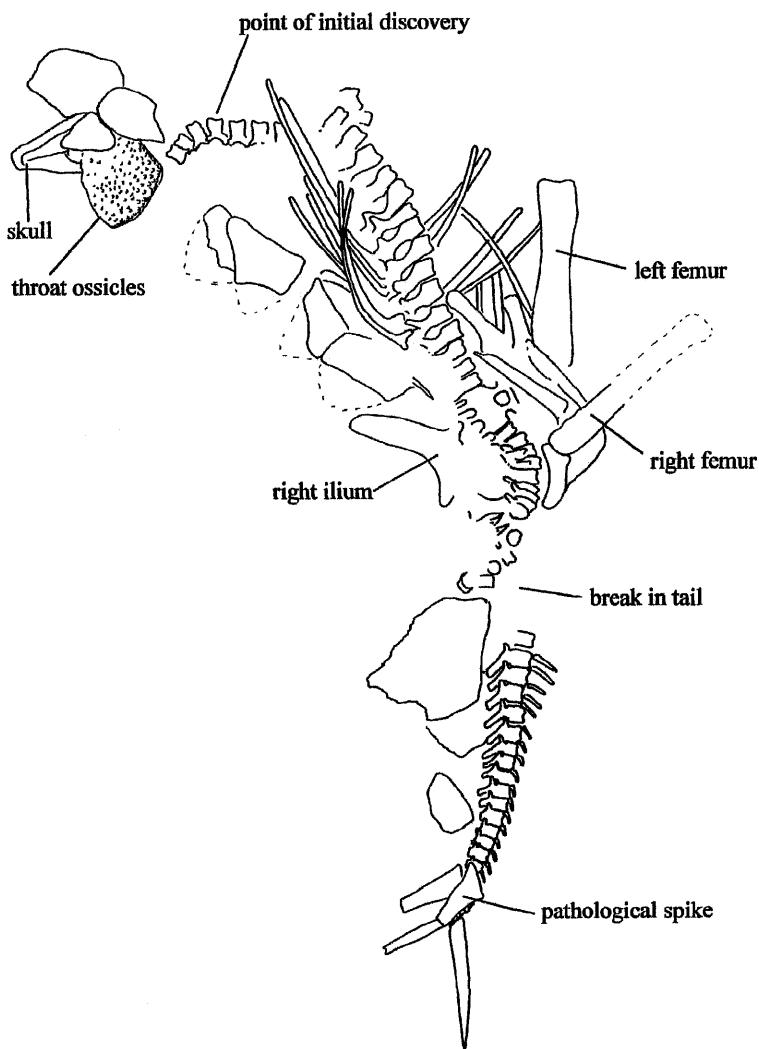


FIGURE 2 Quarry map of the Small *Stegosaurus stenops* specimen. Edges of dorsal plates were damaged during excavation. Distal end of right femur, most of a tibia, and most of one pes were found nearby buried in Subrecent sediments.

The articulated condition of the skeleton is consistent with the interpretation that mortality was drought related. As Hillman and Hillman (1977) have observed in East Africa, carcass production during droughts is so great that scavengers are unable to keep pace. As a result, many carcasses are left untouched. The nearly untouched condition of the Small *Stegosaurus*

also supports drought fatality (Carpenter, 1987a). The only evidence of scavenging are tooth marks on a metatarsal and the apparent absence of forelimbs (preparation is not complete as of this writing).

The *Stegosaurus* apparently died in a small pond based on the sediments, although whether or not there was any water present is unknown. Behrensmeyer and Boaz (1980) and Cornfield (1973) have noted that large ungulates seek refuge in swamps, ponds and rivers during droughts to avoid heat stress. Nevertheless, these animals die, not because of the lack of drinking water, but because of malnutrition and associated problems (see Evanoff and Carpenter, this volume; and Carpenter, 1987a for additional discussion). The cause of mortality in the *Stegosaurus* may be due to malnutrition or to the animal being in a weakened condition due to illness. As Hillman and Hillman (1977) and Foster (1965) have noted, an individual's fitness at the time of the drought is the key factor in its survivability. That the *Stegosaurus* was not well during the drought is evidenced by a pathological tail spike.

The first right spike is missing about half its length and the surface has a "melted candle wax" appearance (Fig. 3). The bone is very flattened, thinning to a feather edge at the broken end. The spike was evidently broken during life and infection, osteomyelitis, spread into the bone (McWhinney, Rothchild and Carpenter, in preparation). A considerable amount of



FIGURE 3 Tail spikes of DMNH 2818 as preserved. Arrow points to a pathological spike.

internal bone loss occurred as evidenced by the thinness of the spike. A normal first spike of an animal about the same size (DMNH 1438), is 6.5 cm thick (dorsoventrally). This compares with 1.5 cm in total thickness for the pathological spike. Both spikes were measured about 8 cm above the base. Liquification and loss of bony matrix is common with the loss of blood supply to the bone (Rothchild and Martin, 1993).

After its death, the *Stegosaurus* lay on its left side decaying and bloating with decomposition gas. The pressure may have caused the legs to splay apart, pushing the animal partially onto its back, as apparently happened to dead ankylosaurs (Carpenter, 1984). This action bent the plates on the body back so they were partially under the skeleton. The rotation of the body apparently caused the base of the tail to twist apart because the tail, lying in a stable position, resisted the rotation of the body. Several of the vertebrae are jumbled, indicating that the muscle tissue was in an advanced state of decay, but that ligaments still connected the vertebrae. These ligaments prevented the tail from twisting off cleanly. Body gases vented soon after, possibly as a result of the twisting of the tail or by scavenging of the abdominal cavity. In any case, the body collapsed upon itself, with the right leg laying across the pelvis.

It is not known how long afterwards that the drought was broken. It is possible, based on observations in Africa (e.g., Hillman and Hillman, 1977) that mummification of the carcass occurred. When the drought finally broke a nearby river flooded and spilled a crevasse splay towards the *Stegosaurus* carcass. The carcass apparently trapped most of the sand on one side of the body, sheltering the pond from infill. Evidence for this is seen in a thin wedge of fine sand covering some of the bones on the animal's left side (right side of Fig. 2). A thin layer of dark mudstone (~15 cm) separates this splay deposit from another, thicker splay deposit over much of the skeleton. The amount of time separating the two crevasse splay events is unknown, but may represent the next flood during the same rainy season. This second, as well as successive splays completely buried the skeleton to a depth of at least 2 m. Identification of these sandstones as crevasse splay deposits is based upon the cyclicity of the thin sandstone lenses, the presence of climbing ripples and rip-up clasts internally, and finally, the progressive thickening of the sandstones above the initial splay as successive crevasse events prograded into the pond.

As the carcass was buried deeper with each crevasse event, decomposition continued using up the available oxygen, especially from the pore water in the sediments. The decomposition process set up a local alkaline environment due to the production of ammonia and other bases (Berner, 1968;

Carpenter, 1987b). This high pH environment caused the precipitation of calcium ions as calcium fatty acid salts (adipocere). Later this adipocere was converted to calcium carbonate by loss of the hydrocarbons. The calcium as a carbonate and fibrous calcite formed a rind 5–30 mm or more thick around the skeleton. This early diagenetic rind partially blocked mineralized ground water from the skeleton. The result is that permineralization of the bones is poor and much of the bone is punky except where splay sands are in contact with the bone.

At some point during the Sub-Recent or Pleistocene erosion of the gully where the *Stegosaurus* skeleton was found, the hind appendicular elements were exposed. Some of these eroded out in blocks of matrix and rolled into the gully. There, they were buried by sand and were found later during our excavation. It is possible that loss of the forelimbs is due to the Sub-Recent erosion of the gully, but the presence of a complete vertebral column and no pectoral girdles is puzzling unless a scavenger removed the limbs.

THE “PLATE PROBLEM”

Ever since Marsh (1877) first described *Stegosaurus*, the arrangement of the plates on the body has been a problem. An illustrated history of plate arrangement was presented by Gilmore (1914) and repeated by Czerkas (1987). Marsh placed great emphasis on the armor as a driving factor in the evolution of *Stegosaurus*, stating that the “high specialization [of the skeleton] was evidently acquired gradually as the armor itself developed” (Marsh, 1891, p. 180). One species, *Stegosaurus duplex*, Marsh (1887) suggested may not have had any armor, but whether he considered this the ancestral condition or not, he did not say.

Marsh (1877) first suggested that the dermal plates were supported in part by the tall neural spines and that they lay on the body forming a turtle-like shell. Perhaps this turtle analogy is why he also suggested that *Stegosaurus* was aquatic. On land, *Stegosaurus* must have been bipedal because the forelimbs were shorter than the hind (Marsh, 1880; 1881). Later, however, he abandoned this idea, arguing that the large bulk of the animal indicated slow locomotion on four feet (Marsh, 1891; 1896). He still argued that it could stand bipedally, using its tail as a prop.

A few years after Marsh thought of the turtle analogy for *Stegosaurus*, he suggested that the plates stood upright because of the asymmetry of the long axis of the bases (Marsh, 1880). The plates, he suggested, might have been in multiple rows on each side of the back and tail. So placed, they

would protect the animal from attack. Support for a vertical arrangement came a few years later based upon a skeleton from Felch Quarry 1 named *Stegosaurus stenops* (see Evanoff and Carpenter, this volume). Marsh (1887) claimed that the plates were arranged in pairs that increased in size posteriorly from behind the head to the pelvis. From the pelvis rearward, only a single row of plates stood over the expanded neural spines.

A skeletal reconstruction showing the arrangement of the plates was presented by Marsh in 1891. Although only a single row is visible in the figure, it is possible that the plates on the left side hide the mates on the right side (Czerkas, 1987, disagrees with this suggestion). That both spikes of a pair are visible may be due to the divergence of the spikes from the midline. This reconstruction of Marsh's is a composite of different species, despite his having the wonderful skeleton of *Stegosaurus stenops* (USNM 4934). The reconstruction was based upon *Stegosaurus ungulatus*, supplemented by *S. duplex*. Only the pattern of the armor plates of *Stegosaurus stenops* was used, possibly because preparation of the skeleton was not completed at that time.

Lull (1910a) examined the question of plate arrangement while mounting a skeleton of *Stegosaurus armatus* (= *S. ungulatus*). His purpose was to determine whether the plates were in one row or two, paired or alternating, erect or recumbent. He concluded that Marsh was correct about the plates being paired and that they stood erect above the ends of the diapophyses where they attached to the ribs (Lull, 1910a,b). While Marsh (1887) suggested the tail had a single row of plates, Lull concluded instead that these were paired.

A different conclusion was reached by Gilmore (1914, 1915, 1918), who argued for two alternating rows. Gilmore reached this conclusion after completing the preparation of the holotype of *Stegosaurus stenops*. In this, he was in agreement with an unpublished manuscript by Lucas (cited in Gilmore, 1914). This manuscript was apparently the source for Lucas' earlier suggestion that the plates of *Stegosaurus* were in two probably alternating rows (Lucas, 1901). Gilmore further differed from Lull in concluding that the plates were close to the tops of the neural spines rather than over the diapophyses.

Gilmore's conclusion regarding the arrangement of plates in *Stegosaurus* was accepted as evidenced by later mounts of this dinosaur (e.g., American Museum of Natural History – Brown, 1932; Carnegie Museum of Natural History – McIntosh, 1981; previous mount of DMNH 1483).

More recently, Czerkas (1987) reexamined the plate problem, and came up with an ingenious alternative suggestion. He agreed with Gilmore that the

holotype *S. stenops* showed the plates alternating. However, Czerkas departed from Lull (1910a) and Gilmore (1914) by placing the plates in a single row above the neural spines. In this position, the plates leaned alternately towards the left or right, except those on the tail which stood vertically.

The recent discovery of three new *Stegosaurus* specimens shed additional light on the "plate problem." These three, listed in the Introduction, retain plates in life position relative to the vertebral column. In each of these specimens, the plates are alternating, therefore it is doubtful that the alternating plates associated with the holotype *S. stenops* is due to shifting of one plate row relative to the other as suggested by Lull (1910a).

In addition, the UFHMNH and DMNH specimens have matrix separating the plates and their bases of one side from those of the other (e.g., Fig. 1). This separation of the plates indicates that the plate rows were separate and that they did not diverge from a single row above the neural spines. From this evidence, I can only conclude that Gilmore was correct as to plate arrangement.

PLATE FUNCTION

The function of the plates has long been assumed to be defensive (Marsh, 1877; Lull, 1910a; Gilmore, 1914). Colbert (1945) suggested the plates were passive defensive structures to protect the spinal cord. However, this suggestion is doubtful because the tall neural arches and neural spines provide adequate protection for the spinal cord. Furthermore, the plates would leave the more vulnerable gut region exposed to attack. Recumbent plates, either permanent or movable, might offer some protection to the sides of the body, but plate morphology does not support such a position. de Buffrénil *et al.* (1986) note that the mechanical forces acting on recumbent plates would result in asymmetrical attachment scars on each side of the base, and asymmetrical fiber structure within the plate. Such asymmetry is not seen leading de Buffrénil *et al.* to conclude that the plates were oriented vertically.

In addition, if the plates had been movably recumbent, the musculature involved in raising or lowering the plates would have to be oriented perpendicular to the axis of the body. This orientation eliminates the epaxial muscles for consideration, because these muscles are oriented parallel to the body axis so that they can move the vertebral column. The dorsal subcutaneous muscles could not be used to move the plates either because these are also oriented parallel to the body axis in extant vertebrates (e.g., *Caiman* sp., personal observation). For these muscles to have been used to

move the plates would require considerable modification in their orientation, and a massive increase in size from the thin slips they are in extant animals. Also, considerably more rigid origin sites would be needed to move the large plates than the fascia between the skin and epaxial muscles.

In extant crocodiles, the armor is embedded in the skin and it is most likely that the same was true of the plates in *Stegosaurus* (cf. de Buffrénil *et al.*, 1986). Being supported by fibrous skin tissue, the skin could slide over the underlying muscles as the body is turned. If the plates were embedded in the muscles, they would interfere with the epaxial muscles, such as the transversospinalis and latissimus dorsi muscles. Considering how high the rugose attachment scars are on the bases of some plates, the dorsal skin must have been very thick, up to 10 cm for the largest plates. Such skin may have extended down the flanks of the body, offering some protection from predator attack. Among extant ungulates the skin is thickest on the back for protection against predators (personal observation), therefore it is reasonable to assume the same was true of *Stegosaurus*.

The use of the plates for defense was recently challenged by Farlow *et al.* (1976) and de Buffrénil *et al.* (1986). They suggest that the plates may have functioned in thermoregulation by acting as heat dissipaters to regulate internal body temperatures. This was accomplished by controlling blood flow to the plates and by orientation of the body with respect to the wind direction (Farlow *et al.*, 1976). There are, however, several problems with the thermoregulation model. First, the model is developed for *Stegosaurus stenops*, which is only one of several stegosaurs world wide. Second, this species of stegosaur is unusual for having the largest known plates. More common among stegosaurs are smaller plates and spine-like plates (e.g., *Huayangosaurus*, *Tuojiangosaurus* and *Chungkingosaurus*, Dong, 1990; *Kentrosaurus*, Galton, 1982; *Stegosaurus armatus*, Lull, 1910a). Some of these stegosaurs (e.g., *Kentrosaurus*, Hennig, 1925; *Stegosaurus armatus*, Lull, 1910b) had a mass equal to that of *Stegosaurus stenops*, yet had smaller plates. Third, many of these stegosaurs from other countries lived in environments comparable to the Morrison in that the climate was strongly seasonal and semiarid (e.g., Russell *et al.*, 1980). Under such conditions, a need to thermoregulate should be just as necessary and plate size should be closer to that in *S. stenops*. That this does not occur suggests that thermoregulation was not the main function of the plates, although they may have functioned incidentally in that role by virtue of their arrangement as noted by Farlow *et al.* (1976).

The visual prominence of plates in stegosaurs suggests that display may in fact have been more important than de Buffrénil *et al.* (1986) acknowledged.

That these plates are most noticeable in side, rather than front view, implies that lateral display may have been important in stegosaurs, especially *S. stenops*. As Leuthold (1977) has observed, lateral display can be used both in sexual and agonistic encounters. In agonistic encounters an enlarged profile makes the animal appear larger when the body is turned towards the antagonist. Analogous behavior is seen in a house cat arching its back and fluffing its fur.

In *Stegosaurus*, lateral threat display towards another *Stegosaurus* or towards a predator would enhance the size of the individual. The visual effect might have also been embellished by pumping more blood into the plates causing them to blush. This blushing capacity, rather than thermoregulation, may be the reason the plates are well vascularized (contrary to Farlow *et al.*, 1976 and de Buffrénil *et al.*, 1986). In addition, any weapon (e.g., horns, teeth) the animal has is prominently displayed signaling a willingness to use it (Leuthold, 1977). *Stegosaurus* may have slowly waved the tail to draw attention to the spikes.

In sexual encounters, display is often a modified or toned down version of agonistic display (Leuthold, 1977). Weapons may be displayed, but not in a threatening manner. Furthermore, among animals in which the males do the courting, they are often showy and colorful. With *Stegosaurus*, the lateral display with blushing plates might have been a method of mate attraction. The spikes would not be displayed in a threatening manner, possibly by keeping the tail still or turning the tail away.

This alternative hypothesis for plate function does not negate thermoregulation as occurring because the large size of the plate could not help but dump some body heat. Furthermore, the difference between the large plates of *Stegosaurus stenops* and the smaller plates of *Stegosaurus armatus* would aid in quick species recognition.

THE "SPIKE PROBLEM"

Spikes on the end of the *Stegosaurus* tail have been less controversial than the arrangement of plates on the back. Nevertheless, Marsh, Lull and Gilmore have all discussed spikes to some extent. Marsh (1877) first reported the presence of spikes in his initial description of *Stegosaurus armatus*. He tentatively accepted Owen's (1875) suggestion that the spikes were a "carpal appendage", but added there were so many that they must have been elsewhere on the body as well. With spikes on the forelimb, *Stegosaurus* could easily defend itself if attacked. Marsh (1880) later dropped the idea

of spikes on the forelimb when he received an articulated forelimb from Como Bluff, Wyoming.

Marsh (1880; and later Lull, 1910b) suggested that the spikes might be a sexual dimorphic character because they had been found only with one of his two species (species not given). By 1887, Marsh realized that the spikes were associated with the end of the tail. He also thought that the various species and possibly the sexes might differ in the shape, size and number of plates and spikes on the body. He concluded that *Stegosaurus ungulatus* was characterized by four pairs of spikes, in another unnamed species there were three pairs, in *Stegosaurus stenops* and *Diracodon laticeps*, there were two pairs, and in *Stegosaurus sulcatus* there was only a single pair of spikes.

The first skeletal reconstruction of *Stegosaurus* was presented by Marsh in 1891. Marsh shows the tail spikes projecting upwards but does not give his reasons for this position. We may reason, however, that as offensive weapons they would have had to project upwards if the tail dragged on the ground as he shows.

Lull (1910a) and later Gilmore (1914) maintained the upward diverging spikes in their discussion of *Stegosaurus* armor. Both even showed a cross-section of the tail to illustrate the spike in relationship with the caudal vertebrae. However, while remounting of the Kessler *Stegosaurus* skeleton (DMNH 1438) at the Denver Museum of Natural History, this standard spike placement was re-examined. Several lines of evidence now indicate that the spikes projected posterolaterally.

First, the tail of *Stegosaurus* was most likely carried high in the air parallel to the ground making upward projecting spikes ineffective as offensive weapons. Evidence for the tail in this position is the upward facing posterior face of the last sacral vertebra and the wedge-shaped first caudal. This caudal is anteroposteriorly longer along the ventral margin of the centrum than it is at the level of the neural canal. Both of these conditions in *Diplodocus* were used by Gilmore (1932) to argue that the base of the tail arced upwards, and the same argument holds for *Stegosaurus*. With the rest of the caudal vertebrae articulated so their centra faces are parallel, the tail is almost at the level of the sacrum throughout its length.

In addition, while Marsh (1880) suggested the expanded, bifid neural spines of the caudals were for support of the plates, it is more probable that the expansion was to aid in the support of the tail. By expanding and bifurcating the tops of the neural spines, the surface area for interspinous and supraspinous ligaments is greatly increased. These ligaments connect the adjacent vertebrae together keeping the tail extended horizontally without

the use of the caudal muscles. These ligaments and the need to swing the tail laterally may explain why stegosaurs, of all the ornithischians, lack ossified tendons in the back and tail.

Second, the long base of the plates effectively "lock" segments of vertebrae together. If it is accepted that the base of a plate should be equal distance above the neural spines throughout its length, then this is possible only if the tail is straight. If the tail droops, then the plate over the base of the tail, which is also the largest plate, is not evenly spaced above the vertebrae (Fig. 4). This "locking" of vertebrae explains why articulated tails of *Stegosaurus* are frequently found straight (Figs. 1 and 2).

Third, the spikes have a trough bisecting the base along its long axis. When spikes are mounted in the traditional upward projection, this trough is vertical relative to the caudals. In addition, the base of the spikes is not evenly spaced from the caudals (contra Lull, 1910a, Fig. 8; see also Gilmore, 1914, Fig. 64). When the trough is aligned parallel to the caudals, the spikes project posterolaterally (Fig. 5(C)). This position is also seen in articulated tails in which the spikes are preserved (Fig. 3). If the spikes

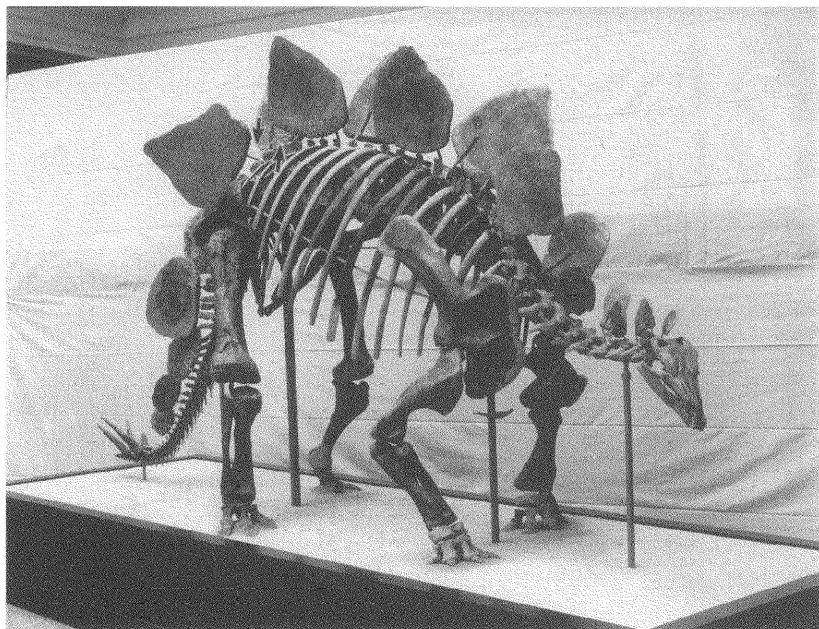


FIGURE 4 Traditional mount of *Stegosaurus stenops* with tail dragging on the ground. Note large gap between anterior edge of plate and tail at arrow. Photograph courtesy of National Museum of Natural History.

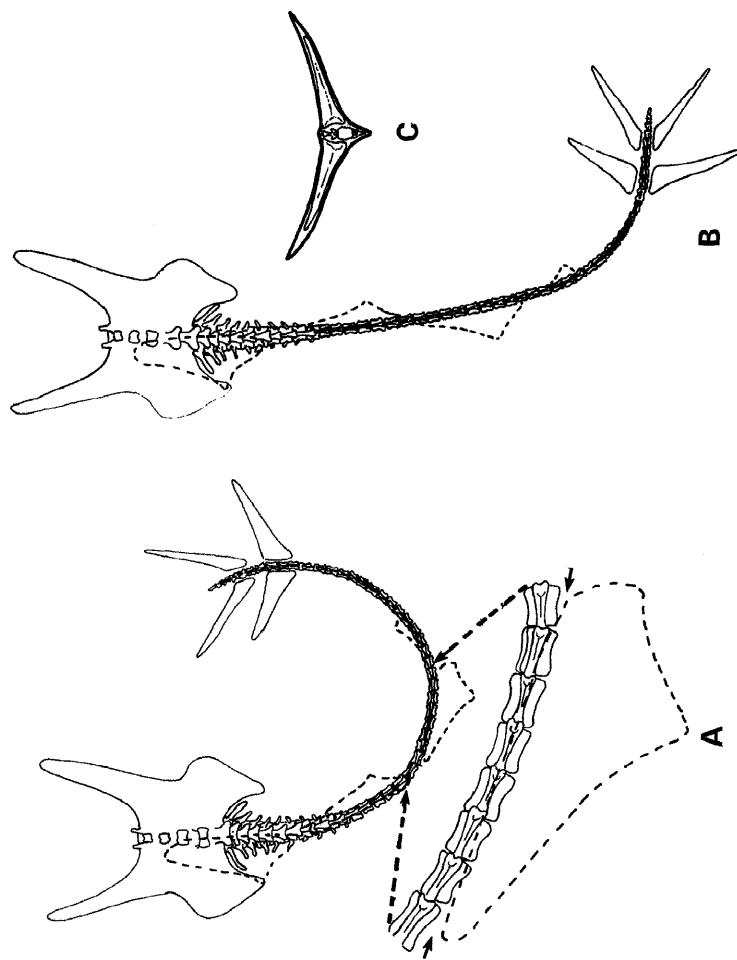


FIGURE 5 Comparison of lateral tail motion in *Stegosaurus stenops*. A, hypothetical tail swing without regard to restrictions of plates (heavy dashed lines). Detail below showing anterior and posterior edge of plate (heavy dashed line) extending laterally beyond the vertebrae. B, more restrictive lateral movement of the tail taking plates (heavy dashed lines) into account. Greatest bending movement is in the posterior third. C, cross-section of tail showing laterally projecting spikes. Not to scale with A or B.

had projected upwards as in the traditional view, then the spikes in the articulated tails should have reflected this position.

With the spikes projecting posterolaterally on the tail, they are situated in a manner that allows their use as an offensive weapon (Fig. 5(B)). Lateral tail movement was limited because of the "locked" segments of vertebrae by the plates, but the small amount of movement between vertebrae was cumulative (cf. Fig. 5(A) and (B)). The result was that at the end of the tail, the spikes could project a little more than perpendicular to the axis of the body (Fig. 5(B)).

THROAT ARMOR

The presence of other armor besides plates and spikes was announced by Marsh in 1881. He briefly reported on the presence of small disk-shaped ossicles in the throat region of *Stegosaurus stenops*. Additional information on these scutes was provided by Gilmore (1914), who noted that the ossicles are pitted and grooved on one side. He also suggested that they might have extended beyond the throat to the top of the skull and possibly the sides of the body. The Small specimen provides a great deal more information about these ossicles.

The ossicles of DMNH 2818 are displaced relative to the skull, but they remain as a group and not scattered as with the Felch specimen (Fig. 2). As may be seen in Fig. 6, the ossicles are somewhat hexagonal and form

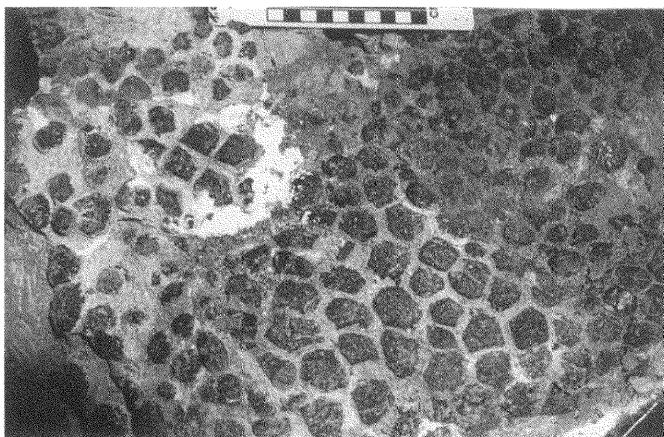


FIGURE 6 Throat ossicles of *Stegosaurus stenops* (DMNH 2818) as preserved. Note rosette patterns of ossicles.

rosette patterns. They measure 4–27 mm in diameter and are about 5 mm apart. Encased in skin, this gap between the ossicles would permit neck movement. The rosette pattern has been reported from molds of dinosaur skin, including various hadrosaurs (Osborn, 1912; Lull and Wright, 1942), ceratopsians (Brown, 1917; Lull, 1933), ankylosaurs (Nopcsa, 1928), and sauropods (White, 1967). This evidence suggests that the rosette pattern was typical of dinosaur skin. At present, there is no evidence that the ossicles extended onto the skull or body as suggested by Gilmore (1914).

CONCLUSIONS

Several new specimens of *Stegosaurus stenops* provide evidence about the plate arrangement on the neck, body and tail. The three-dimensional preservation of the plates demonstrate that, in this species at least, the plates were arranged in two alternating rows along the neck, back and tail. In addition, the throat ossicles were arranged in rosettes and the tail spines projected posterolaterally. Lateral body and tail movement was restricted by the long base of the plates overlapping several vertebrae. On the other hand, these plates and a well developed system of ligaments enabled the tail to be carried in the air without the use of muscles. With the tail in this position, the spines projected posterolaterally so they could be used as a threat device or as defensive weapons.

Finally, the rigidity of the tail imposed by the plates makes it very improbable that *Stegosaurus* could stand tripodally. This idea, first suggested by Marsh (1891), has more recently been advocated by Bakker (1986). Many of the same arguments about the pelvis, such as tall sacral neural spines, have also been used to argue for a tripododal stance in some sauropods (e.g., *Apatosaurus*, Bakker, 1986). Based on the conclusions reached here about *Stegosaurus*, pelvic adaptations by themselves may lead to erroneous stance interpretations. For example, the tall sacral spines in *Stegosaurus* and in *Apatosaurus* probably served for attachment sites for interspinous and supraspinous ligaments in order to keep the tail in the air.

Acknowledgments

Bill Tezak and the Colorado Rock Quarry assisted greatly in the excavation and removal of the Small *Stegosaurus*. The 6,300 kg block containing the body was removed by the A Company, 2/158 Aviation Regiment, Fort Carson, Colorado, with a Chinook helicopter. The Cañon City District

Office of the Bureau of Land Management expedited permitting (BLM permit C49819(c)) to enable the Denver Museum of Natural History to excavate the Small *Stegosaurus*. Numerous volunteers from the Denver Museum of Natural History and the Garden Park Paleontology Society endured gnats and numerous rain storms during the excavation and their help is gratefully acknowledged. Bryan Small, Denver Museum of Natural History, oversaw much of the excavation of the *Stegosaurus* skeleton. Dr. Bruce Rothschild made the first suggestion that the pathological spike might be due to osteomyelitis. Preparation of the main body block was by Dona Engard, Garden Park Paleontological Society, the tail block by volunteers of the Denver Museum of Natural History, and final preparation of the skull by Bryan Small. Finally, thanks to Dan Chure, David Gillette and James Farlow for helpful comments of an earlier draft of this paper.

References

Bakker, R. (1986) *The Dinosaur Heresies*. New York: William Morrow and Co., Inc., 481 pp.

Behrensmeyer, A. and D. Boaz (1980) The recent bones of Amboseli National Park, Kenya, in relation to East African paleoecology. In Behrensmeyer, A. and A. Hill (Eds.) *Fossils in the Making*. Chicago: University of Chicago Press, pp. 72–92.

Berner, R. (1968) Calcium carbonate concretions formed by the decomposition of organic matter. *Science*, **159**, 195–197.

Bollan, H. (1991) The Bollan *Stegosaurus*. In Averett, W. (Ed.) *Guidebook for Dinosaur Quarries and Tracksites Tour*. Grand Junction, Colorado: Grand Junction Geol. Soc., pp. 53–54.

Brown, B. (1917) A complete skeleton of the horned dinosaur *Monoclonius*, and discussion of a second skeleton showing skin impressions. *Amer. Mus. Nat. Hist. Bull.*, **37**, 281–306.

Brown, B. (1932) A spine-armored saurian of the past. *Nat. Hist.*, **32**, 493–496.

Buffrénil, de, J. Farlow, and A. de Ricqlès (1986) Growth and function of *Stegosaurus* plates: evidence from bone histology. *Paleobiol.*, **12**, 459–473.

Carpenter, K. (1984) Skeletal reconstruction and life restoration of *Sauropelta* (Ankylosauria: Nodosauridae) from the Cretaceous of North America. *Canad. J. Earth Sci.*, **21**, 1491–1498.

Carpenter, K. (1987a) Paleoecological significance of droughts during the Late Cretaceous of the Western Interior. In Currie, P. and E. Koster (Eds.) *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. *Occas. Papers Tyrrell Mus. Palaeont.*, **3**, 42–47.

Carpenter, K. (1987b) Potential for fossilization in Late Cretaceous-Early Tertiary swamp environments. *Geol. Soc. Amer. Abstr., Rocky Mtn. Sect.*, pp. 264.

Colbert, E. (1945) *The Dinosaur Book*. New York: McGraw-Hill Book Co., 156 pp.

Cornfield, T. (1973) Elephant mortality in Tsavo National Park, Kenya. *East Afr. Wildl. J.*, **11**, 339–368.

Czerkas, S. (1987) A reevaluation of the plate arrangement on *Stegosaurus stenops*. In Czerkas, S. and E. Olson (Eds.) *Dinosaurs Past and Present*, **2**. Seattle: Univ. Washington Press, pp. 82–99.

Dong, Z. (1990) Stegosaurs of Asia. In Carpenter, K. and P. Currie (Eds.) *Dinosaur Systematics, Approaches and Perspectives*. New York: Cambridge University Press, pp. 255–268.

Dong, Z., Z. Tang, and S. Zhou (1982) Note on the new Mid-Jurassic stegosaur from Sichuan Basin, China. *Vert. Pal. Asiat.*, **20**, 83–87.

Farlow, J., C. Thompson, and D. Rosner (1976) Plates of the dinosaur *Stegosaurus*: forced convection heat loss fins? *Science*, **192**, 1123–1125.

Foster, J. (1965) Mortality and ageing of black rhinoceros in East Tsavo Park, Kenya. *East Afr. J. Wildl.*, **3**, 118–119.

Galton, P. (1982) The postcranial anatomy of stegosaurian dinosaur *Kentrosaurus* from the Upper Jurassic of Tanzania, East Africa. *Geol. Palaeont.*, **15**, 139–160.

Galton, P. (1990) Stegosauria. In Weishampel, D., P. Dodson, and H. Osmólska (Eds.) *The Dinosauria*. Berkeley: University of California Press, pp. 427–455.

Gilmore, C. (1914) Osteology of the armored Dinosauria in the United States National Museum, with special reference to the *Stegosaurus*. *U.S. Nat'l Mus. Bull.*, **89**, 1–136.

Gilmore, C. (1915) A new restoration of *Stegosaurus*. *Proc. U.S. Nat'l Mus.*, **49**, 355–357.

Gilmore, C. (1918) A newly mounted skeleton of the armoured dinosaur *Stegosaurus stenops*, in the United States Museum. *Proc. U.S. Nat'l Mus.*, **54**, 383–390.

Gilmore, C. (1932) On a newly mounted skeleton of *Diplodocus* in the United States Museum. *Proc. U.S. Nat'l Mus.*, **81**, 1–21.

Hennig, E. (1925) *Kentrurosaurus aethiopicus*; die Stegosaurier-Funde vom Tendaguru, Deutsch-Ostafrika. *Palaeontogr. Suppl.*, **7**, 103–253.

Hillman, J. and A. Hillman (1977) Mortality of wildlife in Nairobi National Park during the drought of 1973–1974. *East Afr. Wildl. J.*, **15**, 1–18.

Leuthold, W. (1977) *African Ungulates*. Berlin: Springer-Verlag, 307 pp.

Lucas, F. (1901) *Animals of the Past*. New York: McClure, Philips and Co.

Lull, R. (1910a) The armor of *Stegosaurus*. *Amer. J. Sci.*, 4th ser., **29**, 201–210.

Lull, R. (1910b) *Stegosaurus ungulatus* Marsh, recently mounted at the Peabody Museum of Yale University. *Amer. J. Sci.*, 4th ser., **30**, 361–377.

Lull, R. (1933) A revision of the Ceratopsia or horned dinosaurs. *Peabody Mus. Nat. Hist. Mem.*, **3**, 1–175.

Lull, R. and N. Wright (1942) Hadrosaurian dinosaurs of North America. *Geol. Soc. Amer. Spec. Paper*, **40**, 1–242.

Marsh, O. (1877) A new order of extinct Reptilia (Stegosauria) from the Jurassic of the Rocky Mountains. *Amer. J. Sci.*, 3rd ser., **14**, 513–514.

Marsh, O. (1880) Principle characters of American Jurassic dinosaurs, Part III. *Amer. J. Sci.*, 3rd ser., **19**, 253–259.

Marsh, O. (1881) Principle characters of American Jurassic dinosaurs, Part IV. Spinal cord, pelvis, and limbs of *Stegosaurus*. *Amer. J. Sci.*, 3rd ser., **21**, 167–170.

Marsh, O. (1887) Principle characters of American Jurassic dinosaurs, Part IX. The skull and dermal armor of *Stegosaurus*. *Amer. J. Sci.*, 3rd ser., **34**, 413–417.

Marsh, O. (1891) Restoration of *Stegosaurus*. *Amer. J. Sci.*, 3rd ser., **42**, 179–181.

Marsh, O. (1896) The dinosaurs of North America. *U.S. Geol. Surv. Ann. Rep.*, **16**, 142–230.

McIntosh, J. (1981) Annotated catalogue of the dinosaurs (Reptilia, Archosauria) in the collections of the Carnegie Museum of Natural History. *Carnegie Mus. Nat. Hist. Bull.*, **18**, 1–67.

Nopcsa, F. (1928) Paleontological notes on reptiles. *Geol. Hungarica, Ser. Palaeont.*, **1**, 1–84.

Osborn, H. (1912) Integument of the iguanodont dinosaur *Trachodon*. *Amer. Mus. Nat. Hist. Mem.*, **1**, 33–54.

Owen, R. (1875) Monographs on the fossil Reptilia of the Mesozoic formation, Part II, genera *Bohriospondylus*, *Cetiosaurus*, *Omiosaurus*. *Palaeontogr. Soc. Mon.*, **29**, 15–93.

Rothchild, B. and L. Martin (1993) *Paleopathology: Disease in the Fossil Record*. Boca Raton: Florida, CRC Press, 386 pp.

Russell, D., P. Béland, and J. McIntosh (1980) Paleoecology of the dinosaurs of Tendaguru (Tanzania). *Mém. Soc. Géol. France*, **139**, 169–175.

White, T. (1967) *Dinosaurs at Home*. New York, Vantage Press, 232 pp.