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The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs

Russell P. Main, Armand de Ricqlès, John R. Horner, and Kevin Padian*

Abstract.—The evolution of scutes in thyreophoran dinosaurs, based on *Scutellosaurus*, *Scelidosaurus*, *Stegosaurus*, and several ankylosaurs, began with small rounded or ovoid structures that typically had slight, anteroposteriorly oriented keels. These scutes were elaborated in two general and overlapping ways: they could flare laterally and asymmetrically beneath the keels that mark the anteroposterior axis, and they could be hypertrophied in their distal growth to produce plates, spikes, and other kinds of ornamentation. *Stegosaurus* plates and spikes are thus primarily hypertrophied keels of primitive thyreophoran scutes, sometimes with elaboration of dermal bone around their pustulate bases. Histologically, most thyreophoran scute tissues comprise secondary trabecular medullary bone that is sandwiched between layers of compact primary bone. Some scutes partly or mostly comprise anatomically metaplastic bone, that is, ossified fibrous tissue that shows incremental growth.

The ''plumbing'' of *Stegosaurus* plates was not apparently built to support a ''radiator'' system of internal blood vessels that communicated with the outside of the plates and coursed along their external surfaces to return heated or cooled blood to the body core. Possibly a purely external system supported this function but there is no independent evidence for it. On the other hand, many of the vascular features in stegosaurian plates and spikes reflect *bautechnisches* artifacts of growth and production of bone. Surface vascular features likely supported bone growth and remodeling, as well as the blood supply to a keratinous covering. When the gross and microstructural features of the plates and spikes are viewed in phylogenetic context, no clear pattern of thermoregulatory function emerges, though an accessory role cannot be eliminated in certain individual species. It seems more likely, as in other groups of dinosaurs, that the variation of dermal armor form in stegosaurs was primarily linked to species individuation and recognition, perhaps secondarily to inter- and intraspecific display, and rarely to facultative thermoregulation.

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Introduction

The problems that concern the position and function of the plates of *Stegosaurus* and related forms have a long and colorful history. De Buffrénil, Farlow, and de Ricqlès (1986) reviewed this history and tested three major hypotheses by studying the histology of the bone tissue of a plate of *Stegosaurus*. They discounted the hypothesis that the plates served as armor because ''the plate structure is extremely light and hollow,'' and the orientation of Sharpey's fibers in the bone did not suggest muscle attachments that would have supported an oblique or recumbent position of the plates. The hypotheses that the plates were either ''intraspecific agonistic or sexual display structures'' or ''interspecific deterrent display structures'' were not strongly tested by their study, although the vertical orientation and light construction of the plates were accepted as generally consistent with both. The final hypothesis, that the plates were thermoregulatory devices, appeared most likely because they are so extensively vascularized. De Buffrénil et al. suggested the possibility that blood could have flowed arterially through the inside of the plates to the outside, where in the course of venous drainage on the surface the blood could be warmed or cooled as

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circumstances dictated. Or such thermoregulatory circulation could have been entirely external, some evidence of which would be marked by the external grooves on the *Stegosaurus* plates. The thermoregulatory model, they noted, would make more sense if *Stegosaurus* were an ectotherm but would not rule out endothermy.

A distinct advance in de Buffrénil et al.'s study over earlier work (e.g., Wheeler 1978, which considered thermoregulatory functions in a variety of dinosaurian structures) is that it used tissue microstructure to test functional hypotheses that were based on gross morphological features. They avoided the ''story-telling'' pitfalls of the ''adaptationist program'' criticized by Gould and Lewontin (1979) by using, as far as possible, a hypothetico-deductive approach to formulating and testing such hypotheses. On the other hand, it is not clear that their model, which was developed on the basis of the stegosaur with the largest known plates, would work with other stegosaurs that have different sizes and configurations of scutes (Carpenter 1998).

Our study, in part, builds on theirs by providing more of a phylogenetic component to the histological approach that they used. Like them, we agree that '''bizarre structures' (Gould 1974) constitute an especially challenging problem to paleontologists interested in functional morphology.'' Bizarre structures do not come from nowhere, but rather are obviously the byproducts of macroevolutionary as well as morphogenetic processes. To complement the morphogenetic aspect, it is important to test adaptive hypotheses in a phylogenetic sense in order to see how those functions may have evolved (e.g., Padian 2001).

For this study, therefore, we analyzed the bone tissue histology of several plates, spikes, and throat ossicles of *Stegosaurus*, and of scutes from ankylosaurids and the basal thyreophorans *Scutellosaurus* and *Scelidosaurus*. (Thyreophora represents ankylosaurs, stegosaurs, and their closest relatives separate from other ornithischian dinosaurs [Sereno 1986].) De Buffrénil et al. (1986) constructed a model of stegosaur plate growth based on successive sections through the plate they studied. We wanted to ask whether that plate form was elaborated from or different from the pattern of scute growth in other, more basal thyreophorans. We also wanted to know if the hemocirculatory patterns that de Buffrénil et al. (1986) proposed for the stegosaur plate that they studied could be seen in other stegosaur plates and spikes, and in the scutes of other thyreophorans. Finally, we wanted to ask whether we could establish homologous features and modes of development in the tissues of all thyreophorans.

Materials and Methods

Thin-sections were processed and observed according to standard techniques (e.g., Wilson 1994; Horner et al. 2000). We used specimens of *Scutellosaurus* (V85010/130580) and ankylosaurs (V83232/179282) from the University of California Museum of Paleontology (UCMP); of *Scelidosaurus* (BMNH 39516) from the Natural History Museum, London (NHM); and of *Stegosaurus* from the UCMP (courtesy of Ken Stadtman of the Earth Sciences Museum, Brigham Young University, BYU 881/13698), the National Museum of Natural History (USNM V6135, 6531, 7947) and the Yale Peabody Museum (YPM 1856/ acc. 1512Y, including sections made by de Buffrénil, Farlow, and de Ricqlès).

Our choice of taxa from which to obtain histological materials was based on phylogenetic proximity. Ankylosaurs are accepted as the sister group of stegosaurs. *Scelidosaurus* is traditionally regarded as a basal thyreophoran, although some evidence suggests that it may be a very basal ankylosaur (Carpenter 2001; Norman 2001b). *Scutellosaurus* was described by Colbert (1981) as a ''fabrosaurid,'' but its scutes and other features make it the most basal well-known thyreophoran (Sereno 1986; Rosenbaum and Padian 2000).

Because scutes occur on the flanks of the body as well as the back, we use the terms ''proximal'' and ''distal'' to refer to the directions and surfaces that are respectively closest to and farthest from the anteroposterior body axis.

Histological Observations

Scutellosaurus.—Colbert (1981) described six gross scute forms in the small basal thyreophoran *Scutellosaurus*, though they intergrade somewhat (see also Rosenbaum and Padian 2000). The scutes that we studied resemble those of phytosaurs and some other pseudosuchians in being roughly ovoid with a ridgelike or apical distal surface. They are about 1.2 cm broad and 1.5 cm long, and about 0.6 cm from base to apex. Their proximal surfaces can be flat to concave, or even internally peaked, and they bear pits, especially near the center. Some of these pits connect to radially directed grooves. As the grooves intersect the lateral edges they tend to create a ''scalloped'' pattern. The distal surfaces of the scutes are pitted and grooved, especially near the apex.

These grooves and pits are further reflected in histological cross-sections (Fig. 1A–C). Most of the bone tissue is typical dermal bone, rather compact throughout, and highly birefringent under polarized light in some regions. The peripheral bone tissue comprises a flat zone of mostly avascular, sheetlike bone (Fig. 1C). It has a layered structure, and at least one line of arrested growth (LAG) is present in the individual that we studied. This outer region surrounds a region of better vascularized bone that contains medium to large erosion rooms (Fig. 1A). These erosion rooms are surrounded by reconstructed osteonal tissues that are deposited centripetally. The outer layer contains many bundles of radially oriented Sharpey's fibers, particularly in the keel near the apex (Fig. 1B). There are a great many osteocyte lacunae, some flattened parallel to the surface of the bone, especially near the perimeter, but there are no visible canaliculi, and we found no evidence of typical periosteal bone anywhere in the scute.

The proximal, nearly avascular cortical tissue is interrupted by a few erosion rooms set within a regularly organized matrix, with numerous flattened osteocyte lacunae (Fig. 1C) and some evidence of lines of arrested growth (LAGs) and annuli. A few large vascular canals enter from the edge and can be seen to be continuous with the erosion rooms (Fig. 1B). Many fibers lie parallel to these canals (mainly in a proximodistal direction) in the matrix surrounding the canals. There are fewer fibers in the deep cortex, but they are still present, especially in the unreconstructed portions of the proximal region.

Scelidosaurus.—Scutes of *Scelidosaurus* can also take a number of forms (Owen 1861, 1863; Padian 1987), from nearly round, caplike peaks with short, flat or concave hollowed bases to elongated bilateral ovoids with weak to strong keels (Fig. 1D–F). The scutes that we studied were approximately 4 cm broad and ranged from about 4 to 6 cm in length and from 3.5 to 5 cm in height. The nearly round scutes often bear a slight crest along the anteroposterior axis that may be reflected as a channel along their hollowed undersides. Generally these scutes have taller apices and less lateral flaring than those of *Scutellosaurus* or of pseudosuchians such as crocodiles, aetosaurs, and phytosaurs. In scutes with concave or hollowed bases, the bases are formed by the periphery of the flared surfaces that extend laterally from the keel or apex of the scute. Small vascular pores are present on the hollowed proximal surface. When the scute bottoms are flattened, they are often provided with vascular pores that are from 1 to 5 mm in diameter, and that often have superficial grooves that extend laterally from them. These pores and grooves are seen on the outer surfaces of all scutes.

In cross-section, the scutes are composed of an outer, highly compact layer of bone that is no more than a few millimeters thick (Fig. 1D). This layer thins toward the top; throughout the scute it surrounds a network of lightly built, open, latticelike trabecular bone that occupies most of the basal thickness of the scute but is reduced to nearly nothing at the top (Scheyer and Sander 2004). The undersides of the scutes, whether flat or hollow, are also composed of thin compact bone. In these scutes we found no evidence of a complement of outer avascular bone, perhaps because the bone was growing too rapidly or was not near cessation of growth.

The outer cortex is made of a highly fibrous dermal bone that is poorly organized and poorly vascularized, and also well provided with fiber bundles (Fig. 2A,B). These bundles are interspersed, and may extend in all directions though they are largely perpendicular to the outer surface. Their individual filaments,

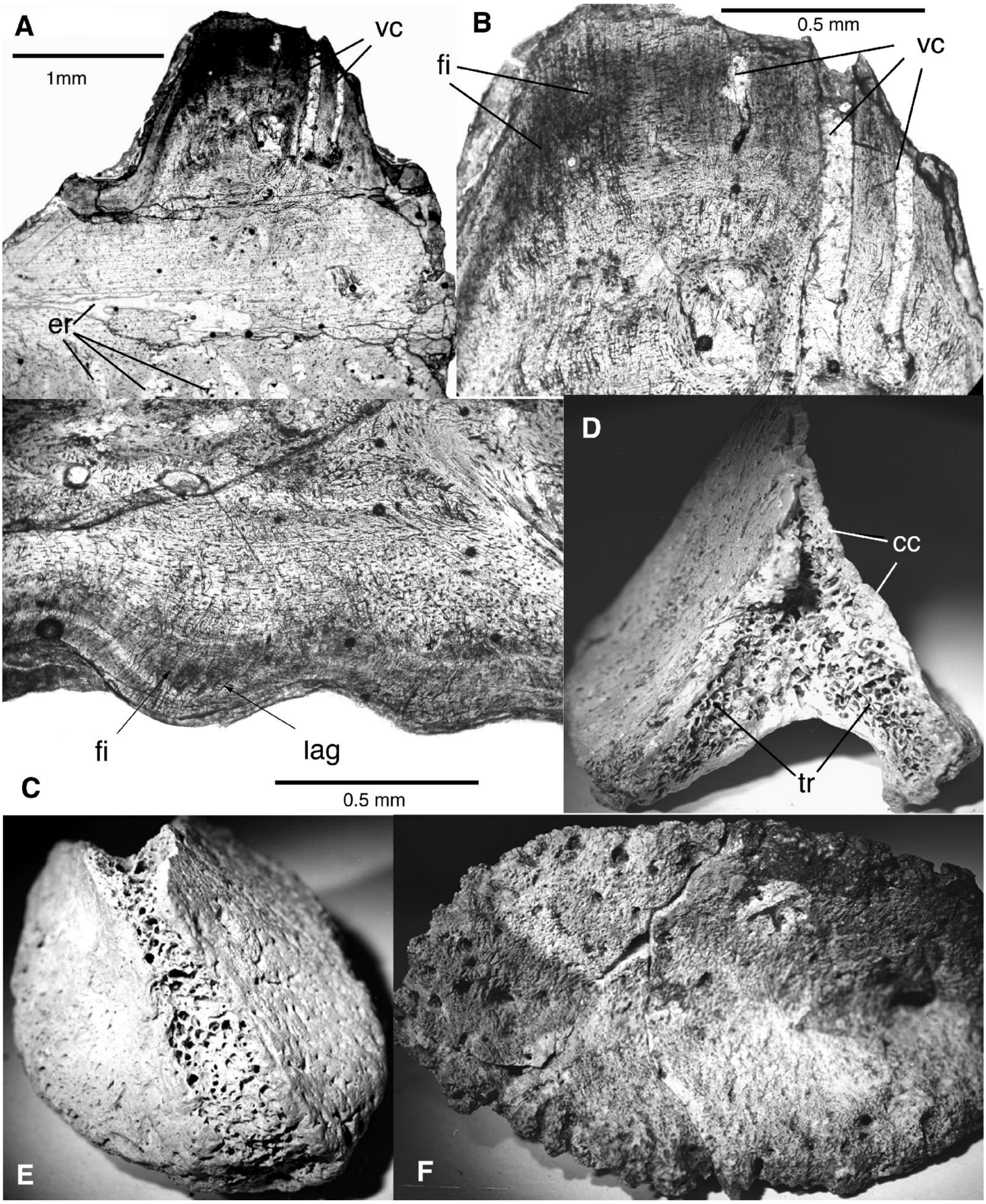

FIGURE 1. Scutes of *Scutellosaurus* (A–C, in thin-section) and *Scelidosaurus* (D–F, gross anatomy). A, Proximodistal thin-section of a keeled scute of *Scutellosaurus* (UCMP 130580), distal edge at top, to show entry of vascular canals into keel, primary cortex, and numerous erosion rooms internally. B, Detail of upper portion of preceding figure, to show primary bone structure of keel with extensive Sharpey's fibers. C, External cortex of base of same scute, showing nearly avascular structure with numerous fibers and at least one LAG. D, Keeled scute of *Scelidosaurus* (BMNH 39516) in end view. Loss of superficial bone reveals the typical internal structure of these scutes: a thin cortical layer covers a network of internal trabecular bone. Height of scute is 5 cm. E, Another scute of *Scelidosaurus* (BMNH 39516) in end view. This more globose scute, which lacks a prominent keel and has a flat bottom, has the same histological structure as the keeled scute. Length of scute is 5 cm. F, Keeled scute of *Scelidosaurus* (BMNH 39516) shown in Figure D, proximal view, to emphasize pits, grooves, and vascular pores on this concave surface. Abbreviations: cc, compact cortex; fi, bone fibers; lag, line of arrested growth; tr, trabecular bone; vc, vascular canal. Scale bar for A, 1 mm; for B and C, 0.5 mm.

however, course mostly parallel to each other in each bundle. Almost the entire outer cortex may be formed of this very fibrous bone, where a few developing osteons may also be present. In some senses this bone should be described as ''metaplastic,'' but the term has a meaning and a specificity that requires precision (see below, ''Growth and Evolution of Thyreophoran Scutes'').

In the internal cortex of the *Scelidosaurus* scutes, the bone is secondary trabecular cancellous tissue, with very few osteons. Very little dermal bone is left in the internal cortex, apart from some small islands (Fig. 2B); it is mostly found near the outer surface, where the trabeculae tend to be denser and oriented parallel to each other (and mostly perpendicular to the surface). Vascular canals enter the scute in these regions between the parallel trabeculae, and appear to communicate with numerous tiny erosion rooms and marrow spaces that become larger toward the inside.

In taller scutes, large medullary bays may be surrounded by a secondary deposit of regularly concentric tissue (Fig. 2C). These elongated spaces are similar in some respects to the ''pipes'' described in the plates of *Stegosaurus* (de Buffrénil et al. 1986; Scheyer and Sander in press). They are round or nearly so, larger than the surrounding medullary spaces, and distinct from the rest of the matrix. They may be ringed internally by secondary tissue or retain a scalloped, unfinished perimeter of trabecular bone. They may communicate with the distal face of the scute, as in *Scutellosaurus*.

Stegosaurus.—The gross morphology of *Stegosaurus* plates was very well illustrated by Marsh in the later 1800s (Ostrom and McIntosh 1966: Plates 59–64). The outside of the plate has a generally smooth surface of compact bone that is marked by grooves for blood vessels and by perforations for capillaries (Figs. 2D–F, 3). These grooves are very obvious in oblique light; they course in straight lines, occasionally with irregular curves, sometimes branching, and mostly in a proximodistal direction. They resemble in these respects similar grooves on the antlers of moose and elk and the frill and horns of *Triceratops*. They are seldom more than 1–2 mm deep and usually cannot be traced along the entire length of the bone. It is common to see grooves extend distally to the very edge of the plate, sometimes converging as the anteroposterior length of the plate is reduced distally (Fig. 2D). These grooves occasionally, but not usually, lead to or coincide with pits that appear to conduct blood vessels to the inside of the plate (Fig. 2E); isolated pits may also appear. The base of the plate is usually slightly expanded and may have a lumpy, pustulate appearance. The plates that appear to come from the shoulder region (e.g., USNM 7617; Fig. 1F) have a broadly expanded base that resembles the primitive condition in the much smaller flat scutes of *Scutellosaurus* and *Scelidosaurus* described above.

Many of these observations also apply to the tail spikes (Figs. 4, 5A), taking into account the general difference in shape. External grooves, pits, and perforations appear much as they do in the plates, and the base is slightly expanded and pustulate. The throat ossicles, in contrast, are shaped like disks approximately 2.5–3 cm in diameter and 0.8 cm in typical thickness, slightly convex on their distal surface and flat to slightly concave or convex proximally.

The histology of a *Stegosaurus* plate was described by de Buffrénil et al. (1986), and our observations of the plates we studied are largely concordant with theirs. The plates are formed of two layers of thin, compact bone tissue that surround an internal cancellous medullary layer of trabecular bone in which medium to large erosion rooms appear (Fig. 2G), much as in *Scelidosaurus*. Near the apex there is poorly vascularized cortical bone that can be extensively remodeled by secondary (Haversian) substitution internally; the deepest medullary region is secondary cancellous trabecular bone with evidence of extensive erosion-reconstruction cycles (Fig. 5B). Around it, the extent of remaining primary bone and of secondarily reworked bone tends to vary locally within the plate. De Buffrénil et al. determined that the types of bone tissue deposited in various parts of the plate suggested that the base of the plate was where the highest rates of growth took place, and that because more secondary reworking took place in

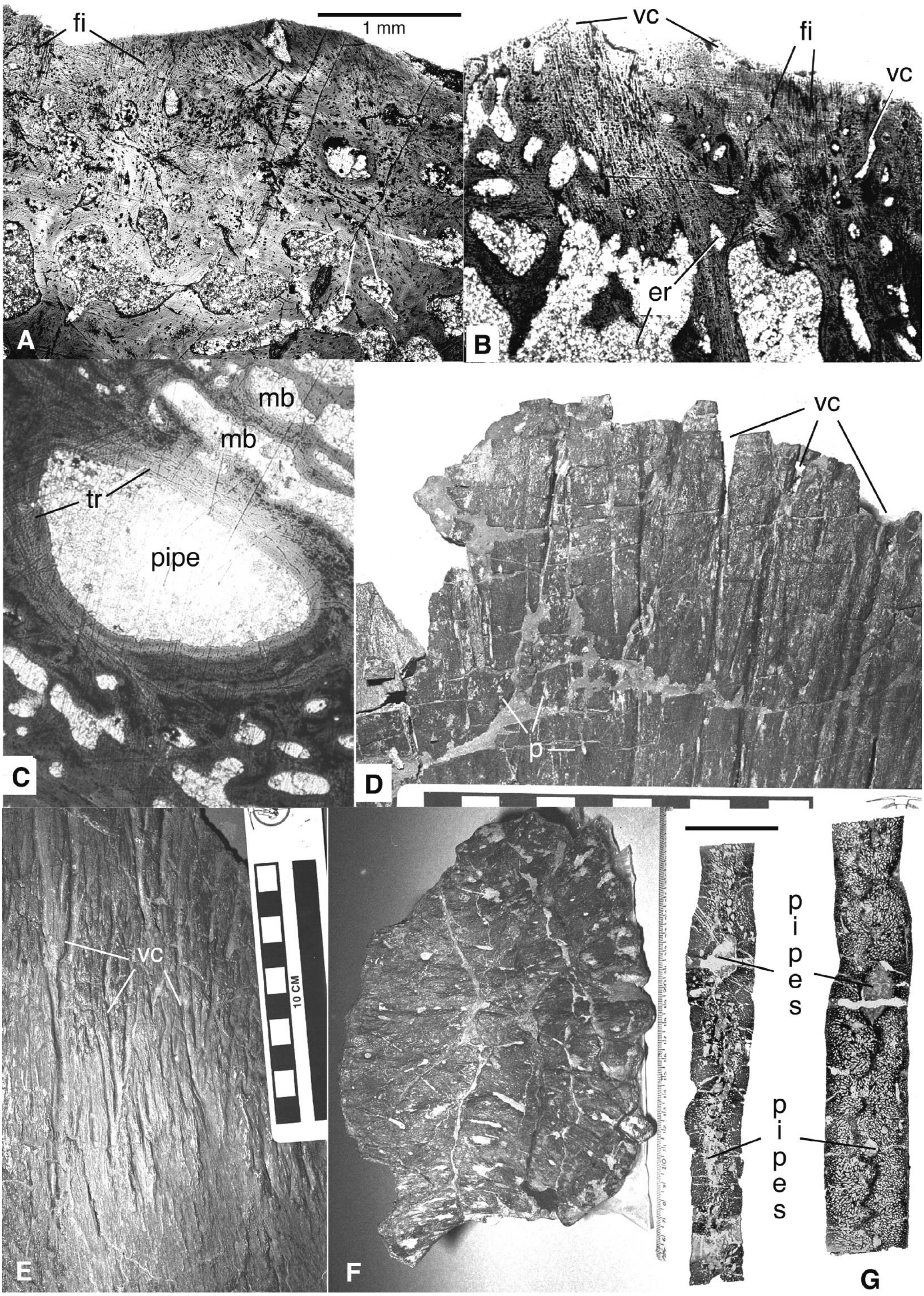

FIGURE 2. Scutes of *Scelidosaurus* (A–C, in thin-section; scale bar, 1 mm) and *Stegosaurus* (D–F, gross anatomy, G in thin-section). A, Cross-section of a scute of *Scelidosaurus* (BMNH 39516), showing the histological structure near the surface. The outer compact bone tissue (distinguished by the many bundles of fibers that course in all directions, but largely perpendicular to the surface) is invaded by vascular pits at the surface and hollowed by secondary erosion rooms internally. B, Same section, different field, to show the large internal erosion rooms and the strutlike vertical columns of trabecular bone. C, Same specimen, to show a particular kind of medullary bay that is very

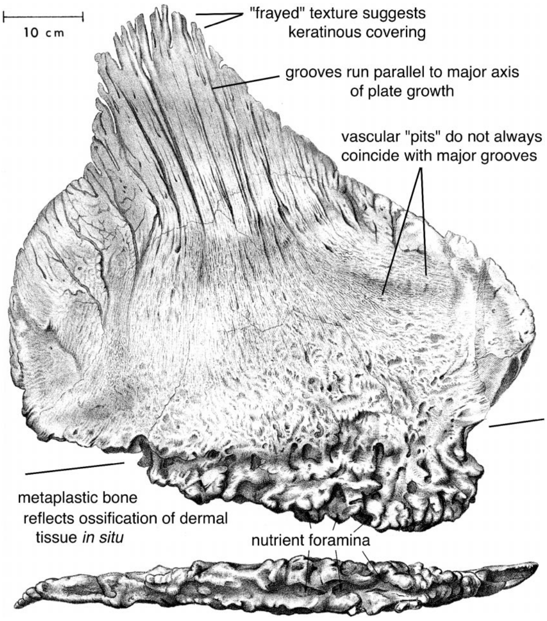

FIGURE 3. Marsh's illustration of a typical large plate of *Stegosaurus* from Como Bluff (USNM 4714, anterior at right) in lateral (top) and proximal (bottom) views, to show the extent and direction of the vascular grooves on the surface of the plate, and the expanded, pustulate appearance of the bone at the base of the plate. The line indicates the minimum distal prevalence of metaplastic bone, which represents ossification of adjacent fibrous tissue and hence must be deposited within the dermis. Adapted from Ostrom and McIntosh 1966: Plate 61.

the upper regions, the uppermost regions were progressively older ontogenetically than the basal regions. However, bone continued to be deposited periosteally both on the outer surfaces of the plate and at its base (de Buffrénil et al. 1986: Fig. 6). The apex of the plate (Fig. 5C) contains many osteocyte lacunae and fibers; thin secondary deposits of bone can be seen within the vascular spaces. In Figure 5D, two canals of moderate size at the apex appear to communicate with the local internal region of the bone, as in the scute of *Scutellosaurus* described above.

De Buffrénil et al. also noticed that bony trabeculae form the walls of several ''pipes'' or vertically continuous cylindrical channels that run proximodistally in the innermost medullary region of the plates. They used the term ''pipe'' as a morphological descriptor, not necessarily in a functional sense. We have observed these ''pipes'' in other *Stegosaurus* plates (Figs. 2G, 5B). They are 0.7–1.2 cm in diameter, depending on their position in the bone, and spaced at intervals of about 1.0–1.5 cm at the middle height of the plate. Their diameters and intervals decrease toward the distal edge, and they do not reach the surface of the distal edge; that is, they are confined to the medullary region, which in the distal section of the plate is pinched out, leaving only the external compact cortical bone. Nor do they exit along the sides of the plate. In some specimens (e.g., USNM 46130), external grooves that reach the tips of the plate lead to pits that appear to enter the cortex, but these are not contiguous with the ''pipes'' (Figs. 2D, 3, 5D). Structurally, the ''pipes'' do not show characteristics of osteons; that is, there is no evidence of regular centripetal deposition of a continuous layer of secondary bone around their peripheries, and their walls are locally formed of secondary lamellar tissue, often

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similar to the ''pipes'' observed in *Stegosaurus* plates. This structure differs from the surrounding medullary bays in being larger, more regularly shaped, rounder, and ringed internally by secondary endosteal tissue. D, Detail of *Stegosaurus* plate, USNM 7585, showing the distal edge of the plate and the grooves that run to the edge without diminishing in diameter or entering the plate. These features suggest that these grooves contained the vascular canals that supplied blood to the presumably keratinous covering. Scale bar in cm. E, Detail of *Stegosaurus* plate, USNM 2274, showing the vascular channels that are indented into the bone surface. Scale bar in cm. F, Shoulder plate of *Stegosaurus*, USNM 7617, in lateral view (ventral side to right edge). This plate morphology is unusual because the keel is not as high as in most plates, the base is bilaterally expanded, and the proximal surface is concave; in these respects the plate resembles scutes of more basal thyreophorans and the intermediate condition of a moderately pronounced keel is evident. Note the many pits and channels on the surface. Scale bar in cm. G, *Stegosaurus*, USNM 6531, two successive cross-sectional segments from the upper region of a typical high, flat plate. Note the compact cortical surface bone, the trabecular internal bone, and the many small medullary bays. Of particular interest are the larger, rounded ''pipes,'' which can be seen to be continuous from one section to the next and are likely a kind of large, elongated, regular-shaped tubular system. Compare these unusual large erosion rooms with the similar structures in *Scelidosaurus* (C). Scale bar for G, 1 cm. Abbreviations as in Figure 1; er, erosion room; mb, medullary bay; p, vascular pits.

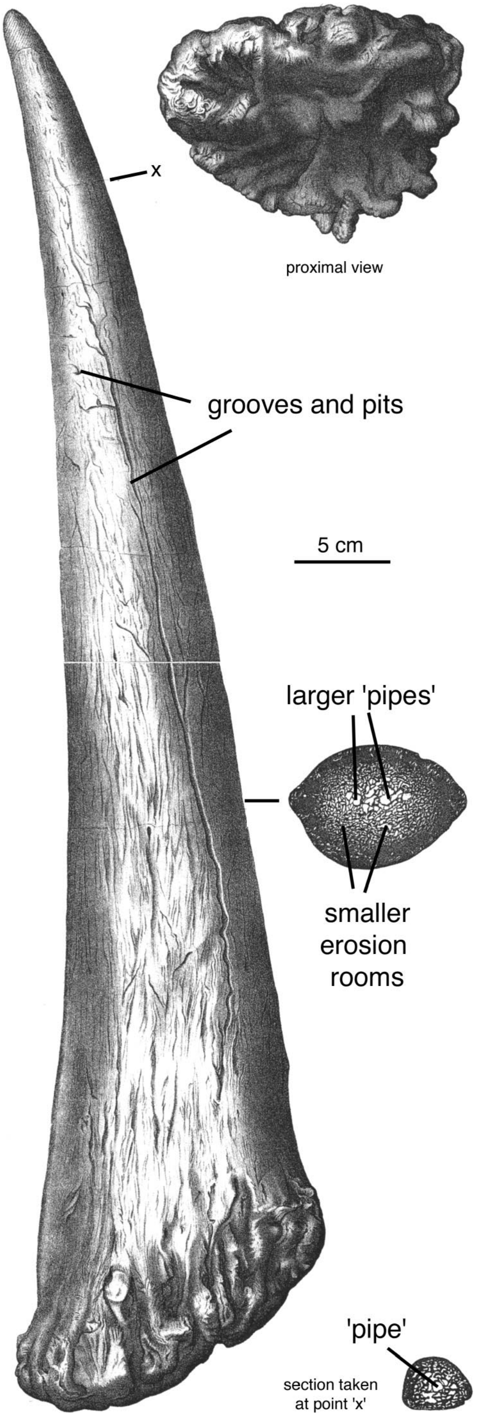

FIGURE 4. Marsh's illustration of a typical tail spike of *Stegosaurus* from Como Bluff (YPM 1853) to show the extent and direction of the vascular grooves on the surface of the plate, and its cross-section. Note presence of both large (''pipes'') and small medullary bays, as in the *Stegosaurus* plate in Figure 3. Adapted from Ostrom and McIntosh 1966: Plate 55.

with a scalloped erosional surface (Fig. 5B,E). Where bony tissue that surrounds the periphery of the ''pipes'' can be observed clearly (e.g., USNM 46130), it is of the same character and thickness as the trabecular bone that surrounds the many smaller medullary bays associated with erosion rooms in the same local area. Nutrient foramina, perhaps continuous with these ''pipes,'' can be seen along the base (proximal end) of the plate.

The spikes of *Stegosaurus* (e.g., USNM V6135), despite their difference in gross morphology from the plates, are similar to them in general organization. There is an outer layer of compact, mostly primary bone that encircles an inner cortex of trabecular bone that includes numerous medullary bays, and finally a medullary cavity or canal of variable diameter (Figs. 4, 5A). Secondary osteons can invade the internal and external cortex virtually to the external limit of the bone.

A cross-section taken about midway along the length of the spike (Figs. 4, 6A) illustrates the general histological organization of the bone, which can vary locally. The bone has an amorphous organization and incorporates many collagenous fibers. There can be numerous vascular canals in the bone that mainly course radially and longitudinally, but some sections are poorly vascularized (Fig. 6A,B). Most of these osteons, though small like the primary osteons typical of denser regions, show the circumferential organization of tissue typical of secondary osteons. Bundles of fibers tend to run parallel to some osteons in the primary bone, which suggests that these are primary osteons. Other fiber bundles are cut by ostensibly secondary osteons. In the deep cortex the bone is mostly trabecular; occasionally islands of primary bone can be seen (Fig. 6B). One or two ''pipes'' may be present at various cross-sections along the spike's length (Fig. 4).

Toward the apex of the spike is a relatively thick outer layer of primary bone that contains numerous longitudinal osteons and numerous obliquely oriented fibers. This outer layer grades inward into a region of medullary resorption spaces that reflect the development of secondary osteons. Interior to this region is a thick region of secondary osteons, with rare primary osteons in the few remaining islands of primary bone. The Haversian systems are multigenerational, as their encroachment upon their neighbors indicates. Near the apex there is almost no central cancellous region or medullary cavity.

The throat ossicles (Fig. 6C) present quite a similar picture. A very thin layer of compact bone surrounds the outer perimeter of the ossicle (USNM 7947; Fig. 6D). Again, this tissue is almost entirely coarsely woven primary dermal bone, except where it has been replaced in the cortex by secondary osteons and in the medullary cavity by trabecular bone. Reid (1996: p. 26) noted for a similar specimen that it ''showed bone formed from irregularly interwoven ossified fiber bundles, with some replacement by compact secondary osteons but no periosteal content.'' Secondary osteons can be found almost to the edge of the bone. As with the other tissues examined, medullary bays are common; in addition, small holes with scalloped edges that appear to be incipient erosion rooms are common in the internal cortex. Numerous fibers run parallel to the surface through the tissue and contact the outer surface of the ossicle. The highly remodeled medullary region is rich in endosteal tissue, which also surrounds the remaining islands of primary dermal bone and osteons.

Ankylosaurs.—Ankylosaurs present a complex situation (Scheyer and Sander 2004). They have many different types of dermal ossicles and scutes that are thicker and more extensively distributed over the body than in other thyreophorans (Carpenter 1997, 2001; de Ricqlès et al. 2001). Externally, many ankylosaur scutes are similar in gross respects to those of *Scutellosaurus* and *Scelidosaurus*: they are flat and ovoid and bear low anteroposterior keels, they are sculptured by external grooves and pits, and they appear to consist of a compact outer layer that surrounds a spongy internal layer. The composition of these scutes is essentially as in the thyreophoran scutes discussed thus far, but metaplastic bone has also been detected. Cooper (in Blows 1987) recognized metaplastic bone in the armor of *Polacanthus*, and Reid (1996: p. 26) noticed this tissue type and its unusual construction in other ankylosaur scutes (and the throat ossicles of *Stegosaurus*, as noted above):

> The fibrous tissue seen in the lower parts gives a very strong impression of being of metaplastic origin, and it also gives an impression of being formed initially as compact bone, despite the lack of a compact basal plate, because cancellous spaces in it cut through fiber bundles. . . . Flat-lying armor from the early ankylosaur *Polacanthus* and an unnamed Late Cretaceous species from Alberta again showed bone ossified from large irregularly interwoven fiber bundles, but a sample from *Sauropelta* was instead formed mainly from reconstructed (Haversian) cancellous bone, with fiber bundles seen only in a thin basal layer of periosteal bone.

Scheyer and Sander (2004) hypothesize that this variation of scute composition is diagnostic among the three subgroups of ankylosaurs (polacanthids, nodosaurids, and ankylosaurids). Our observations were confined to ankylosaurids and agree with theirs. In some scutes or areas of scutes, a relatively thin, somewhat fibrous outer compact cortical layer surrounds an internal medullary region of trabecular bone. But in most scutes, highly fibrous, compact metaplastic bone predominates throughout the interior (Fig. 7A). The large fiber bundles typically have a strongly interwoven, zigzag pattern (see also de Ricqlès et al. 2001, on another ankylosaur from Antarctica). Some fiber bundles are generally oriented more or less perpendicular to the surface of the scute. Color changes reflect bursts of mineralization of the fibers parallel to the osteoderm's free surface. The fibers are orderly and often fan-shaped in orientation within the bundles, much like the structure of ossified tendon. The cell spaces are also orderly in their arrangement, unlike typical periosteal tissue. These metaplastic tissues are far less vascularized than those of typical thyreophoran scutes.

Incremental growth lines (Fig. 7B), parallel to the bone surface or to each other, show cycles of deposition of bone, which have been described for the metaplastic osteodermal tissue of lizards (Levrat-Calviac and Zylberberg

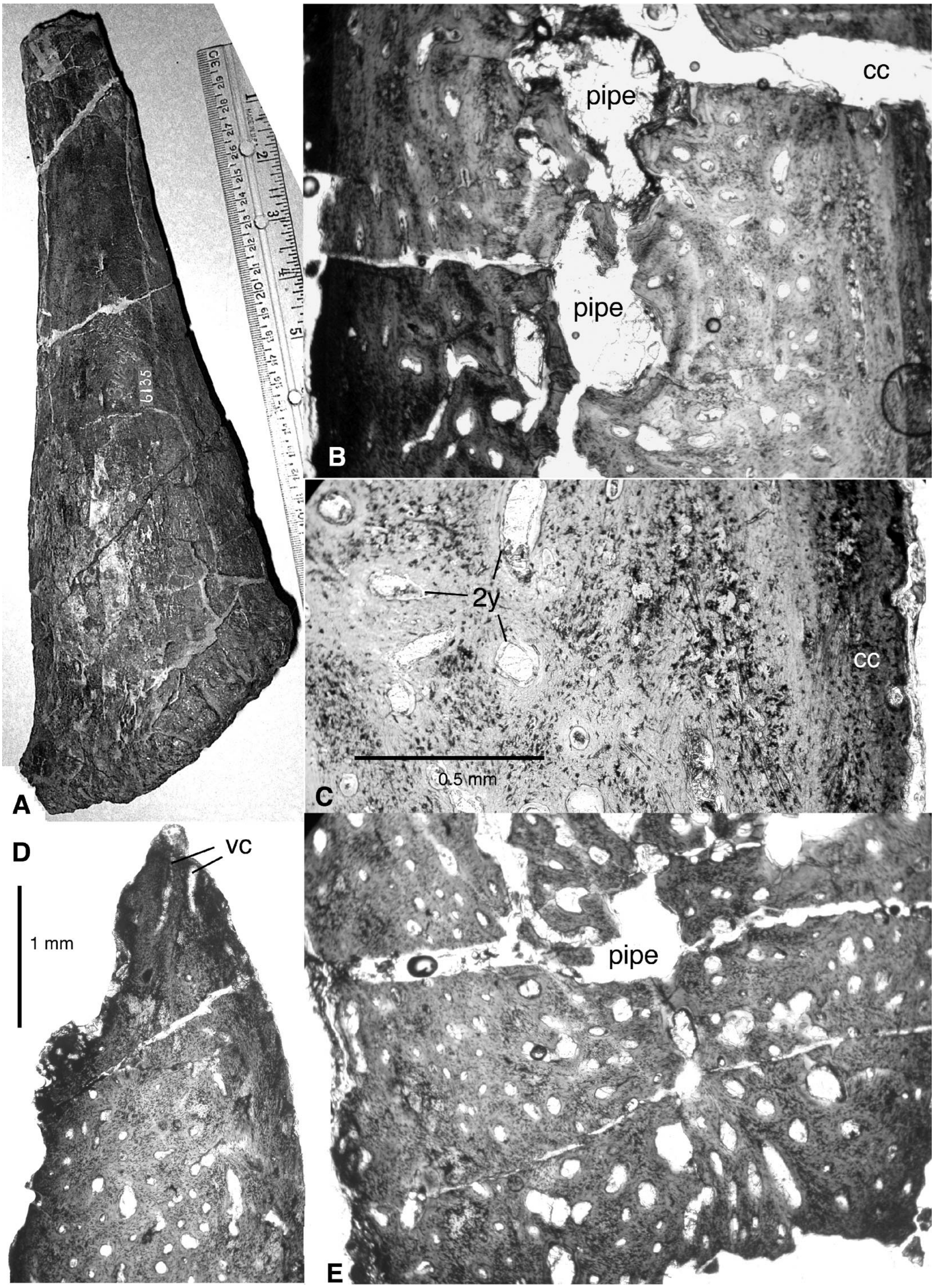

FIGURE 5. Spike and plates of *Stegosaurus*. A, Tail spike of USNM 6135, showing pustulate base, and longitudinal blood channels and pits on the outside of the spike. Scale in cm and inches. B, Plate of USNM 6531, transverse section through plate to show compact external bone (left and right edges), and details of internal ''pipe'' and surrounding structures that are largely built of primary bone. Note scalloped erosional edges around the upper ''pipe''; some centripetal bone is deposited in the upper right part of the lower ''pipe.'' C, Plate of USNM 46130, transverse thin-section of the superficial cortex in detail. The cortex is built mostly of primary, irregularly woven bone tissue, crossed by primary osteons, that becomes more compact toward outer edge (right); secondary bone is

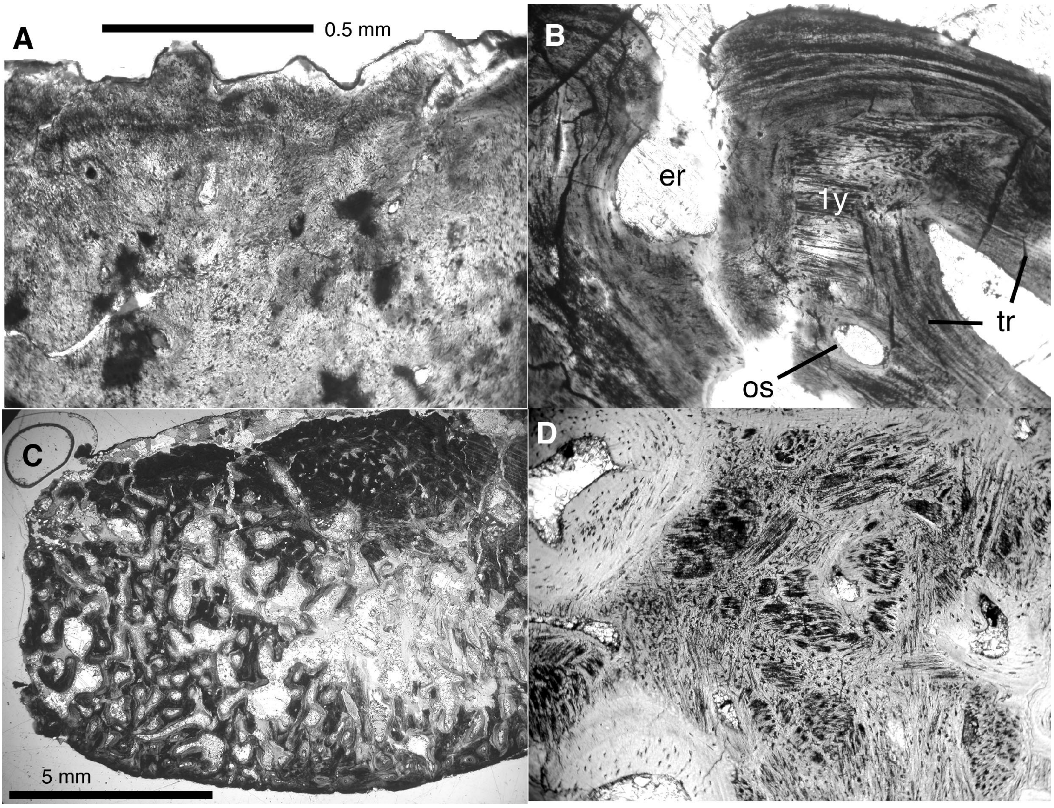

FIGURE 6. Thin-sections of spike and throat ossicle of *Stegosaurus*. A, USNM V6135, partial cross-section about midway along the length of a large tail spike, to show metaplastic-like bone tissue with scarce vascular canals and one ''cycle'' of growth. B, Detail of previous slide to show apparent erosion-reconstruction processes close to the bone periphery, engulfing an ''island'' of metaplastic-like bone tissue with extensive systems of fiber bundles. The unconformity of osteonal deposition (os) is evidence that it is secondary. C, USNM 7947, vertical section through a typical throat ossicle, with distal edge above. Notice the same arrangement of external cortical bone surrounding a lightly constructed, trabecular interior. D, Transverse section of same throat ossicle, showing an apparently metaplastic bone matrix with numerous fiber bundles in various orientations and large secondary osteon-like medullary bays. The few small vascular canals may be incipient erosion rooms. Scale bar for A, B, and D, 0.5 mm; scale bar for C, 5 mm. Abbreviations: er, erosion room; tr, trabecular bone; 1y, primary bone.

1986); there is also evidence of modest cycles of erosion and reconstruction of bone deep within the scute. The tissue is dense even well within the bone; there is no spongy bone, and the construction of the tissue is quite complex and fibrous throughout. Osteocyte lacunae are numerous but they are small and difficult to observe; we have been unable to find canaliculi surrounding the osteocyte lacunae of any thyreophoran scute, although at times their flattened appearance gives the impression of lateral extensions resembling canaliculi (and Martin Sander [personal communication 2003] noted that he and Torsten Scheyer have found them both in ankylosaurs and in *Scelidosaurus*). Scheyer and Sander (2004) identify ''pipes'' in the scutes of the polacanthid *Gastonia* and ankylosaurids as canals for large

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centripetally deposited around some erosion rooms. D, *Stegosaurus*, USNM 6531, a longitudinal section through the apex of the plate, to show the entry of two vascular canals at the tip. Note that these have not been found to communicate with the internal ''pipes.'' E, Same slide, different field, showing internal structure just below the apex. Most of the cortex is well vascularized and still primary in structure. Erosion-reconstruction processes result in a more cancellous medullary region. Abbreviations as in Figure 1; 2y = secondary bone. Scale bar for B, D, and E, 1 mm; scale bar for C, 0.5 mm.

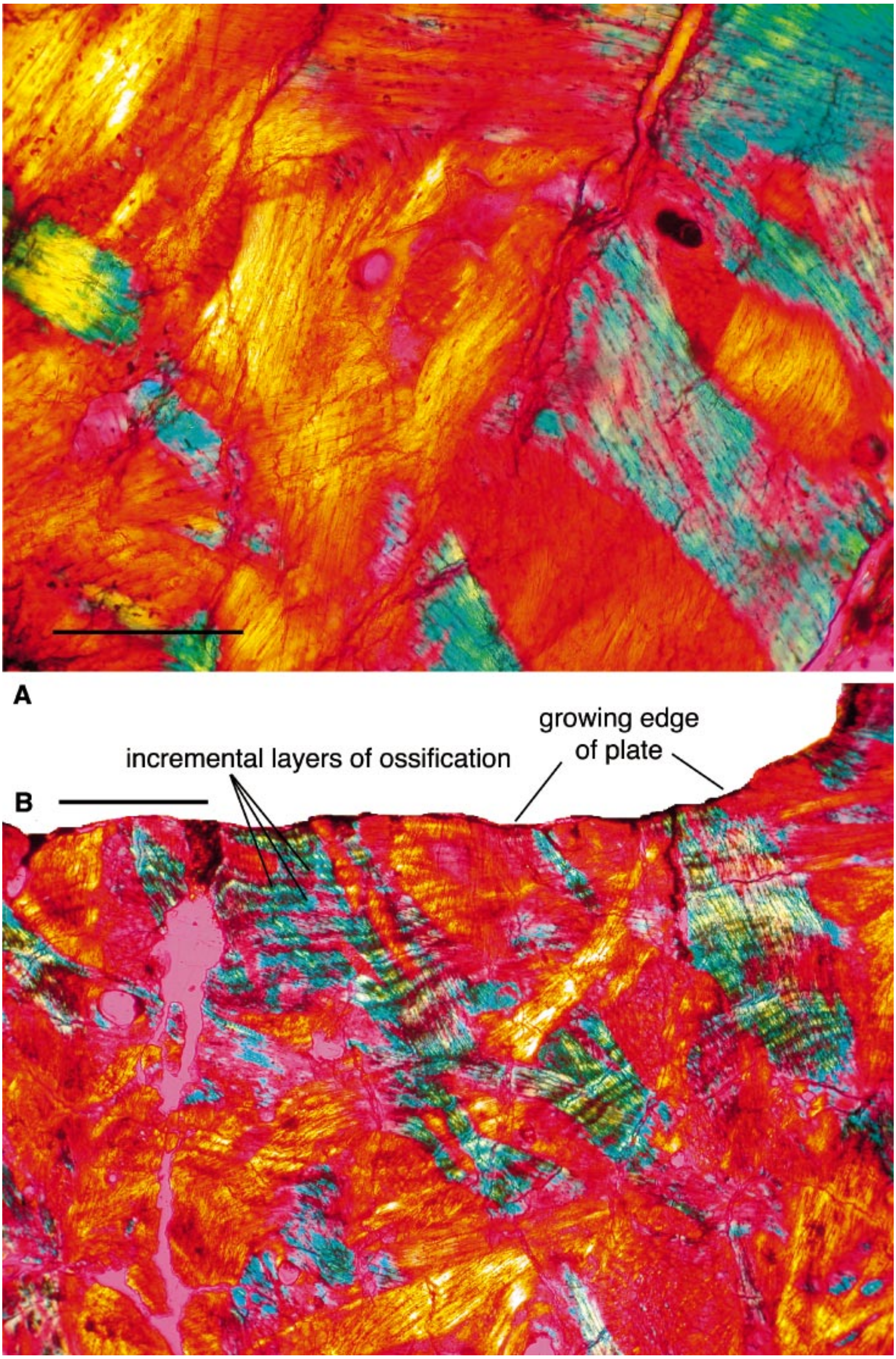


FIGURE 7. Cross-section through an ankylosaur scute from the Judith River Formation of Montana (UCMP 179282). A, Metaplastic bone birefringes, reflecting different orientations of ossified tissue bundles, characterized by fibers that tend to course in the same direction. Small osteocyte lacunae appear in line with the bundles. Vascular canals are extremely scarce. B, Same specimen, taken at the edge of the scute. Clear incremental layers of ossification can be seen in the fibrous tissue bundles that course peripherally. Scale bar for A, 0.5 mm; scale bar for B, 1 mm.

blood vessels. Such canals are often ringed internally by lamellar bone, as in stegosaurs.

Growth and Evolution of Thyreophoran Scutes

On the Problem of "Metaplastic" Bone.—By ''metaplastic bone'' (Haines and Mohuiddin 1968), we refer to a major component of thyreophoran osteoderms: a poorly vascularized, amorphous dermal bone tissue in which fibers are very numerous and oriented in many directions. This is metaplastic bone in a general sense, as distinguished from bone that is clearly of periosteal origin but may nevertheless contain numerous fibers (which are often directed perpendicular to the periosteal surface). Metaplastic bone may have many osteocyte lacunae, but they apparently lack canaliculi (Levrat-Calviac and Zylberberg 1986). The tissues we describe as metaplastic are obviously primary because they do not replace existing bone (they replace connective tissue); however, they do not have a typical periosteal origin. Furthermore, without more evidence we cannot distinguish metaplastic bone from neoplastic bone, that is, avascular, amorphous bone that forms dermally but does not replace preexisting tissue of any kind.

Considerable attention has been paid in the literature to the problem of bone formation by simple mineralization of preexisting tissue, generally a densely fibered connective tissue such as tendons, ligaments, dense dermis, or even cartilage (e.g., Beresford 1981; Haines and Mohuidden 1968; Reid 1996). Fossil material does not allow direct observation of the ossification process itself, but the structure of the resulting tissue can nevertheless provide hints to how it was produced. We have noticed above, in several specimens of *Stegosaurus* (throat ossicles) and especially in ankylosaurs, peculiar bone structures that are best interpreted as metaplastic bone (see also Reid 1996; Ricqlès et al. 2001).

Generally, metaplastic bone (distinguishing metaplastic from neoplastic bone) would not need a specialized layer of new, actively differentiated osteoblasts (e.g., a periosteum) for its production. It would require instead that the preexisting cells of a tissue begin to behave as osteoblasts (including local mineralization of the extracellular fibrillar matrix), and ultimately as osteocyte lacunae. These conditions may often be met in ligaments, tendons, and the *stratum compactum* of the dermis. In such cases, the resulting metaplastic bone would retain all the histological characteristics of the preexisting soft tissue, plus its permineralization by hydroxyapatite crystals. On the other hand, new bone formed by neoplasy (such as periosteal or ''typical'' membrane bone) integrates newly generated osteoblasts that turn into osteocytes as they synthesize a new extracellular collagenous matrix de novo (neoplasy). However, many intermediate situations may exist between the two extremes of this spectrum. During its deposition, periosteal or dermal bone may integrate a small or large number of ''extraneous'' fibers (the so-called Sharpey's fibers). Hence, depending on their proportions, the bone can change from ''typical'' periosteal into more or less ''metaplastic.'' This intermediate condition probably prevails in the bases of osteodermal plates and spikes in *Stegosaurus*, and in many regions of the osteoderms of *Scutellosaurus* and *Scelidosaurus*.

Ankylosaurs show an even more typical condition of metaplasy. Indeed, their osteoderms seem to match in every detail the structure of a dermis *stratum compactum*. The large fiber bundles running in several directions, the apparent ''in phase'' orientation of fibers and fibrils within bundles, the alignment of cells along the main axis of the fibers, and the low vascularization are the main structural characteristics of these osteoderms similar to dense dermis. One may also note, in the large scutes of ankylosaurs observed here, that the main diameter of bundles does not seem to change from within the osteoderm to its periphery, as would certainly be the case if the neoplastic ossification of a dense connective tissue previously in situ had taken place. This was discussed in the case of the tiny ankylosaur osteoderms described by Ricqlès et al. (2001). Also, evidence of osteoderm ''growth'' (actually of its mineralization) is provided by the concentric ''modulations'' parallel to the osteoderm surface and to each other, observed especially in the bundles perpendicular to the osteoderm surface. This would be evidence of successive ''bursts'' in the advance of the mineralization front in the preexisting bundles, progressively increasing the overall size of the osteoderm as an accretionary process. The osteoderms formed by metaplasy may be ultimately more or less remodeled inwardly into more ''typical'' secondary bone by erosion/reconstruction processes, as also happens in the mineralized tendons of ornithischian dinosaurs. At this stage, in spite of their peculiar ontogenetic origin, metaplastic osteoderms ''behave'' much like regular bone.

Growth Patterns of Thyreophoran Scutes.—The distribution of bone tissues in thyreophoran scutes appears to reflect two principal means of formation, a conclusion independently reached by Scheyer and Sander (in press) and Reid (1996). The primary bone of the external, unreworked regions of most scutes is typical dermal bone (Figs. 1A–C, 2A,B). It is not highly vascularized and often contains many fibers that course in all directions, often quite densely. The second means of formation also produces highly fibrous bone, but in this case entire bundles of fan-shaped, parallel fibers may be ossified in a preexisting matrix of dermal soft tissue. This type of bone, which corresponds to the ''metaplastic'' type discussed above (and see below, ''Evolution of Thyreophoran Scute Form''), differs from the first because the fiber bundles are highly birefringent under polarized light and the tissue is poorly vascularized (Fig. 7A). Bands of alternating light and dark tissue suggest incremental ossification that cuts across various fiber bundles and tissues, regardless of their orientation (Fig. 7B).

These tissues may seem quite different in some respects, but they both have strong complements of fibers and both are clearly variations of dermal bone. They are therefore only somewhat different manifestations of the same process. This is clear, for example, in the throat ossicles of *Stegosaurus* (Fig. 6C,D), where in different regions of an apparently homogenous bone, different tissue types may be locally and perhaps temporarily produced. The ''metaplastic'' bone is ostensibly a more direct ossification of preexisting fibrous bundles. The type of tissue produced may in part depend on what types of soft tissues are locally present before ossification begins; the presence of such local tissues themselves could reflect a phylogenetic signal, as Scheyer and Sander (2004) suggest. However, as noted below, the thickness of metaplastic bone is limited because it lacks canaliculi and is poorly vascularized.

This anatomical description is agnostic with respect to whether the bone originally formed around a fibrous ''template'' that approximated the form of the scute (true metaplastic bone), or whether the bone formed in place without a precursor (neoplastic bone). De Ricqlès et al. (2001) noted the same problem in the ankylosaur scutes that they studied. At present a sufficient ontogenetic series is not available to test this hypothesis.

Are these kinds of tissue homologous? Systematists distinguish between taxic homology, in which all taxa under consideration manifest a given feature, and ''biological'' or ''deep'' homology (Gould 2002), in which phenotypic manifestation may vary but the common ability to express these features phylogenetically is established. In the present instance, the topological relationships, the outward form, means of development, and composition of the various dermal ossicles are the same among thyreophorans, even though the type of tissue produced may vary according to local (ontogenetic) circumstances and perhaps also from taxon to taxon. The gross phenotypic features that allow us to recognize these bones as homologous scutes do not change. It is therefore a case in which the developmental processes may vary but the phenotypic outcome is still ostensibly homologous.

Through ontogeny, successive layers of primary dermal bone were laid down along the periphery of the scutes while that part of the bone was in contact with the dermis. This bone varied in the degree and orientation of vascularization, depending on the growth trajectory of the scute. As it grew, this bone was replaced in the medullary cavity through processes of erosion and redeposition. The outer compact cortical layer was also replaced, rapidly in some areas, by secondary (Haversian) tissue that is found in the deeper layers of this outer cortex. In other parts of thyreophoran scutes, bone that appears to have been originally metaplastic (Fig. 7) is sometimes replaced by secondary bone. This replacement is necessary in metaplastic bone, as Levrat-Calviac and Zylberberg (1986) noted: there is a limit to its possible thickness because it lacks canaliculi and is sparsely vascularized. This process left an internal structure of relatively sparsely constructed, branching trabeculae of secondary bone tissue. This tissue frequently contains marrow bays that connect with vascular channels that lead to the surface of the bone. This tissue is first seen in *Scutellosaurus* (Fig. 1A,B); the broad, elongated channels are also present in *Scelidosaurus* (Fig. 2C), and we suggest that the ''pipes'' in the plates and spikes of *Stegosaurus* (Figs. 2G, 4) are probably homologous with these medullary bays or channels, in even more elongated form. Scheyer and Sander (2004) have also identified such ''pipes'' in ankylosaurid scutes.

De Buffrénil et al. (1986) developed a model of the growth of *Stegosaurus* plates that suggests that growth took place simultaneously at the base and along the sides of the plates, and Reid (1996) agreed. This is clear in the simpler scutes of, for example, *Scutellosaurus*, which show growth both on the proximal side and along the other edges (Fig. 1C). However, the plates and spikes of stegosaurs are remarkable for the hypertrophy of their distal growth, and so there is frequently considerable evidence of rapid rates of growth at the peripheral margins of the plates, as de Buffrénil et al. indicated. Metaplastic bone is more likely to have formed at the bases of plates, as new bone incorporated previously existing fibrous bundles that connected the bony plates to surrounding dermal tissues.

General Structural Homologies of Thyreophoran Scutes.—Thyreophoran scutes share extensive histological similarities that are typical of dermal scutes (Scheyer and Sander 2004) as well as of platelike bone in general; i.e., compact outer cortical layers of primary bone surround a secondary medullary region of trabecular bone, and features of secondary reworking and cycles of erosion and redeposition of bone largely reflect the mature age of that part of the bone. The outer surface has pits, grooves, and perforations that represent traces of vascular structures. Whether the scute is expanded laterally, as seen in ankylosaurs, *Scutellosaurus*, most *Scelidosaurus* scutes, and in a few broad-based *Stegosaurus* plates, or is expanded distally, as in *Stegosaurus* plates and spikes, this pattern remains the same.

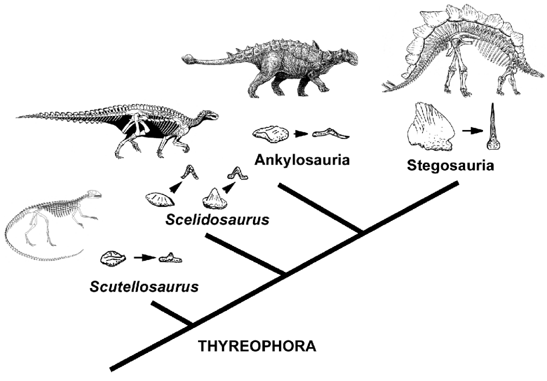


FIGURE 8. Phylogeny of Thyreophora (based on Sereno 1986 and other sources), with evolution of scute features added. For explanation see text. Figures of *Scutellosaurus* by Pamela Lungé (from Colbert 1981), of *Scelidosaurus* (courtesy of Greg Paul), of an ankylosaur by John Sibbick (from Norman 1985), and of *Stegosaurus* from Marsh (after Ostrom and McIntosh 1966).

We suggest, therefore, that these types of scutes should be regarded as specially and serially homologous (Owen 1846). That is, the scutes are homologous in different taxa (special), and in their various forms along the body axis and laterally they are corresponding structures (serial). They appear in the same approximate positions in the skeleton; they are made of the same kinds of tissue (dermal or membranous bone of mostly metaplastic construction), and they show evidence of developing in the same way. These features of the scutes satisfy the criteria of homology developed and synthesized by Owen in a pre-Darwinian context. The phylogenetic underpinning of these homologies can also be established: a phylogeny based on many characters (e.g., Sereno 1986) shows that these features were inherited from a common thyreophoran ancestor, and that the more elaborate forms of stegosaur plates and spikes, as well as the simpler ankylosaur scutes, appears to be derived directly from the patterns of more basal thyreophorans (Fig. 8).

Evolution of Thyreophoran Scute Form.—Thyreophoran phylogeny (Fig. 8) suggests a model of scute evolution that begins with a relatively flat plate, anteroposteriorly oriented, that has a low keel along this axis (as in *Scutellosaurus*). The two sides of this flat plate can expand laterally, as in many ankylosaur scutes, or they can adjust their orientation to form the arched sides and even the rounded, caplike shapes found in *Scelidosaurus*. Another evolutionary process, mediated by developmental rates like the first, is the hypertrophy of growth along this distal keel in a vertical direction. In this way, given a flat, rounded scute model, the spikes of stegosaurs can be produced; given an elongated scute model, the plates of stegosaurs can be produced. In nearly all scutes, both processes of expansion operate to a greater or lesser degree.

Like Reid (1996) and de Ricqlès et al. (2001), we are not able to answer the question of whether the primary bone that predominates in some scutes of thyreophorans formed on a template of preexisting fibrous tissue (true metaplastic bone), directly with no template (neoplastic bone), or both in different regions and at different times. Both processes may be in a kind of ontogenetic competition, and local circumstances of growth, size, or age of the tissue may determine which type of tissue predominates in a given scute. Systematic studies of ankylosaur and other such scutes, in ontogenetic and positional context, may illuminate this problem (Scheyer and Sander 2004).

Functional Hypotheses for Stegosaur Plates

General Remarks.—Given the generally accepted phylogenetic outline of thyreophoran evolution (Sereno 1986), it is reasonable to conclude (1) that this branch of ornithischians primitively had scutes over most of the body, as in *Scutellosaurus* (Colbert 1981), and (2) that these were retained and augmented in several ways in ankylosaurs, and lost from the sides of the body in stegosaurs (Fig. 8). Our histological findings also suggest that scutes were present in the common thyreophoran ancestor, because the tissue composition of the scutes, the distribution of these tissues among various scutes, and the morphological continuum of histological structure that emerges in phylogenetic context are consistent with each other. For our purposes it does not matter if *Scelidosaurus* is a basal ankylosaur (Norman 2000, 2001a,b; Carpenter 2001) or a basal thyreophoran, because the general histological pattern of basal thyreophorans is continued in ankylosaurs (with modification in some scute types as noted above).

Armor.—De Buffrénil et al. (1986) rejected the hypothesis that plates and spikes were protective, because the internal trabecular structure seemed to have low resistance to crushing, such as a powerful bite from a carnosaur would deliver (see also Carpenter 1998). Most thin-sections of plates that they and we studied bear out this statement: diagenetic crushing has almost without exception distorted the medullary regions.

Display.—This broad category includes ''intraspecific agonistic, deterrent, or sexual display structures'' or ''interspecific deterrent display structures.'' Neither de Buffrénil et al's. (1986) study nor ours could eliminate these possibilities. However, given the lack of demonstrated sexual dimorphism in stegosaurs, we find intraspecific (sexual) display functions unsupported. Whereas it is possible that unusual structures may be present in both sexes but functional in only one, this situation is so unusual that it requires another type of evidence to be plausible in a given case. Without such independent evidence in stegosaurs, the hypothesis is weak.

It is possible that the large plates of *Stegosaurus*, seen from the side, made the animal appear much larger to predators (or rivals [Carpenter 1998]). However, this would not be as effective in stegosaurs that had smaller plates, some plates and some spikes, or all spikes (Fig. 9). One could argue that the abundance of very large predators in Late Jurassic environments (such as those represented in the Morrison Formation) was a critical selective force for large plates, but this hypothesis requires several kinds of unavailable evidence.

Thermoregulation.—De Buffrénil et al. (1986) concluded that this was the most likely function of the plates of *Stegosaurus*. Our study suggests that the potential role of the plates in thermoregulation depends on several factors that can only be partly assessed, if at all. Moreover, it depends on the model of vascular flow that is postulated for the plates, some aspects

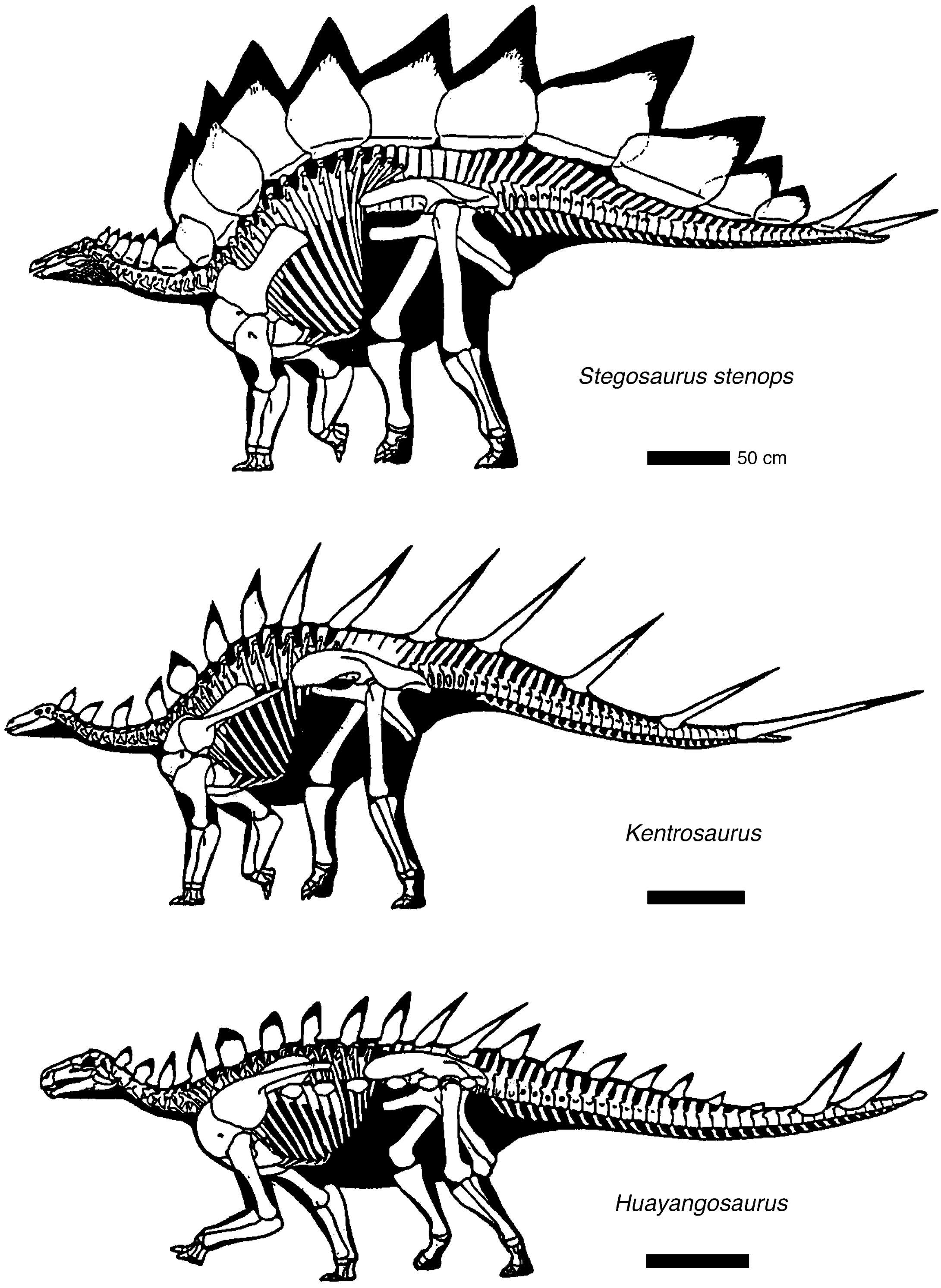


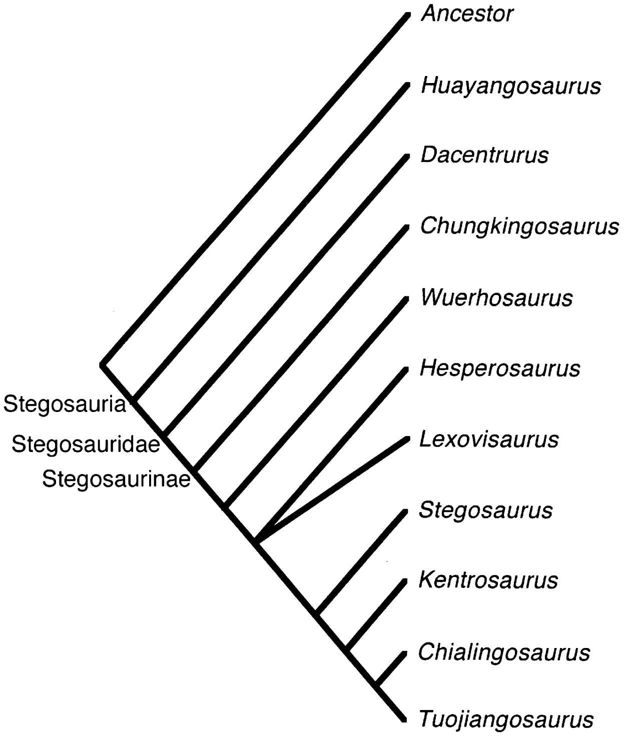
FIGURE 9. Three stegosaurs, restored by Greg Paul, to show variation in plate configuration on three genera of similar size. Areas in white represent actual bony tissue extent; black silhouettes around plates and spikes represent hypothesized keratinous extent. The horizontal line along the bases of the plates in *Stegosaurus* approximates the skin line.

of which we think may be eliminated or weakened by the available evidence.

First, de Buffrénil et al. (1986) suggested that the internal ''pipes'' in the plates may have carried blood from the body through the plates, and these may have communicated with the grooves on the outer surface of the plates to return warmed or cooled blood to the body core along the outside of the plates. We think this is unlikely for two reasons. The ''pipes'' by themselves show no clear evidence of efferent vascular structures; they are surrounded by secondary trabecular bone. This trabecular bone is locally organized as secondary osteonal bone, but this cannot be readily compared to the primary osteons that form the periphery of typical vascular canals in periosteal compact bone. Sometimes the ''pipes'' have only scalloped edges that reflect erosion by osteoclasts. In these respects, they are more similar to and may be homologous to the elongated medullary bays that are seen in *Scutellosaurus* (Fig. 1A,B), *Scelidosaurus* (Fig. 2C), and ankylosaurs (Scheyer and Sander 2004). Also, the ''pipes'' do not communicate directly with the outside of the plate, because they do not pass directly through the outer layers of compact cortical bone on the lateral surfaces of the plates, including the distal edge. Furthermore, vascular channels that have left grooves on the external surface of the plates course mostly proximodistally, and course right to the distal edges of the plates without communicating with any internal channels along this edge (Fig. 2D). Although there are scattered, sparse pits up to several millimeters in diameter on the outer surface of the plates that reflect vascular communication with the inside of the plates, blood inside the plates would mostly have to perfuse through small perforations of less than 1 mm in diameter in order to reach the external surface of the plates. These perforations are too small and few to carry the flow of blood suggested by the diameter and location of the ''pipes.''

Second, we consider whether vascular structures that enhanced thermoregulation could have been present mainly in the tissues external to the plates. In other words, leaving aside the internal vascular structures, could the vessels on the outside of the plates alone have supported substantial thermal cooling? In one sense, this model would structurally resemble the situation in deer antlers, in which efferent vessels course through the velvet internal to the afferent vessels, both of which have branching rami that run inside the bony core of the antler (Waldo et al. 1949). However, although antlers have some function in thermoregulation, the extent of their role is disputed (e.g., Stonehouse 1968; Geist 1968), and their utility is certainly not indispensable, because in most cases the females lack them yet thermoregulate as well as males. Moreover, whereas the vascular structure that we describe above for the antlers does not clearly have a function in thermoregulation, it does have a demonstrated function in building the bone of the antler (Waldo et al. 1949). Antler is the fastest growing bone among the vertebrates. It typically is considerably warmer than the ambient temperature when covered with velvet; but this is because it is growing so fast and radiating heat, not absorbing it. Naked bone, such as antlers become after velvet is shed, cannot function in heat transmission because their blood supply is lost. But the deep grooves in the bone that transmitted the blood supply during growth remain.

Other such structures, if covered by blood vessels and a horny, protective covering such as keratin, could still function in this capacity, but that must be established independently. Horns are in this general sense more appropriate than antlers to compare with stegosaur plates and spikes. Information from living horned ungulates suggests that the vascular supply both to the horns and to the adjacent sinuses can have a significant role in thermoregulation (Taylor 1966), and that geographic and altitudinal variation in horn core sizes within species may be correlated with thermoregulatory potential (Picard et al. 1996, 1999; Hoefs 2000). However, there is also a general understanding that these same animals use behavior to regulate body temperature (e.g., in migrating geographically and altitudinally, and in using sun, shade, and wind) and that this contributes at least as significantly as horn core morphology in most cases. As with antlers, the hypothesis that horns evolved largely in the context of a ther-



Huayangosaurus	two rows small plates, pointed spines close to sagittal plane; ≥ one row of osteoderms
Dacentrurus	large tail spines; apparently small anterior dorsal spines, but poorly known
Chungkingosaurus	triangular, flattened platelike spines without laterally expanded bases over neck and trunk; tailspines have central rodlike thickening and some basal expansion
Wuerhosaurus	poorly known, but plates short
Hesperosaurus	cervical plates longer than high; dorsal plates parallelogram-shaped and larger; caudal plates become longer than high posteriorly. Tail spikes.
Lexovisaurus	poorly known. Gradation of armor from anterior plates to posterior spines. Plates relatively large.
Stegosaurus	very large plates with angled, sometimes expanded bases; most plates taller than long; two pairs tail spikes
Kentrosaurus	large elongate spines with expanded bases; gradation of armor from anterior plates to posterior spines
Chialingosaurus	relatively small, platelike spines
Tuojiangosaurus	large, elongate spines with expanded bases over posterior 2/3 of back and most of tail. Smallest spines are anterior to tail spikes

FIGURE 10. Phylogeny of selected genera of Stegosauria (after Upchurch and Galton 2004); for explanation see text. Characteristics of size, plates, and spikes (based on information in Blows 2001 and other references) are listed next to the names of genera.

moregulatory function is generally rejected (Taylor 1966; Hoefs 2000). Barrick et al. (1998) have suggested that the frill of *Triceratops* had a thermoregulatory function, on the basis of oxygen isotope analysis of its skull and postcranial bones. It will be interesting to see if larger samples and greater phylogenetic scope provide further support for this hypothesis.

For a model of external vascularization to work, the efferent and afferent vascular structures have to be identified. On the surface of the plates, grooves that carried these channels run almost exclusively proximodistally, but there is no indication of the direction of blood flow. If a system of canals circled the plate surface and returned blood to the body core for thermoregulatory functions, there is no evidence of it. We agree with de Buffrénil et al. (1986) that it is implausible that the plates were naked, and we suppose that a keratinous covering was likely. This would be consistent with the situation in ungulate horns. If blood vessels associated with thermoregulatory enhancement were external to the plates, no clear evidence remains of their configuration, so the thermoregulatory hypothesis reduces to speculation.

Finally, why would *Stegosaurus* ''need'' plates to shed heat? Other dinosaurs lacked them, and the forms of plates and spikes vary among stegosaurs without respect to body size (Fig. 10). Farlow et al. (1976) showed that the plates in *Stegosaurus* were well arranged to shed heat, but the staggered arrangement could have had other functions, none of which was (or perhaps could be) treated in their study. Dinosaur bones show no evidence of ectothermy; Mesozoic dinosaurs deposited tissues that in living tetrapods grow at rates that suggest basal metabolic rates significantly higher than those of any living non-avian reptiles (Padian et al. 2001). The thermoregulation hypothesis may simply be unnecessary. Nevertheless an accessory role in cooling cannot be ruled out, and the external grooves on stegosaur plates resemble in some ways the pattern of vessels in elephant ears, which have an important function in cooling (Phillips and Heath 1992).

Species Recognition.—The simplest explanation of the diverse features of stegosaurian plates and spikes (and, we would argue separately, for most cranial ornamentation in dinosaurs) is species recognition. To make this argument, which does not itself falsify or deny any possible role in mate recognition, we must first separate species recognition from various other kinds of what has traditionally been called ''display.''

Behaviors that involve signals and recognition of those signals evolve in animals that have distinct features and the ability to perceive them. Mesozoic dinosaurs must have been highly visual animals, as the large size of their eyes suggests. Although features that apply to species recognition are frequently called ''mate-recognition'' features, recognizing mates is not the only possible advantage of the ability to identify conspecifics. Individuals of the same species can band together for protection, for example, provided social groups do not reject outsiders of their own species.

The term ''display,'' in the context of behavioral signals, has several possible functions that may or may not be associated. A structure may be displayed for aggressive purposes, but warning off a rival for a mate and discouraging a potential predator have different selective regimes. The first involves sexual selection, the second natural selection. Either function could presumably be co-opted for the other, but it is impossible to tell which (if either) was the case in extinct forms—unless another kind of evidence confirms that the plesiomorphic condition of a clade could function in one way but not the other.

Vrba (1984) remarked that structures that differentiate closely related species ''should involve a shift in morphology (for example, structure and color, that are not only visible to conspecifics and members of the parent species, but may also be visible to us).'' And Sampson (1999: p. 183) noted: ''as in extant groups, such signals are frequently important taxonomic characters . . . . This should come as no surprise, since the animals themselves surely used the very same visual cues in the recognition of conspecifics and in competition for mates.'' We agree that this amounts to common sense, with the proviso that the functions of conspecific recognition and mate competition still require differentiation. Although, as for stegosaurs, we have no independent evidence of mate competition, we can use the features of their plates to identify species. And, because we can perceive no male-female differences in these structures, we have no evidence to support mate recognition; but we can support species recognition.

Phylogenetic Considerations.—A phylogeny of stegosaurs has been elusive. Peter Galton and Paul Upchurch have kindly shared with us the results of their analysis (2004) of stegosaurian genera for which an adequate number of phylogenetically informative characters can be coded. They stress that missing data and character conflicts make resolution difficult. The tree reproduced in Figure 10 resulted from a Strict Consensus analysis of three most parsimonious trees produced by an Exhaustive Search in PAUP 4.0, but Galton and Upchurch urge caution about relationships within Stegosaurinae (taxa ''above'' *Huayangosaurus*, *Dacentrurus*, and *Chungkingosaurus*).

We have listed some characters of the plates next to individual genera in Figure 10. Even accounting for size differences and similarities in larger stegosaurs (Fig. 9), it is difficult to find any phylogenetic signal in the expression of plate patterns. A different resolution of the phylogeny, or the discovery of enough new taxa, could affect it, but we conclude that there is at present no clear pattern of directional evolution in the features of stegosaurian plates, beyond those generally correlated with body size. Coupled with the lack of evidence for sexual dimorphism, we conclude that the simplest explanation of the diversity of plate patterns in stegosaurs is species recognition, a function also noted by Carpenter (1998).

If natural selection is playing an important part in shaping the morphology of features in a clade, then derived members of the clade might be expected to continue the selective pattern as a trend, except when exaptation turns the structure to another purpose. Similar trends should be seen under Fisherian sex-

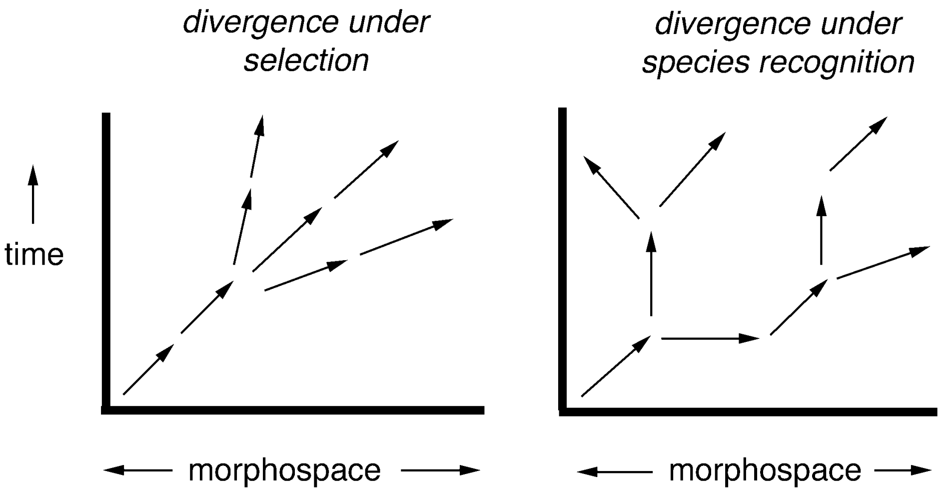


FIGURE 11. Expected differences in macroevolutionary patterns of morphology between regimes governed by natural selection (or Fisherian sexual selection) and species recognition. Although these are extremes of a continuum of patterns, it would be expected that natural selection would cause more or less linear morphological trends through time as the function of a structure improved. Sexual selection might also direct the orthal elaboration of a difference into a morphological trend. But when species recognition is selected for, the object is to be recognizably different, not necessarily functionally better or more visually elaborate; so a range of morphology is possible, as long as the result is divergence.

ual selection, although if mate recognition features are important in isolated populations (whether by peripheral or vicariance models), divergence through sexual selection could occur in a variety of directions (e.g., Price 1998; Sampson 1999). On the other hand, species recognition factors should (*ceteris paribus*) evolve *only* randomly with respect to morphologic trends, because there would be no reason to follow any single selective trajectory; in fact, there would seem to be an advantage in differentiating one's recognition signals from those of related congeners (Fig. 11).

Conclusions

The scutes of thyreophoran dinosaurs, in their various forms of ossicles, plates, spikes, and so on, are homologous to each other. The simplest form was a bilateral, slightly keeled structure (*Scutellosaurus*) that seems to have developed largely from a template of compact dermal bone that was ontogenetically replaced internally with secondary incursions of canals and erosion rooms. Larger, more complex scutes were peaked (*Scelidosaurus*, ankylosaurs) and comprised a relatively thin outer layer of cortical bone and an internal lattice of trabecular bone, again with occasional erosion rooms and canals. The primitive keels of thyreophorans were sometimes modified by hypertrophy to form high plates or spikes (stegosaurs), but internally they retained the same histological construction. In these plates and spikes the oldest bone is generally toward the apex, and secondary remodeling can proceed throughout growth (de Buffrénil et al. 1986). The ''pipes'' inside stegosaur plates and spikes are a well-defined system anatomically, but the variable structure of their walls does not allow us to identify a precise function for them in blood circulation or other purposes. They are very similar to the elongated medullary bays seen in more basal thyreophorans. The vascular grooves on the outside of stegosaur plates and spikes, like those of ungulate horns and antlers, supplied blood for the growth of the bone and presumably continued to supply the non-osseous tissues (dermal, epidermal, and probably keratinous) that covered the bone. In short, these ''pipes'' form a distinct system that may have contained blood vessels, but the system of internal ''pipes'' and external vascular grooves seems much more strongly linked to the overall growth dynamics of the plates themselves than to another specialized function, such as thermoregulation.

Stegosaurian plates show little evidence of a biomechanical function in defense, because they comprise trabecular bone sandwiched by thin layers of cortical bone. Because the internal ''plumbing'' of the plates and spikes is not consistent with the conduction of efferent and afferent blood vessels, the internal structures have no apparent connection to any role in thermoregulation played by the external surface of the plates and spikes. The vessels that course along the outer surface of the plates and spikes could have had such a function, depending on how actively the blood supply was maintained to these structures; this is not possible for antlers once they finish growing but has been established for horns. This role is accessory in horned ungulates and is complemented by behavioral factors, which cannot be measured in stegosaurs. Thermoregulation that involved the external blood vessels of stegosaur plates cannot be assessed without knowledge of their extent, their circulatory rates, their mechanisms of control, and associated behavioral factors. Whereas an accessory role for stegosaur plates in thermoregulation is possible, it is based on analogical comparisons, not on functional, phylogenetic, or ontogenetic evidence.

Some sort of function in display is likely for stegosaur plates. However, sexual selection and other mate recognition functions are difficult to substantiate because there is no apparent evidence of sexual dimorphism. It is difficult to distinguish between the hypotheses of mate recognition and simple species recognition. If juvenile (sexually immature) stegosaurs displayed characters of adult members of their species to the extent that they could be recognized as members of that species, then the mate recognition hypothesis would be countered and species recognition supported.

Species recognition is particularly important where several species coexist sympatrically, and these species differences can persist long after differential extinction has affected the morphological and taxonomic diversity of clades (Vrba 1984; Sampson 1999). Carpenter (2001) identified the presence of six distinct stegosaur taxa in the Upper Jurassic Morrison Formation (not all at the same stratigraphic level), which would appear consistent with the inference of species recognition. It cannot be discounted that mate recognition was involved, if stegosaurs tended to differentiate populations as a result of sexual selection (as Price [1998] has argued for birds). (This may have been a mechanism of speciation, but there is no direct evidence.) Birds are highly dimorphic sexually, and imprinting is important; however, stegosaurs (like other dinosaurs) do not appear to be highly dimorphic sexually, and the role of imprinting in dinosaurs cannot be assessed.

We conclude that species recognition, the simplest manifestation of signal and response behavior, was the most probable and defensible function of stegosaurian plate diversity. Other functions may not be ruled out, but they still require support from other independent lines of evidence. When the gross and microstructural features of the plates and spikes are placed in phylogenetic context, no clear pattern of thermoregulatory or other function emerges, though an accessory role cannot be eliminated in certain individual species. We accept that functions of structures can be both multiple and mutable, and that ''bizarre'' structures such as large scutes may have been pulled by various evolutionary forces toward various and even conflicting functions during the course of evolution. However, we conclude that evidence for such alternative functions is weaker than it has historically appeared. It seems more likely, as in other groups of dinosaurs, that the diversity of dermal armor form in stegosaurs was linked to species individuation and recognition, and perhaps secondarily exapted to inter- and intraspecific display or (rarely) to facultative thermoregulation.

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