APPENDIX.

ART. XXXI. — *Principal Characters of American Jurassic Dinosaurs;* by Professor O. C. MARSH. Part III. With six plates.

IN the previous articles of this series, the writer has recorded the more important characters of several groups of Dinosaurs from the Jurassic deposits of the Rocky Mountain region.* In the present communication, some of the peculiar features in the structure of the *Stegosauria* are made known. This suborder proves to be one of the most specialized of the known Dinosaurs, and differs widely from the other groups.

Stegosaurus, Marsh, 1877.

The type genus of this group (*Stegosaurus*) may be taken as the representative of the suborder. Among the characters which at present distinguish this genus from the other known groups of Dinosaurs are the following:

(1) All the bones of the skeleton are solid.

(2) The femur is without a third trochanter.

(3) The crest on the outer condyle of the femur, which in Birds separates the heads of the tibia and fibula, is rudimentary or wanting.

(4) The tibia is firmly coössified with the proximal tarsals.

(5) The fibula has its larger extremity below.

Various other important characters of the present group, which are shared in part by some aberrant Dinosaurs, will be given below.

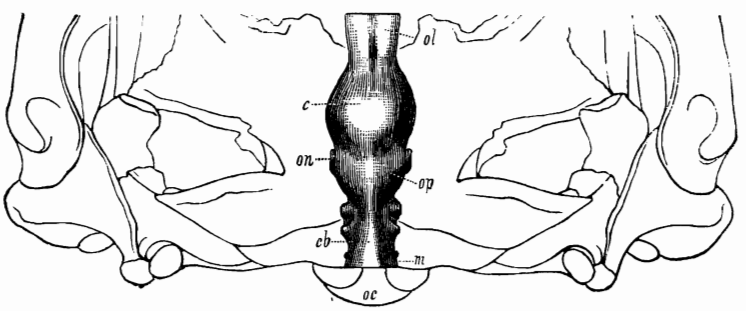
THE SKULL AND BRAIN.

The skull in the *Stegosauria*, so far as known, was remarkably small. In its main features it agreed more nearly with that of the genus *Hatteria*, from New Zealand, than with any other living reptile. The quadrates were fixed, and there was a quadrato-jugal arch. The jaws were short and massive.

* This Journal, xiv, 513; xv, 241; xvi, 411; xvii, 86; and xviii, 501.

Little has been known hitherto of the brain of Dinosaurs, but fortunately in one specimen of *Stegosaurus* the brain-case is well preserved, and apparently without distortion. Figures 1 and 2 of Plate VI show the form and general characters of this brain-cavity. The brain of this reptile was much elongated, and its most striking features were the large size of the optic lobes (*op*), and the small cerebral hemispheres (*c*). The latter had a transverse diameter only slightly in excess of the medulla. The cerebellum was quite small. The optic nerve (*on*) corresponded in size with the optic lobes. The olfactory lobes (*ol*) were of large size. As a whole, this brain was lacertilian rather than avian. A brain-cast of a young Alligator (figure 3) is given on the same plate for comparison. The contrast in the development of the cerebral region is marked, but in some other respects the correspondence is noteworthy.

In comparing the proportionate size of the brain of this living reptile with that of *Stegosaurus*, as given on Plate VII, the result proves of special interest. The absolute size of the two brain-casts is approximately as 1 to 10, while the bulk of the entire bodies, estimated from corresponding portions of each skeleton, was as 1 to 1000. It follows that the brain of *Stegosaurus* was only $\frac{1}{100}$ that of the Alligator, if the weight of the entire animal is brought into the comparison. If the cerebral regions of the two brains were alone compared, the contrast would be still more striking. This comparison, gives, of course, only approximate results, and some allowance should be made for the proportionally larger brain in small animals.



Outline of posterior part of skull and brain-cast of *Morosaurus grandis*, Marsh; superior view, one-fourth natural size; *ol.* olfactory lobes; *c.* cerebral hemispheres; *op.* optic lobes; *on.* optic nerve; *cb.* cerebellum; *m.* medulla; *oc.* occipital condyle.

The brain of *Stegosaurus ungulatus* is clearly of a lower type than that of *Morosaurus*, which, as the writer has shown, was several times smaller in diameter than the neural canal in its

own sacrum.* In the latter genus, the brain was proportionally shorter, and the cerebral region better developed, as shown in the cut above. The absolute size of this brain as compared with that of *Stegosaurus* is about 16 to 10, the brain of the Alligator figured being regarded as 1. Taking again the body of the Alligator as the unit, and *Stegosaurus* as 1000, that of *Morosaurus* would be about 1500. *Stegosaurus* had thus the smallest brain of any known land vertebrate. These facts agree fully with the general law of brain-growth, made out by the writer in extinct mammals and birds.

The Teeth.

The teeth of *Stegosaurus* are very numerous, and mostly cylindrical in form. Those from the maxillary figured on plate VI may be regarded as typical. The series represented in figure 4 consists of functional teeth in position, although separated from the jaw. The crowns are more or less compressed transversely, and are covered with thin enamel. The fangs are long and slender, and the pulp cavity is continued nearly or quite to the crown. The jaws contain but a single row of teeth in actual use. These are rapidly replaced as they wear out by a series of successional teeth, more numerous than hitherto observed in these reptiles. Figure 5, on Plate VI, represents a transverse section through the maxillary, immediately behind the fourth tooth. The latter is shown in place (1), and below it is a series of five immature teeth (2 to 6), in various stages of development, preparing to take its place. These successional teeth are lodged in a large cavity (*c*), which extends through the whole dental portion of the maxillary. The teeth in use were loosely implanted in separate sockets, and were readily displaced. The entire dental series evidently formed a very weak dentition, adapted to a herbivorous life.

The Vertebræ.

The vertebræ of *Stegosaurus* preserved all have the articular faces of their centra concave, although in some the depression is slight. They are all, moreover, without pneumatic or medullary cavities. On Plate VII, a selection from the vertebral series of one skeleton is given, which shows the principal forms. Figures 1 and 2 represent a median cervical. The other neck vertebræ have their centra of similar length, but the diameter increases from the axis to the last of the series. Some of the anterior cervicals have a small tubercle in the center of each end of the centra, a feature seen also in some of the caudals. All the cervicals supported short ribs.

* This Journal, vol. xvii, p. 87.

The dorsal vertebræ have their centra rather longer, and more or less compressed. The neural arch is especially elevated. The neural canal is much higher than wide. The head of the rib fits into a pit on the side of the neural arch. Figures 3 and 4, Plate VII, represent a posterior dorsal, with characteristic features. The ribs are massive, and strengthened by their form, which is **T** shaped in transverse section.

The sacral vertebræ are coössified, but their exact number in the present genus has not yet been fully determined.

The caudal vertebræ offer the greatest diversity, both in size and form. The anterior caudals are the largest in the whole vertebral series, and highly modified to support a portion of the massive dermal armour. The articular faces of their centra are nearly plane, and very rugose. The neural spine has an enormous development, and its summit is expanded into a bifurcate rugose head. These caudals are very short, and their neural spines nearly or quite in apposition above. These vertebræ have no distinct faces for chevrons. The transverse processes are expanded vertically, and their extremities curve downward. Further back, the same general characters are retained, but the centra are more deeply cupped, and the spines less massive. Figures 5 and 6, Plate VII, show a caudal vertebra from this region. The chevrons here have their articular ends separate, and rest upon two vertebræ. In the median caudals, the spine has greatly diminished in height, and the faces for chevrons are placed on prominent tubercles on the postero-inferior surface. The lower margin of the front articular face is sharp, and the chevrons do not meet it. In the more distal caudals (figures 7 and 8), the neural spine and zygapophyses are reduced to mere remnants, but the chevron facets remain distinct. These vertebræ, as well as those further back, have their centra much compressed. The caudal vertebræ are remarkably uniform in length throughout most of the series.

The Fore Limbs.

On Plate VIII, some of the bones of the scapular arch and anterior limbs of *Stegosaurus* are figured. The scapula and coracoid are of the true Dinosaurian type. The former has its upper portion rather short, and moderately expanded (figure 1). The coracoid was closely united to the scapula by cartilage. It is perforated by the usual foramen, which in some cases may become a notch.

The humerus (figure 2) is short and massive. It has a distinct head, and a strong radial crest. The shaft is constricted medially, and is without any medullary cavity. The ulna (figure 3) is also massive, and has a very large olecranal process. Its

distal end is comparatively small. The radius is smaller than the ulna. The fore limb, as a whole, was very powerful, and adapted to varied movements.

The Hind Limbs.

The pelvic arch of *Stegosaurus* is not complete in the specimens at present known, but its main characters agree with the Dinosaurian type. The acetabulum is formed by the ilium, ischium, and pubis. The last was apparently directed downward and forward. The ischium is shown on Plate IX, figure 1. It has a large head for union with the post-acetabular process of the ilium, and a thin extended vertical margin where it joins the pubis. At its distal end, it was united with its fellow by cartilage.

The femur of *Stegosaurus* (Plate IX, figure 2) is by far the largest bone in the skeleton. It is remarkably long and slender. There is no distinct head, and the great trochanter is nearly or quite obsolete. The shaft is of nearly uniform width, and very straight. There is no evidence of a third trochanter. The distal end of the femur is peculiar in having very flat condyles, with only a shallow depression between them. The external one has only a rudiment of the ridge which passes between the heads of the tibia and fibula, and is so characteristic of true Dinosaurs and Birds.

The tibia (figure 3) is very much shorter than the femur. Its superior end is unusually flat, indicating that it met the flat condyles of the femur so as to bring the two bones at times nearly or quite into the same line. The shaft of the tibia is constricted medially, leaving a wide space between it and the fibula. The distal end of the tibia is blended entirely with the convex astragalus, so as to strongly resemble the corresponding part in Birds.

The fibula (figure 3) is slender, and has its smaller end above. This extremity is applied closely to the head of the tibia by a rugose suture, so as readily to unite with it. Its upper articular surface is nearly or quite on a level with that of the tibia. The distal end of the fibula is expanded, and in the specimen figured is firmly coössified with the calcaneum. The two coalesce with the tibia and astragalus, and form a smooth convex articulation for the distal tarsals. The latter are distinct. The posterior limbs were more than twice as long as those in front.

The bones of the feet of *Stegosaurus* have not yet been fully identified, although a number have been found. In figure 4, Plate IX, a metapodial bone is shown, and in figure 4, Plate VIII, are views of a very characteristic terminal phalanx.

Dermal Spines and Plates.

The most remarkable feature about *Stegosaurus* is the series of ossifications which formed its offensive and defensive armour. These consist of numerous spines, some of great size and power, and many bony plates, of various sizes and shapes, well fitted for protecting the animal against assaults. Some of these plates are a meter, or more than three feet, in diameter.

The spines were of different forms, and varied much in size. On Plate X, four of these are represented. All of those preserved are unsymmetrical, and most of them are in pairs. One of the largest is shown in figure 1, which gives the more usual form and proportions. This specimen is over two feet (630 mm) in length, and its fellow is of the same size.

This spine has a rugose oblique base, and its sides are marked by vascular impressions and grooves similar to those on the bony horn-cores of ungulate mammals. It was evidently covered by a horny substance, and in life formed a most powerful weapon. The spinous appendage represented in figure 2 of the same plate was very similar in form and proportions, but of smaller size. It agrees closely with its mate, found not far from it. Nine different spines of this character were recovered with this same skeleton, and others may have been lost.

Figure 3 represents a different kind of spine. This also is obliquely truncated at the base, and thus is unsymmetrical, but its fellow has not been discovered. Its sides are flat and covered with vascular markings. There is a distinct ridge near the base, showing the depth this spine was inserted in the flesh. A smaller spine of the same general character was found near it. The small tubercular bone, shown in figure 1, Plate X, is very similar to the base of a spine-core, with the blade aborted.

The position these various spines occupied in life is uncertain, as none of them were found in place with portions of the skeleton fitted to support them. A spine somewhat similar to that in figure 2 was found with the skeleton of *Omosaurus*, in England, and regarded by Owen as a carpal appendage.* *Stegosaurus* may have been so provided, but the number and variety of the spines found with one skeleton indicate that various other parts were equally well armed. There are no indications of the attachment of spines to the tarsal region.

The dermal plates which protected the same animal were much more numerous than the spines. Some of them were so large and peculiar that their position is indicated by the structure of the anterior caudal vertebræ, whose enormous neural spines were especially adapted to support them.

* Palæontographical Society, 1875.

The plate represented on Plate XI, figure 2, was perhaps a dermo-neural spine, which stood erect over the caudal vertebræ. This would imply a deep compressed tail, and of this there are various indications. Several other plates found near the caudals probably occupied a similar position.

The largest plates discovered are similar to the one represented in figure 3. These are unsymmetrical, and their surfaces indicate that their position was on the back, arranged on each side of the medial line. There may have been several of these rows. Some of the smaller plates were discoidal in form, and quite thin. That shown in figure 1, is one of the smallest recovered. With such protection as the plates and spines together afforded, *Stegosaurus* was doubtless more than a match for his larger brained cotemporaries.

In considering the affinities of *Stegosaurus*, it would appear that the nearest known ally was *Omosaurus*. The fore limb, dorsal vertebræ, and one dermal spine are similar. The caudal vertebræ, however, are different, and there is no evidence that the latter genus was provided with plates, or that the skull and teeth were at all like those of *Stegosaurus*. They both may prove to belong in the same sub-order, and perhaps in the same family, *Stegosauridæ*.

The two known species of *Stegosaurus* were about thirty feet in length. They were herbivorous, and probably more or less aquatic in habit. It is possible that the difference between them was only sexual, as spines were found with only one.

The great disproportion in length between the fore and hind limbs, greater probably than in any known Dinosaur, would imply that *Stegosaurus* was more or less bipedal in its movements on land. The very short, powerful fore limbs, admitting of free motion, may have been well armed with spines, and thus used most effectively in defence. The back was evidently armed, as well as protected. When alive, *Stegosaurus* must have presented by far the strangest appearance of all the Dinosaurs yet discovered.

The remains of the animals here described are all from the Atlantosaurus beds of the Upper Jurassic, in Colorado and Wyoming. In bringing them to light, Messrs. Arthur Lakes, W. H. Reed, and S. W. Williston have rendered an important service to science.

Yale College, New Haven, Feb. 18, 1880.

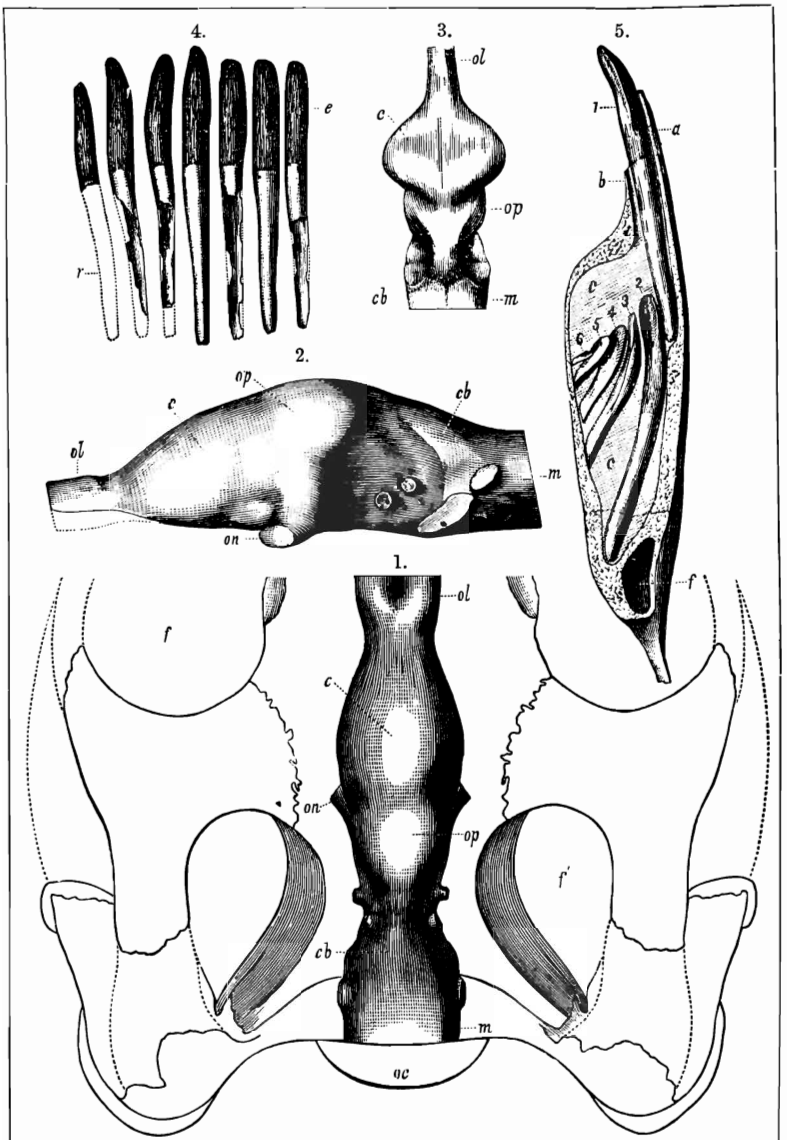


Figure 1.—Outline of skull and brain-cast of *Stegosaurus ungulatus*. Marsh: seen from above. one-half natural size; *ol*, olfactory lobes; *c*, cerebral hemispheres: *op*, optic lobes; *on*. optic nerve; *cb*, cerebellum: *m*. medulla; *f*. orbital cavity; *f'* temporal fossa; *oc*, occipital condyle.

Figure 2.—Same brain-cast; side view, one-half natural size.

Figure 3.—Brain-cast of young Alligator; three-fourths natural size.

Figure 4.—Maxillary teeth of *Stegosaurus armatus*, Marsh; side view, one-half natural size; *e*, enamel; *r*, root.

Figure 5.—Section of maxillary of *Stegosaurus armatus;* showing functional tooth in position, and five successional teeth in dental cavity: *a*, outer wall; *b*, inner wall; *c*, cavity; *f*, foramen.

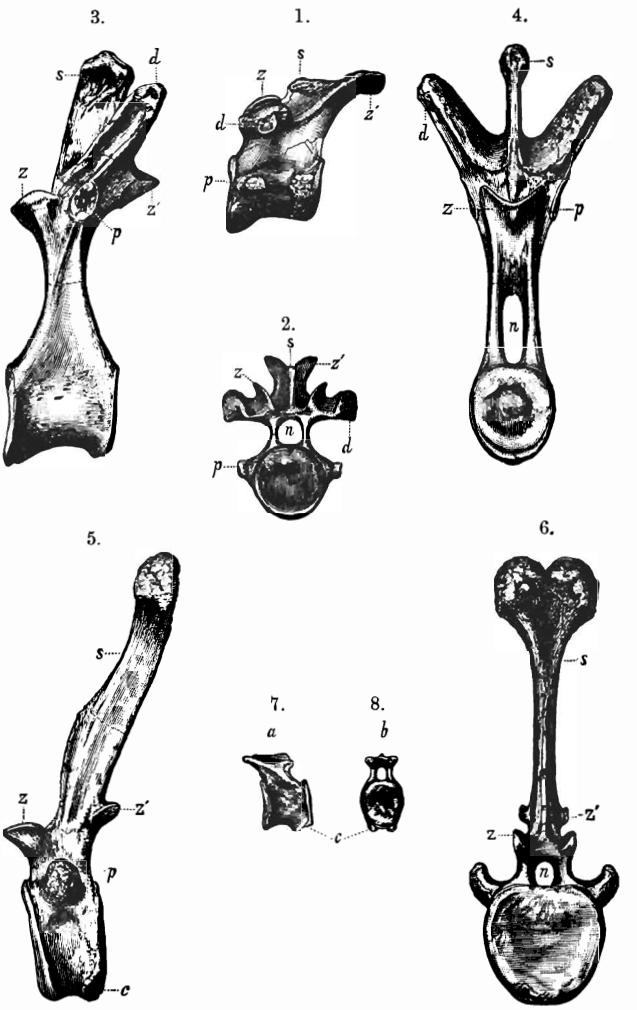


Figure 1.—Cervical vertebra of *Stegosaurus ungulatus*, Marsh; side view; *d*, diapophysis; *p*, parapophysis; *s*, neural spine; *z*, anterior zygapophysis; *z'*, posterior zygapophysis; *n*, neural canal.
Figure 2.—Same vertebra; front view.
Figure 3.—Dorsal vertebra of same series; side view: letters as above.
Figure 4.—Same vertebra; front view.
Figure 5.—Anterior caudal vertebra of same series; side view; *c*, face for chevron.
Figure 6.—Same vertebra; front view.
Figure 7.—Distal caudal of same series; side view.
Figure 8.—Same vertebra; front view.

All the figures are one-eighth natural size.

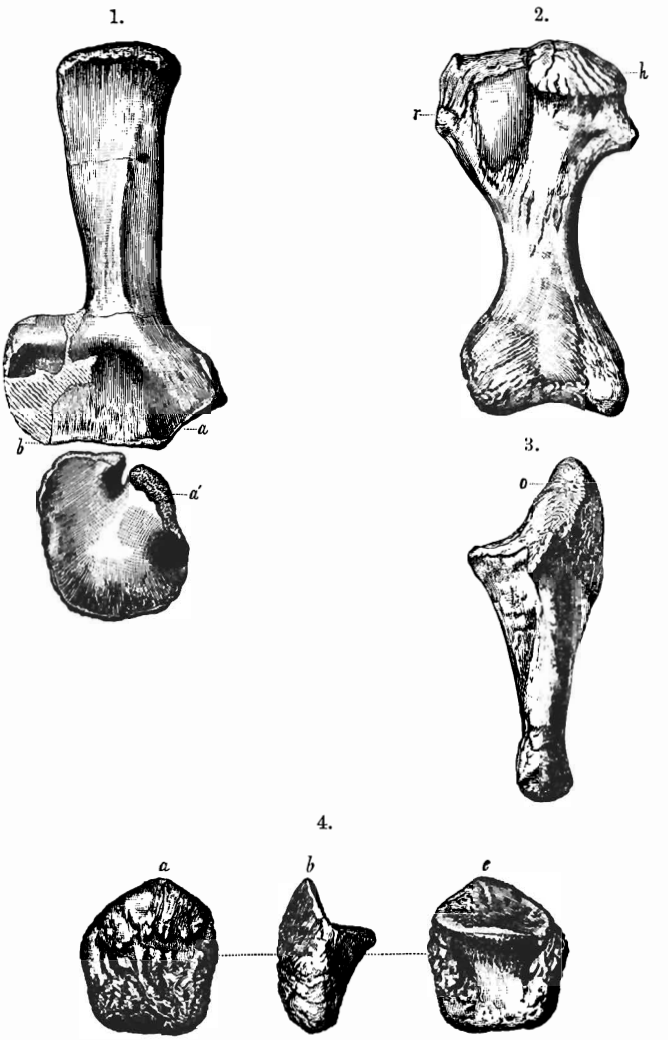


Figure 1.—Left scapula and coracoid of *Stegosaurus ungulatus*, Marsh; side view, one-twelfth natural size; *a*. scapular face of glenoid cavity; *a'*, coracoidean part of same; *b*, surface for union with coracoid.

Figure 2.—Humerus of *Stegosaurus ungulatus;* front view, one-twelfth natural size; *h*, head; *r*. radial crest.

Figure 3.—Ulna of same; side view, one-twelfth natural size; *o*. olecranal process.

Figure 4.—Terminal phalanx of same species; one-fourth natural size; *a*. front view; *b*. side view; *c*, posterior view.

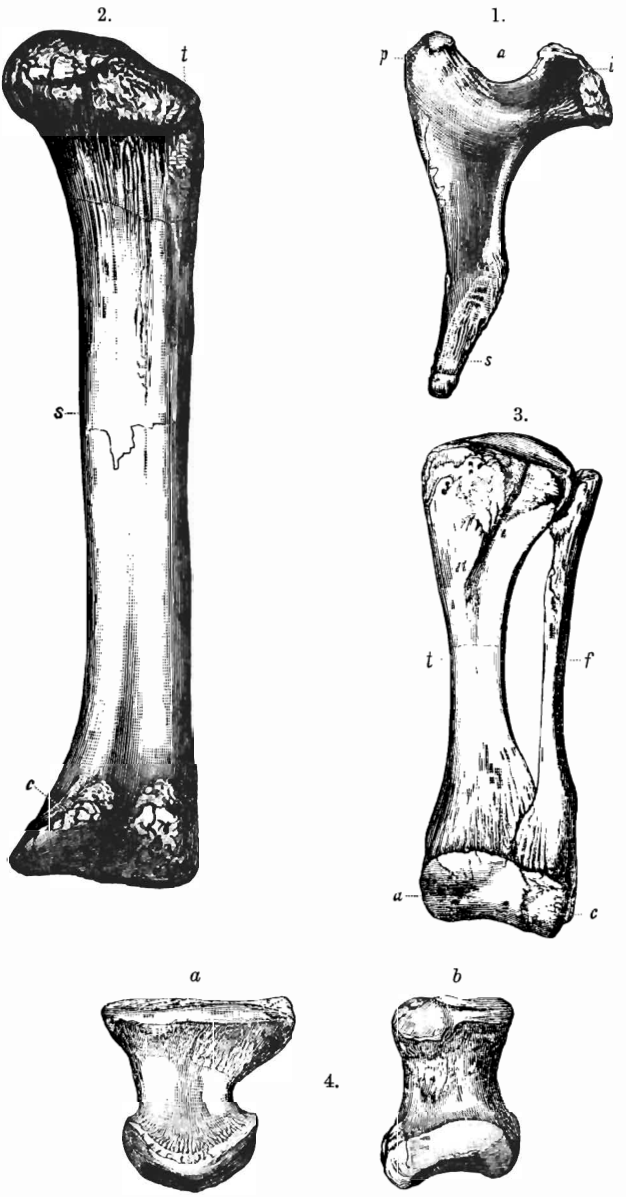


Figure 1.—Left ischium of *Stegosaurus ungulatus*, Marsh: side view, one-twelfth natural size; *a*, acetabulum; *i*, face for union with ilium; *p*, margin joining pubis; *s*, symphysis.

Figure 2.—Left femur of *Stegosaurus ungulatus*: front view, one-twelfth natural size; *t*, position of great trochanter; *s*, shaft, showing absence of third trochanter; *c*, inner condyle.

Figure 3.—Tibia and fibula of same limb; front view, same size; *a*, astragalus; *c*, calcaneum.

Figure 4.—Metapodial bone of same animal; one-fourth natural size; *a*, side view; *b*, front view.

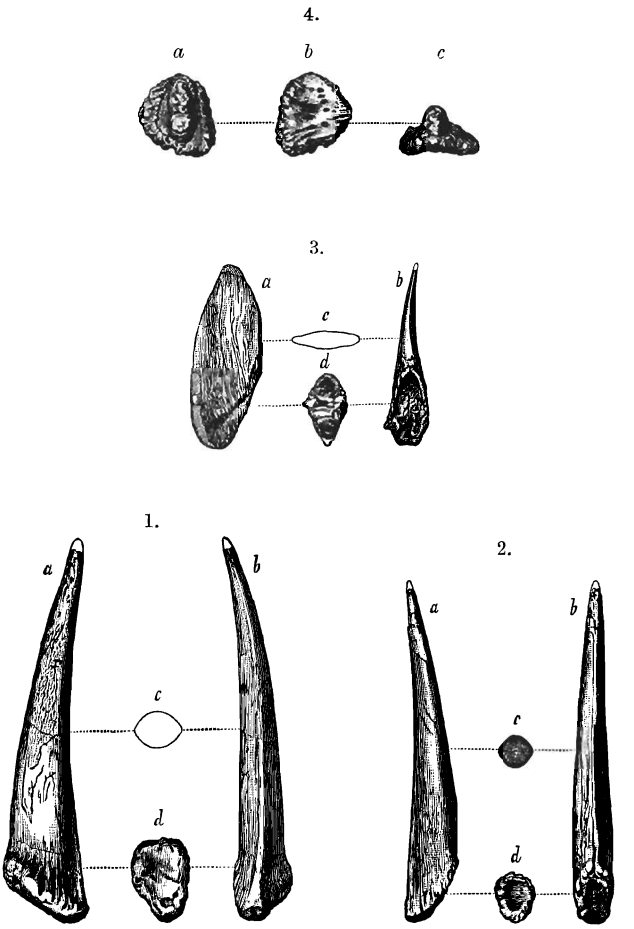


Figure 1.—Dermal spine of *Stegosaurus ungulatus*, Marsh; *a*, side view; *b*, front view; *c*, section; *d*, inferior view of base.

Figure 2.—Smaller dermal spine of same individual; *b*, posterior view; other letters as above.

Figure 3.—Flat dermal spine of same; letters as in figure 2.

Figure 4.—Tubercular spine of same species; *a*, superior view; *b*, inferior view; *c*, fore and aft view.

All the figures are one-twelfth natural size.

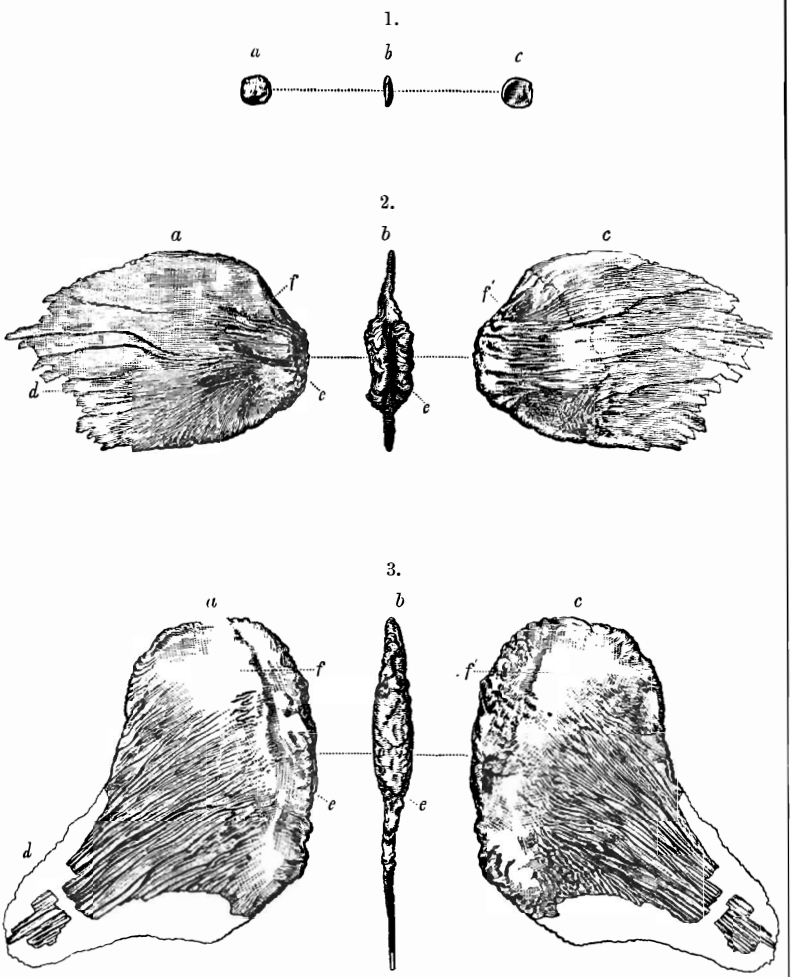


Figure 1.—Dermal plate of *Stegosaurus ungulatus*. Marsh; *a*. superior view; *b*, side view; *c*. inferior view.

Figure 2.—Dermal plate of same animal; *a*. side view; *b*, end view of base; *c*. view of opposite side; *d*, thin margin: *e*, rugose base; *f*, and *f'*, surface marked by vascular grooves.

Figure 3.—Dermal plate of same animal: *a*. superior surface; *b*. thick basal margin; *c*, inferior surface; other letters as in last figure.

All the figures are one-twelfth natural size.