

# Internal vascularity of the dermal plates of *Stegosaurus* (Ornithischia, Thyreophora)

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**Abstract** X-ray computed tomography and petrographic thin sectioning were used to study internal features of the plates of the thyreophoran dinosaur *Stegosaurus* and the osteoderms of *Alligator*. Infrared thermographic imaging of basking caimans was used to examine possible differential blood flow to osteoderms and other parts of the skin. Multiple large openings in the *Stegosaurus* plate base lead to a linear, mesiodistally oriented vestibule, which in turn apically sends off multiply branching “pipes”. The pipes are best developed in the basal half of the plate, and communicate with cancellous regions (some of which presumably were vascular spaces) throughout the plate interior. Some internal vascular features also connect with vascular pits and grooves on the plate surface. Alligator osteoderms show a similar internal vascularity. In crocodylians, the osteoderms serve as armor and help to stiffen the back for terrestrial locomotion, but their vascularity enables them to be used as sources of calcium for egg shelling, as sites of lactate sequestration, and possibly for heat exchange with the external environment, as suggested by our infrared thermographic imaging of basking caimans. Thyreophoran

osteoderms presumably had multiple functions as well. In *Stegosaurus* the potential thermoregulatory role of the plates may have been greater than in other thyreophorans, by virtue of their extensive external and internal vascularity, their large size, thin cross-sections above the plate base, dorsal position, and alternating arrangement.

**Keywords** *Stegosaurus* · Crocodylians · Osteoderms · Reptilian thermoregulation · X-ray computed tomography · Infrared thermographic imaging

## Institutional abbreviations

DMNH	Denver Museum of Nature and Science, Denver, Colorado, USA
HMNS	Hayashibara Museum of Natural Sciences, Okayama, Japan
NSM-PV	National Science Museum, Tokyo, Japan
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

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## Introduction

Dermal ossifications have repeatedly evolved in amniotes: placodonts, pareiasaurs, chelonians, squamates, crocodylians and closely related archosaurs, ceratosaurs, titanosaurs, thyreophorans, and cingulates (cf. Moss 1972; Buffrénil 1982; Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986; Scheyer and Sander 2004; Hill 2005, 2006; Hill and Lucas 2006; Scheyer and Sánchez-Villagra 2007; Maidment et al. 2008; Vickaryous

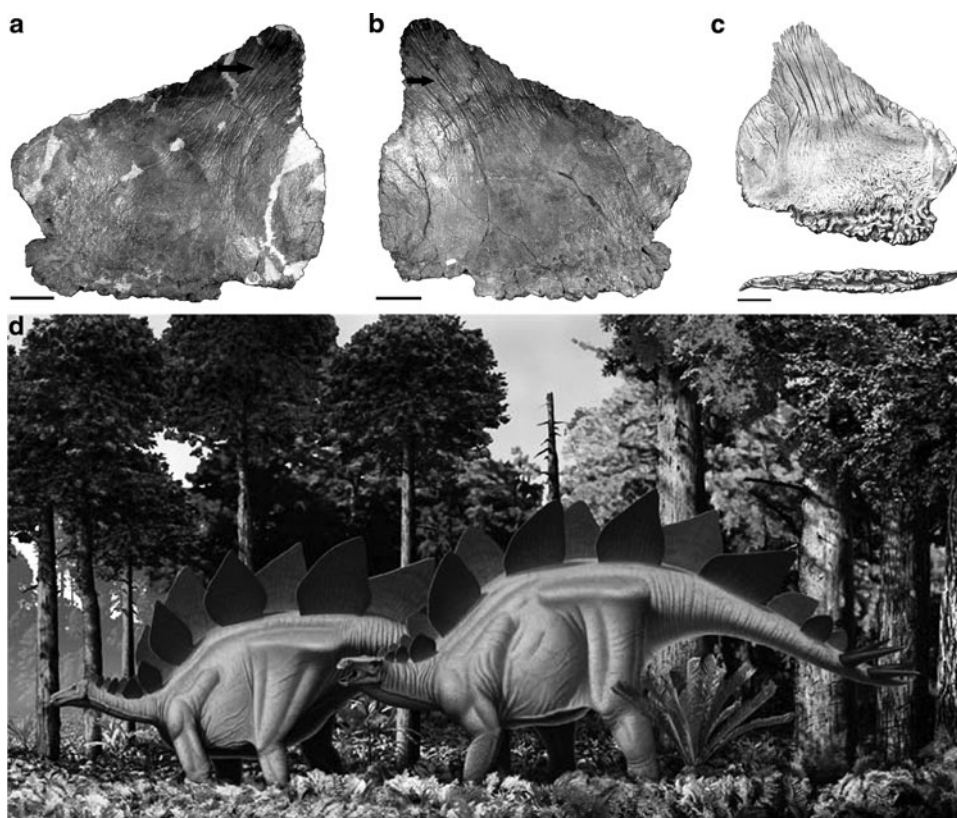
and Hall 2008; D’Emic et al. 2009; Dilkes and Sues 2009; Gower and Schoch 2009; Vickaryous and Sire 2009). Thyreophorans show a particularly exuberant development of osteoderms, with various taxa sporting a variety of small, disc-like ossifications, plates, spikes, clubs, and intergradations among them (Gilmore 1914; Colbert 1981; Czerkas 1987; Carpenter 1998; Ford 2000; Blows 2001a, b; Molnar 2001; Galton and Upchurch 2004; Scheyer and Sander 2004; Maidment et al. 2008; Hayashi et al. 2009, 2010; Mateus et al. 2009; Siber and M ockli 2009). Functions hypothesized for thyreophoran osteoderms are similarly varied (and not necessarily mutually exclusive), and include their use as armor and/or defensive or offensive weaponry (Marsh 1896; Gilmore 1914; Colbert 1981; Bakker 1986; Czerkas 1987; Carpenter 1998; Blows 2001b; McWhinney et al. 2001; Scheyer and Sander 2004; Carpenter et al. 2005; Redelstorff and Sander 2009; Hayashi et al. 2010), structures to stiffen the back or tail (Carpenter 1998; Blows 2001b), features for display and/or species recognition (Carpenter 1998; Main et al. 2005; Hayashi et al. 2009, 2010), and thermoregulatory devices (Farlow et al. 1976; Buffr enil et al. 1986; Blows 2001b; Hayashi et al. 2009, 2010).

Functional interpretations of thyreophoran osteoderms must be consistent with their deployment on the animals’ bodies, as well as their external and internal morphology.

The latter of these concerns has led to investigations of the histological structure of thyreophoran osteoderms (Buffr enil et al. 1986; Reid 1996; Scheyer and Sander 2004; Main et al. 2005; Hayashi 2009; Hayashi et al. 2009, 2010). Evidence for vascularity on both the external surface (Fig. 1a–c) and inside the large dermal plates of *Stegosaurus*, as well as their large, flat shapes and staggered arrangement on the dinosaur’s back (Fig. 1d), led Farlow et al. (1976) and Buffr enil et al. (1986) to hypothesize that heat exchange with the environment might have been one of the functions of the plates in at least this genus. These authors noted the presence of large “pipes” entering the plate from its base, and suggested that such pipes may have housed distributary blood vessels (arteries and/or veins) that fanned out into the plate interior. Main et al. (2005), however, were skeptical that the “pipes” in fact had such a configuration, and suggested that they were instead artifacts of the way the plates developed during ontogeny.

In this study we reinvestigate the internal configuration of the “pipes” and other external and internal features of *Stegosaurus* plates using X-ray computed tomography (CT) and thin sections. For comparative purposes, we also examine the external and internal vascularity of osteoderms of the American alligator (*Alligator mississippiensis*), and present evidence for a possible thermoregulatory role of the osteoderms in the broad-snouted caiman (*Caiman*

**Fig. 1** *Stegosaurus* and its plates. **a, b** Photographs of *Stegosaurus* dorsal plate USNM 4714; photographs by M.K. Brett-Surman, copyright Smithsonian Institution 2009, all rights reserved. Note well-developed surficial vascular grooves (indicated by arrows) on both sides of the plate apex. **c** Interpretive lithographs of the external surfaces of the side and base of the same plate (Ostrom and McIntosh 1966, p. 354; Plate 61). **d** Life restoration of *Stegosaurus* showing alternating arrangement of the dorsal plates; painting used by permission of the artists, B. Walters and T. Kissinger, copyright Carnegie Museum of Natural History 2007. All scale bars 100 mm (a–c)



*latirostris*). We then consider possible functions of *Stegosaurus* plates in light of our observations.

## Methods and material

### CT scans of *Stegosaurus* and alligator osteoderms

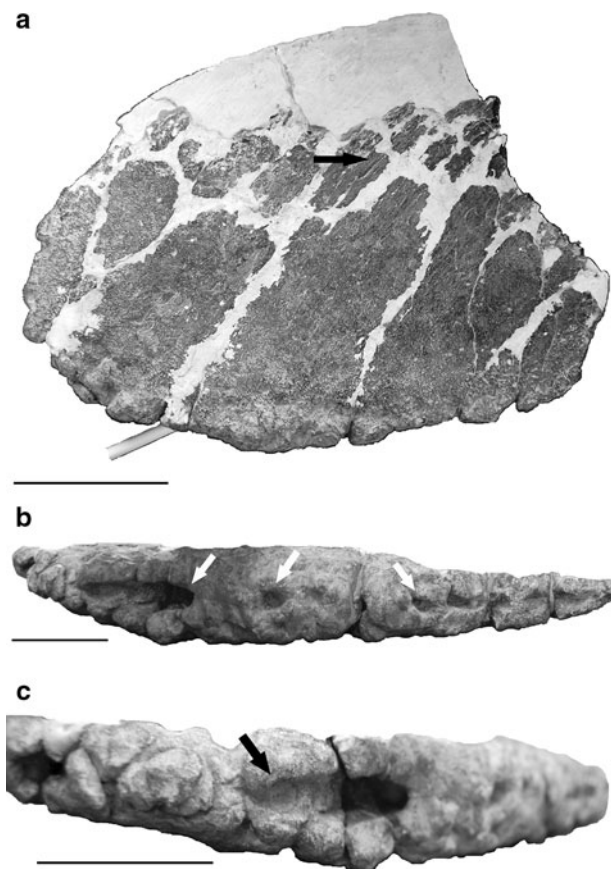
Our study used CT scanners at three institutions: (1) General Electric Lightspeed 8 Slice (140 kV, 240 mA, 1.25 mm slice thickness) medical CT scanner, Dekalb Memorial Hospital, Auburn, Indiana, USA; (2) Hitachi Medical Corporation CT-W2000 (120 kV, 175 mA, 1 mm slice thickness) medical CT scanner, National Institute of Advanced Industrial Science and Technology, Tsukuba, Japan; (3) Tesco Corporation BIR ACTIS+3 (180 kV, 0.11 mA, 200  $\mu$ m slice thickness) micro CT scanner, Tesco Corporation, Tokyo, Japan.

We examined seven plates of five individuals of *Stegosaurus* from the Late Jurassic Morrison Formation of the western United States: DMNH 1483, *S. armatus*, distal caudal plate; NSM-PV 20380, *S. armatus*, proximal caudal plate and distal caudal plate; HMNS 14, *S.* (or *Hesperosaurus*) *mjosi*, proximal cervical plate and distal caudal plate; YPM 1856, *S. armatus* plate; YPM 57716, *Stegosaurus* sp.,? caudal plate. Given present uncertainty about the specific and even generic taxonomy of some of these specimens (Carpenter et al. 2001; Galton and Upchurch 2004; Maidment et al. 2008), we report the current names without expressing an opinion about their validity. The alligator osteoderms in our sample came from wild individuals from the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana, USA.

### Infrared thermographic imaging of basking caimans

The animals were captives kept outdoors at São Paulo State University, Rio Claro, Brazil. The pictures were taken 26 June 2005. Infrared thermal images were taken with a MikroScan 7515 Thermal Imager (Mikron Infrared®). This device produces a 12-bit image (320  $\times$  240 pixels) and stores the temperature information of each pixel at a resolution of 0.1°C. All temperature readings are automatically corrected for non-blackbody properties by assuming an emissivity of 0.95, which is a reasonable estimate for biological tissues (Speakman and Ward 1998). We assessed this assumption by examining the IR from black electrical tape (known emissivity = 0.95) adhering to, and in thermal equilibrium with, caiman skin. Both the tape and the skin were found to exhibit similar temperatures based on the IR analysis, suggesting a similar emissivity of 0.95. The potential for differential emissivity among different regions of the skin is unlikely for two

reasons. Firstly, all regions of the skin surface have similar composition (mainly water and protein), which have known, high emissivity values. Secondly, infrared thermographs of dead caimans were not observed to demonstrate differential changes in temperature between osteoderms and other parts of the skin, even when background temperature was altered. Consequently any thermal differences between osteoderms and other parts of the skin observed in living caimans are likely to represent



**Fig. 2** External views of *Stegosaurus* sp. YPM 57716 (accession number 1388). **a** Side view of the dorsal plate previously X-rayed by Farlow et al. (1976: Fig. 1b). The specimen was glued together, and its apical portion restored, with plaster, which appears as a lighter colour in the photograph. A plastic rod is inserted into a large groove in the plate base that leads to an opening into the plate interior. Black arrow near the apex of the plate (as preserved) indicates one of several faint blood grooves in this region of the plate. **b** Ventral view of the plate base. The large groove leading to the opening into the plate interior in (a) is indicated by the left-most white arrow; the opening itself is adjacent to the arrow. Other white arrows mark two of several more additional openings from the plate base into its interior. Compare with the similarly developed plate base of USNM 4714 (Fig. 1c). **c** Slightly oblique view of the plate base, with the groove leading to the large opening into the plate interior marked by a black arrow. Another large opening (not readily seen in the view in (b)) is at the extreme left edge of the photograph. Scale bars 50 mm (b, c), 100 mm (a)



interactions between solar heat absorption and underlying blood flow, rather than physical differences in surface properties.

## Results

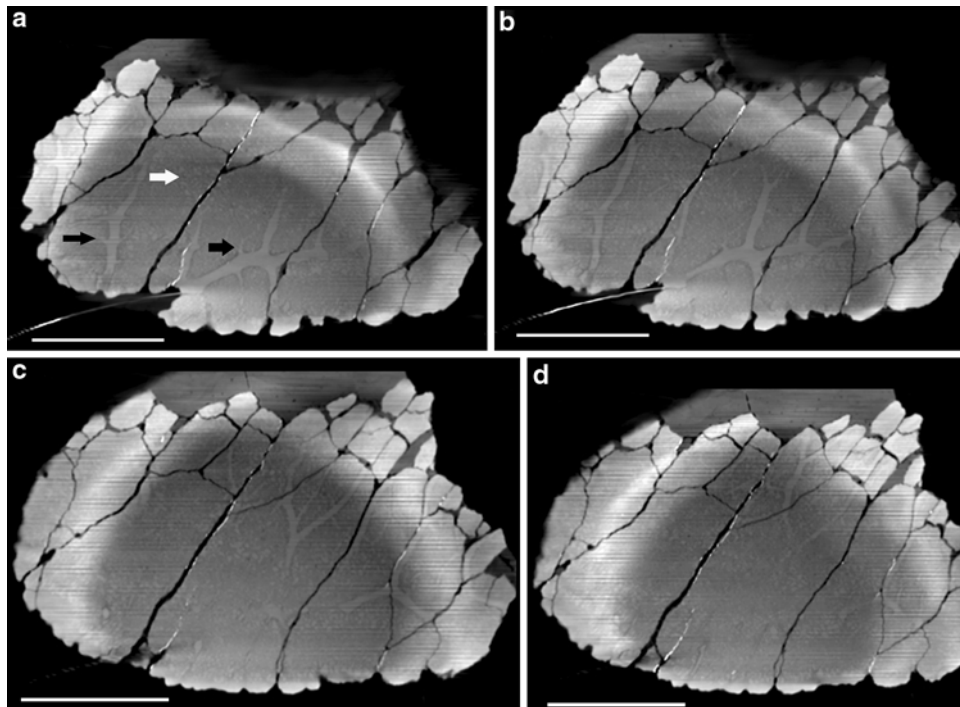
### *Stegosaurus* plates

All plates in our sample, of both species, show similar internal structure, so they will be described using representative specimens. There was no indication of structural variation between large and small plates in a single individual (NSM-PV 20380, HMNS 14).

YPM 57716 (accession number 1388 box 73) is a modest-sized plate, about 356 mm long and 220 mm tall as preserved (Fig. 2a); the apical portion of the plate is

missing. The maximum transverse width of the plate is about 47 mm at its base, which thins to about 10 mm at the apex of the preserved part of the plate. In basal view (Fig. 2b, c) several large, roughly circular openings (mostly sediment-filled; cf. Brinkman and Conway 1985) occur in a row along the midline of the plate base. A particularly large such opening is confluent with a 55 mm long groove in the surface of the plate base. Near the plate apex are some faint linear grooves running longitudinally along the plate surface. These presumably are blood vessel impressions, but are not so well developed as on other stegosaur plates (Fig. 1a–c) (Gilmore 1914; Farlow et al. 1976; Main et al. 2005; Hayashi et al. 2009). The reason for this variable development of external blood grooves among plates is unknown.

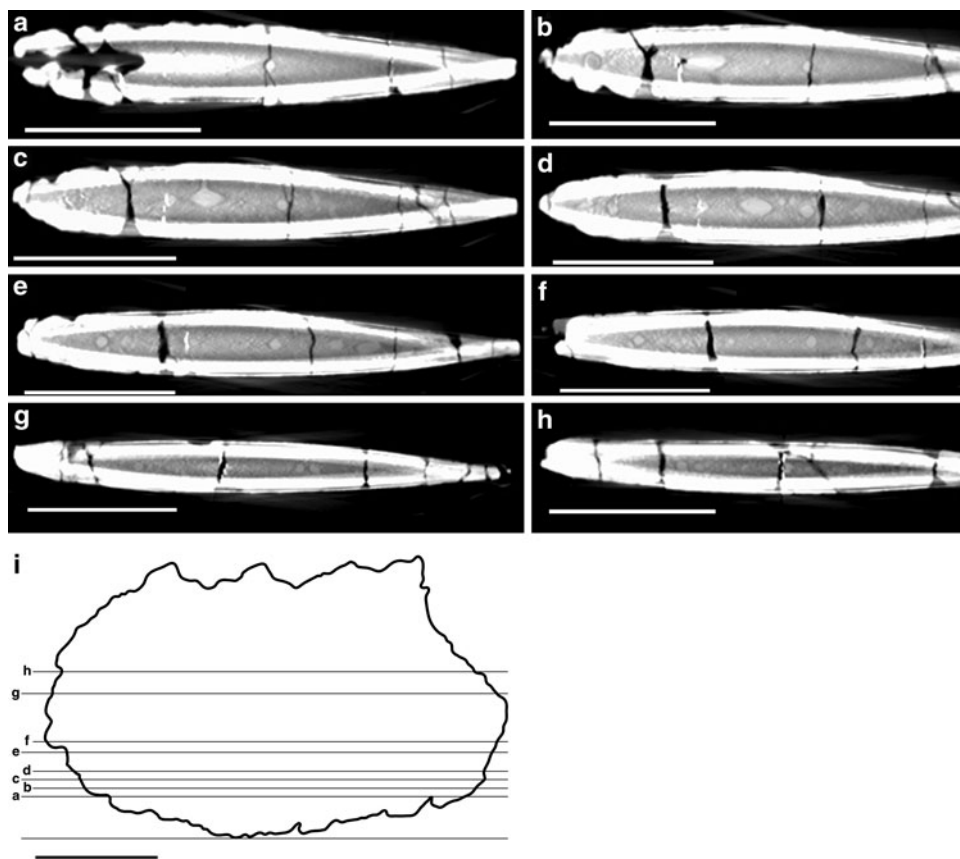
Parasagittal and transverse CT sections (Figs. 3, 4) reveal that the large openings into the plate base communicate with



**Fig. 3** Parasagittal CT images of *Stegosaurus* sp. YPM 57716 (cf. Fig. 2). The plate is oriented in the same direction as in Fig. 2. A piece of wire was inserted into the large groove and opening in the plate base that leads into the plate interior shown in Fig. 2; this wire is visible in (a) and (b) of the present figure. **a** Section about 23 mm into the plate interior below the outermost point on the plate surface (the surface toward the viewer in the image), and close to the plate midline. The large opening from the plate base (marked by wire) leads to a large “main channel” that sends off large branches toward the plate apex, and also connects with other large openings in the plate base. Additional large channels running from the plate base toward its apex can be seen to the left of the main channel. Two of several smaller side branches off the large branches are indicated by *black arrows*; these pinch out as they move away from the plane of

the section. *White arrow* labels a speckled region of cancellous bone. **b** Section about 2 mm deeper (away from the viewer) than the one in (a). A branch from the main channel heading toward the plate apex is beginning to fork. **c** Section about 4 mm deeper than that in (b). The fork in the apex-heading tributary of the main channel is now well-developed, and the left tine of the fork has itself bifurcated. **d** Section about 2 mm deeper than that in (c). A final bifurcation in the left tine of the fork in (b) and (c) can be seen near the most apical edge of the plate (as preserved). Given the arrangement of branches of the internal pipe system, and the close proximity of the branches to cancellous spaces, we suggest that some portion of the cancellous spaces housed minute blood vessels. All scans copyright Yale Peabody Museum. *Scale bars* 100 mm

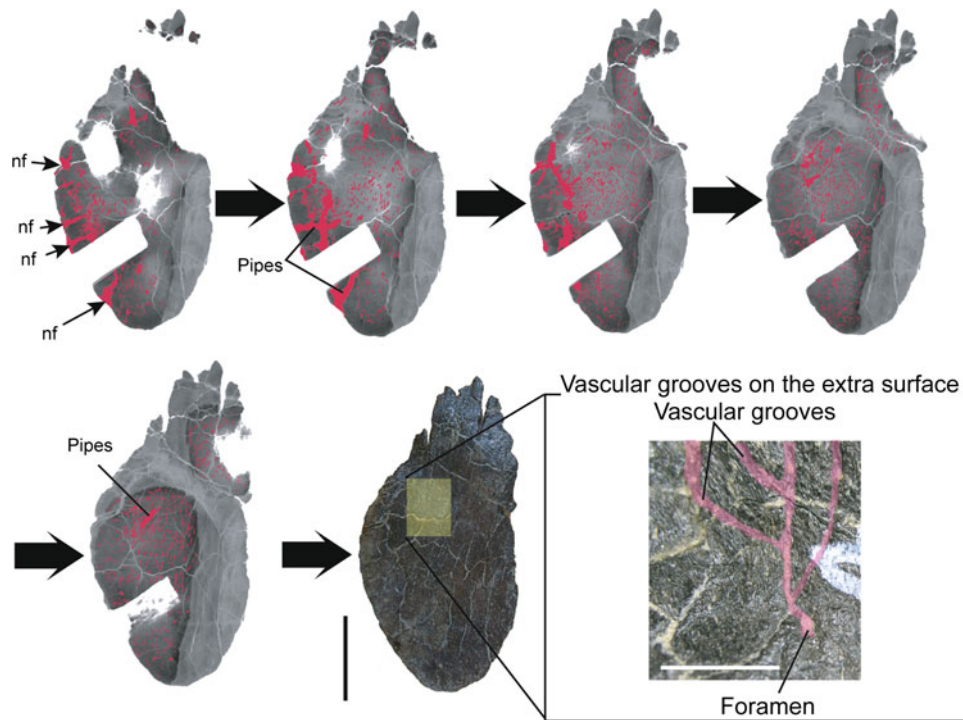
**Fig. 4** Transverse CT sections through *Stegosaurus* sp. plate YPM 57716. **a–h** Sequentially more apical transverse CT scans (cf. Fig. 2). The left end of the plate in all views is the same as the left end of the plate as seen in Figs. 2 and 3. **i** Diagram showing the positions of the transverse scans. Relatively dense bone of the cortex appears in white in (a–h); cortical thickness is about 10 mm. The large groove in the ventral surface of the plate confluent with the opening into the “main” channel (Figs. 2b, c, 3a, b) is seen in (a) as a *large dark region* near the left end of the section. Another, *smaller dark area* at the left-most edge of the section probably leads to the vertical channel immediately to the left of the “main” channel in Fig. 3a. Elliptical to circular sections through internal channels or “pipes” can be seen in all sections, but are most distinct in the basal half of the plate. All copyright Yale Peabody Museum. All *scale bars* 100 mm



**Fig. 5** Computer-generated model of the larger features of the interior distributary system of *Stegosaurus* sp. YPM 57716 (cf. Fig. 2). The “main channel” (Figs. 3, 4) seems to be a linear vestibule running anteroposteriorly near the plate base, with large channels (presumably large nutrient foramina) entering the vestibule from below, and vascular “pipes” branching apically from it. Total mesiodistal length of this distributary system is somewhat less than the external length of the plate (356 mm)

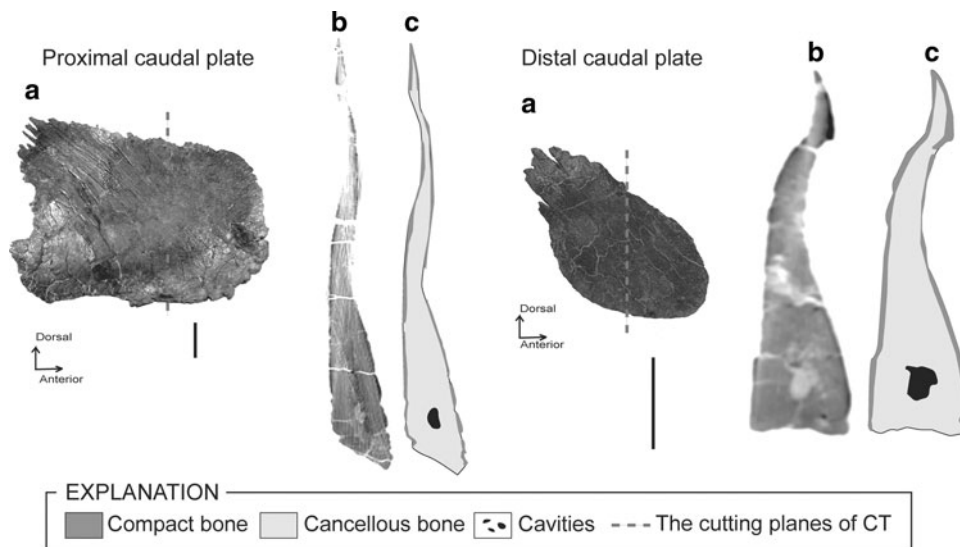
a complex, multiply branching system of tubes in the plate interior. The large “pipes” extend throughout the apical length of the plate as preserved, but are most elaborate and clearly seen in the basal half of the plate (cf. Main et al. 2005; Hayashi 2009). Surrounding these tubes are regions of cancellous bone. A computer-generated model of the

largest components of the interior pipe system (Fig. 5) shows a large, linear basal channel or vestibule running in an anteroposterior manner along the plate base, sending out several “pipes” into more apical parts of the plate interior. CT scans and thin sections of plates of other individual stegosaurs (DMNH 1483; HMNS 14; NSM-PV 20380: Figs. 6–8; also see Hayashi 2009) indicate that the features seen in YPM 57716 are typical for *Stegosaurus*. The pipes inside *Stegosaurus* plates develop ontogenetically from juvenile to subadult individuals (Hayashi 2009), and the histology of osteodermal bone indicates a capacity for continued growth (and the vascular supply to maintain such growth) later in life than in non-osteodermal bone (Hayashi et al. 2009). Older, larger individuals show the same pipe-like vascular canals seen in YPM 57716, which enter the plate interior through roughly circular pits in the plate base. These canals are outlined by trabeculae, and pinch out about midway from the plate base toward its tip (Main et al. 2005; Hayashi 2009). The geometric relationship of the multiply branching pipe system with respect to cancellous spaces within the plate interior (Figs. 3, 6) suggests that some of the cancellous spaces were occupied by minute blood vessels. At least some of the internal porous spaces communicate with pits and grooves on the plate surface (Figs. 6, 9).



**Fig. 6** Pattern of inferred vascular networks in a plate from NSM-PV 20380, a young adult individual of *Stegosaurus armatus*. The digital images were created by microfocus CT scanning, with the pipe-like vascular canals, and spaces within cancellous bone, indicated in red. The sequence of images begins near the sagittal interior, and successive images are progressively closer to the plate surface, ending with a view of the surface itself. Note similarity of the basal vestibular system to that of YPM 57716 (Figs. 3–5); nf, large channels interpreted as nutrient foramina. The arrangement of isolated

red spaces in the cancellous bone with respect to the pipes suggests that at least some of the isolated red spaces represent sections through small tributary blood vessels. The boxed detail enlarges a portion of the plate surface, showing that some of the putative internal vascular canals connect with vascular grooves and foramina on the plate surface. Such connections between interior and surface features of the inferred vascular system occur on both sides of this plate. Scale bars 100 mm for the CT sections, and 10 mm for the inset showing vascular grooves on the plate surface (box)

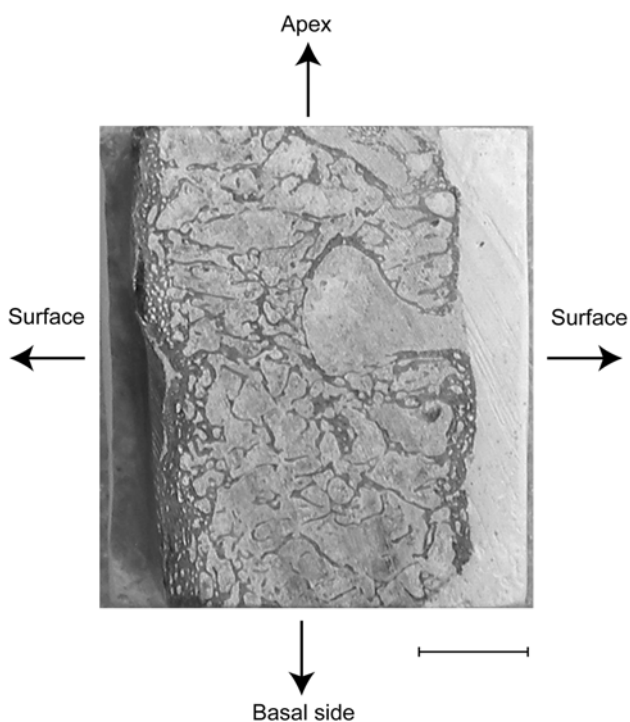
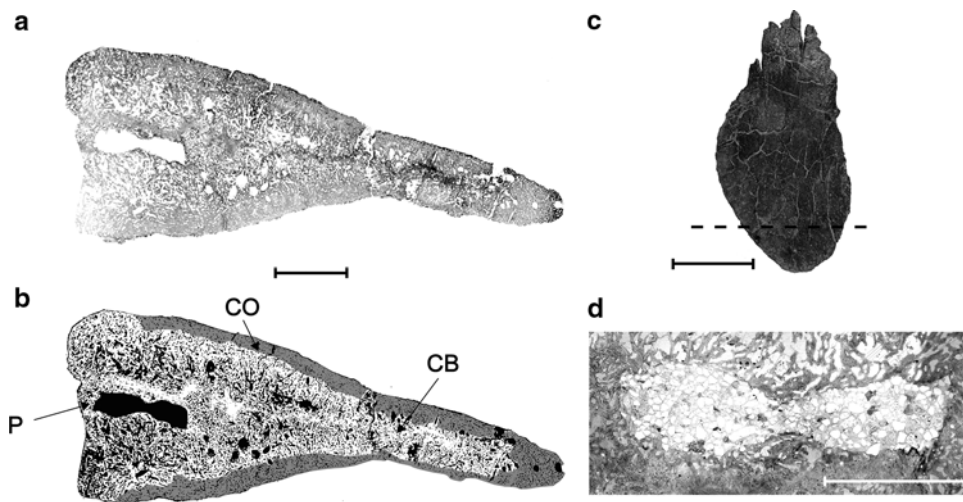


**Fig. 7** Basal to apical CT sections perpendicular to the mesial–distal (anterior–posterior) axes of proximal (left) and distal (right) caudal plates of NSM-PV 20380 (cf. Fig. 6), *Stegosaurus armatus*. Dotted lines on photographs of plates (a) indicate locations of the scans. The CT images themselves are labelled (b) on both plates, and interpretive

drawings are labelled (c). Both plates have highly cancellous interiors surrounded by a thin layer of more compact bone. Near the base of both plates is a large opening, a cross-section through a basal, mesially to distally elongate, vestibular region like that seen in YPM 57716 (Figs. 3, 5). Scale bars 100 mm for photographs of plates



**Fig. 8** Thin section of a distal caudal plate from NSM-PV 20380 (cf. Fig. 6), *Stegosaurus armatus*. **a** Photograph and **b** interpretive drawing of an oblique cut (dotted line in **c**) through the plate. The plate cortex (CO) is very thin. Note the large, pipe-like vascular canal (P) in the basal region of the cancellous bone (CB); the basal portion of this canal corresponds to the vestibule observed in the CT scans (Figs. 3, 5–7). **d** Enlargement of the pipe-like vascular canal. The canal is outlined by trabeculae. Scale bars 10 mm (a, b), 50 mm (d), 100 mm (c)



**Fig. 9** Portion of *Stegosaurus stenops* or *armatus* dorsal plate of YPM 1856, showing an internal pipe connecting with a superficial vascular groove. Scale bar 10 mm

### Alligator osteoderms

In extant crocodylians, a cuirass of osteoderms underlies the horny scales of at least the animal’s back (Richardson et al. 2002; Vickaryous and Sire 2009). The ventral (visceral) surface of an osteoderm is marked by several nutrient foramina (Fig. 10a) (Seidel 1979). The ventral foramina lead internally to a large network of vascular spaces (Fig. 11) (Seidel 1979), branches of which open to the dorsal surface of the osteoderm. The dorsal surface of

individual osteoderms is deeply pitted, with numerous foramina for blood vessels within the pits (Figs. 10b, c) (Buffrénil 1982; Vickaryous and Hall 2008).

### Basking caimans

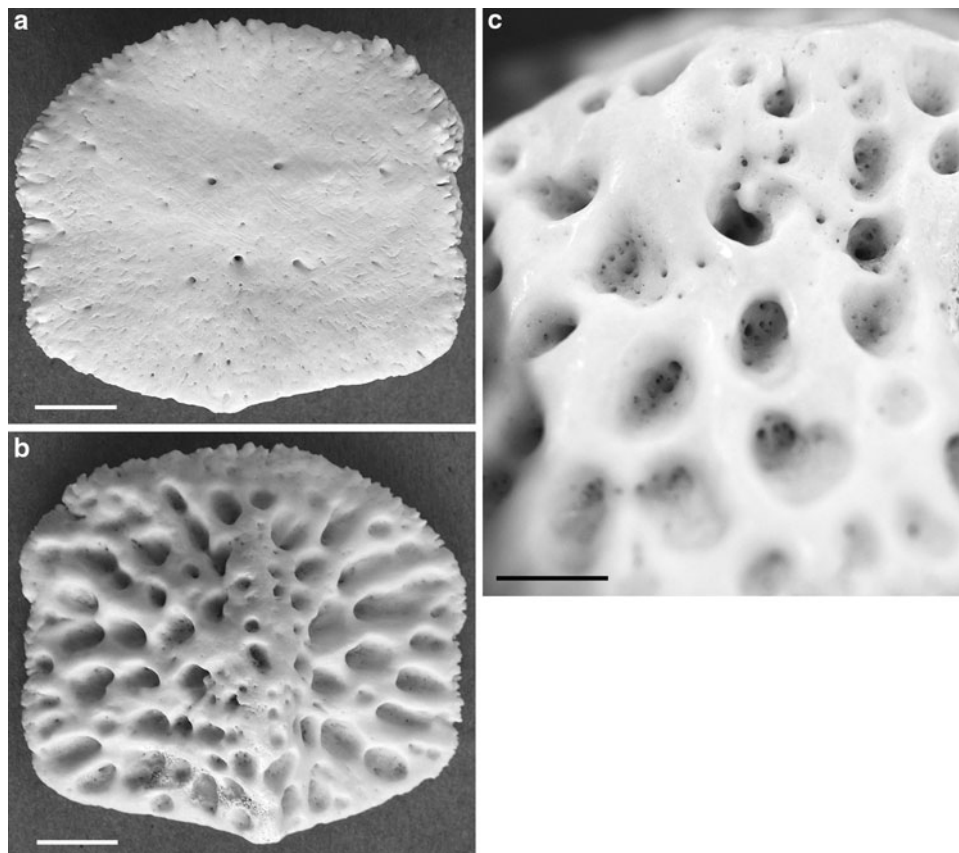
In both caimans the temperature of the animal’s back overlying the osteoderms was cooler than that of skin between the osteoderms (Fig. 12). This suggests that relatively cool blood from the animal’s core may preferentially have been flowing to the osteoderms. Had the osteoderms been an insulating thermal barrier, they would be expected to be as warm as, or even warmer than, the skin in other parts of the back. Thus the osteoderms of these basking caimans may have been involved in heat collection.

### Discussion

#### Interpretation of the vascular system of *Stegosaurus* plates

Both being archosaurs, it seems reasonable to hypothesize that perfusion of *Stegosaurus* plates had some features in common with that of crocodylian osteoderms. Some of the large openings into the plate base are likely to have been nutrient vessels (cf. Buffrénil et al. 1986; Main et al. 2005), but some of them might have been veins rather than arteries, because blood had to exit as well as enter the plate. The large basal openings joined with a large, anteroposteriorly oriented basal vestibule, from which pipes extended apically. Because these structures occur in plates from all individuals examined, they are likely to have been regular features of the stegosaur plate interior, and the multiply branching character of the pipe system suggests that this was a vascular distributary system. The vascular

**Fig. 10** External features of an *Alligator mississippiensis* dorsal osteoderm. **a** Ventral surface; note several nutrient foramina, particularly near the centre of the osteoderm. **b** Dorsal surface; note the numerous pits excavated in the bone. **c** Close-up of the pits, showing the many foramina for blood vessels in the pits. Scale bars 10 mm



pipes presumably broke up into much smaller vessels to service soft tissues in the distal half of the plate, given the necessity of delivering nutrients and oxygen to living bone cells, and of removing metabolic wastes.

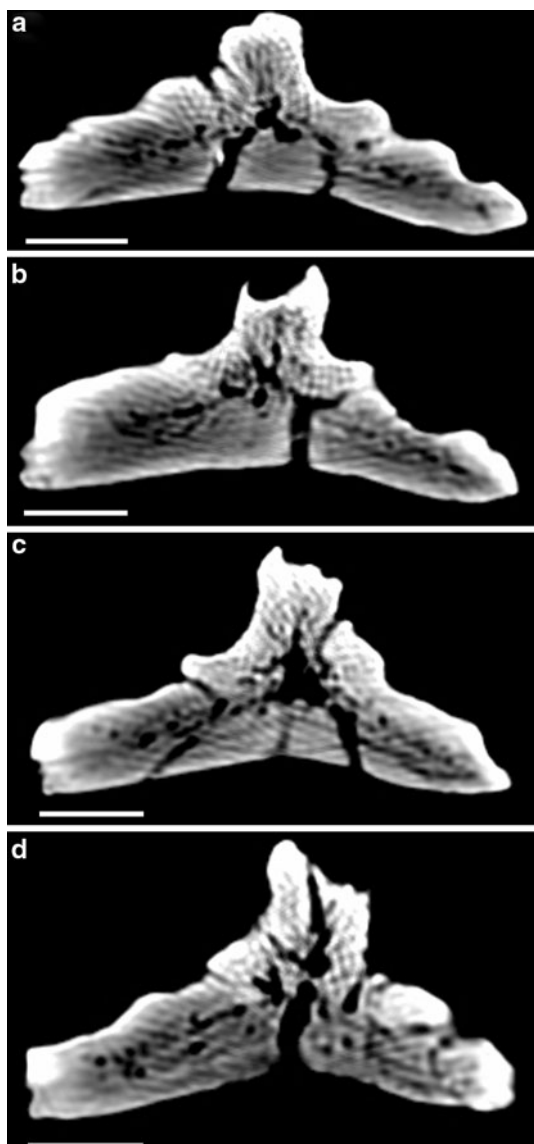
However, perfusion of *Stegosaurus* plates is unlikely to have been identical to that of crocodylian osteoderms. The external surface of mid-level and apical portions of *Stegosaurus* plates shows pinprick openings consistent with the presence of tiny blood vessels leading into the plate interior (cf. Main et al. 2005), but not the great surface density of minute foramina for tiny blood vessels, located in pits, characteristic of crocodylian osteoderms (Fig. 10c). In contrast, *Stegosaurus* plates show an abundance of nearly vertically oriented, superficial vascular grooves, only some of which connect with internal vascular features (Figs. 1, 6, 9; cf. Main et al. 2005), but some of which may have housed superficial blood vessels that spread over the plate from its base, judging from the appearance of plates illustrated by Ostrom and McIntosh (1966, p. 350–361, plates 59–64). The interior of *Stegosaurus* plates (Figs. 3, 4, 6–9) shows a greater proportion of cancellous bone than the interior of *Alligator* osteoderms (Fig. 11). What occupied these cancellous spaces is uncertain, but the proximity of side branches of the internal vascular distributary system described here to the cancellous spaces (Fig. 3) suggests the possibility that some of

the pore spaces housed minute blood vessels. The extensive remodelling seen in trabecular and cortical bone of the plate interior (Buffr nil et al. 1986; Main et al. 2005; Chinsamy-Turan 2005; Hayashi et al. 2009) indicates that blood was reaching bone cells from somewhere, and the internal vascular system described in this paper seems a plausible candidate for at least part of the necessary flow.

#### Function of alligator osteoderms

Because crocodylians are the only extant archosaurian relatives of *Stegosaurus* that bear osteoderms, the role that these dermal ossifications play in the biology of crocodylians may have some bearing on the function(s) of osteoderms in stegosaurs. Crocodylian osteoderms clearly provide some protection for the dorsal surface of the reptile (Richardson et al. 2002), and also function to stiffen the back to facilitate terrestrial locomotion (Frey 1988). In addition, crocodylian osteoderms seem to have some less obvious functions: as sources of calcium for shelling eggs by females (Hutton 1986; Tucker 1997; Klein et al. 2009), and as sites of lactate sequestration via carbonate mobilization during dives (Jackson et al. 2003). Consequently it is too simplistic to talk about single functions of osteoderms in crocodylians, and, by extension, in thyreophorans as well. It is probably more appropriate to think in terms of





**Fig. 11** Four sequential CT scans of an *Alligator mississippiensis* dorsal osteoderm, perpendicular to the long axis of the central keel of the osteoderm. All scans were made near the middle of the fore-aft axis of the osteoderm. Note vascular canals entering vertically and obliquely from the ventral surface of the osteoderm (cf. Fig. 8a), and the network of vascular spaces within the osteoderm interior. Scale bars 10 mm

the primary function(s) of osteoderms (those functions that were most obviously influenced by selection during the evolution of osteoderms) and secondary functions (those functions that osteoderms, by virtue of the characters they developed as a result of selection for their primary function[s], are also able to carry out).

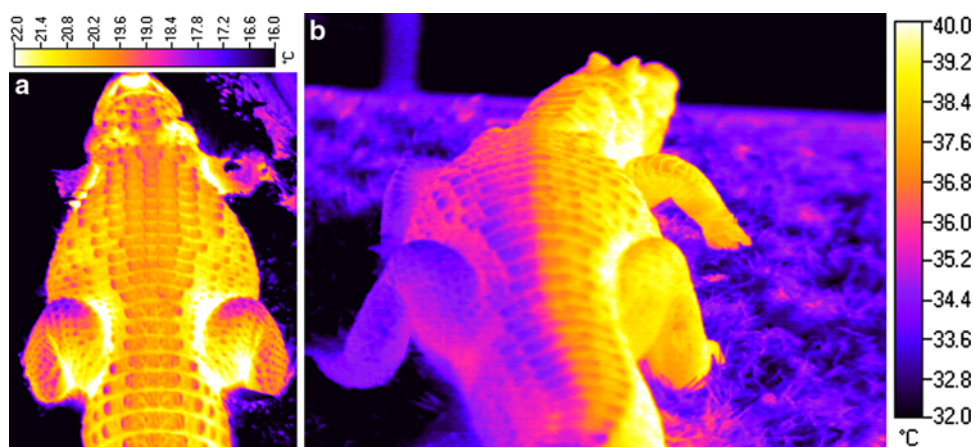
Mobilization of calcium for shelling eggs, and use of osteoderms as sites for lactic acid buffering, as well as continual remodelling of osteoderm surface sculpturing (Buffr n il 1982), all imply a significant blood supply to the osteoderms over a physiologically significant time scale.

Seidel's (1979) observations of the vascularity of *Alligator* osteoderms led him to suggest that one of the roles of the osteoderms might be thermoregulation: "dense bone of the osteoderm is riddled with small holes which are presumably filled with arterioles. Any heat absorbed by the surface of the osteoderm will be rapidly transmitted throughout the entire osteoderm via its compact mineral composition. The arterioles in the osteoderms could readily pick up the absorbed heat and carry it to other parts of the body. To control heat absorption, simple vasoconstriction could reduce osteoderm blood flow and thereby reduce heat transfer rate" (Seidel 1979, p. 379). Richardson et al. (2002), p. 33 likewise reported that crocodylian osteoderms "are well-vascularized and appear to play an important role in heat exchange with the environment. When bloodflow through this arteriole-rich region is increased or decreased it alters rates of heat exchange." We are unaware, however, of published data that quantify the degree to which osteoderms facilitate heat exchange between crocodylians and the environment, but our observations on basking caimans (Fig. 12) provide indirect evidence that Seidel's interpretation could be correct.

#### Blood circulation and temperature regulation in amniotes

In turtles, lizards, and crocodylians, the body typically heats up more quickly than it cools, allowing a warming animal to reach its activity temperature more quickly, and to retain heat longer. This heating-cooling "hysteresis" is associated with increased heart rate and perfusion of the skin with blood during warming, and a reduction in heart rate and perfusion of the skin during cooling (Bartholomew and Tucker 1963; Bartholomew and Lasiewski 1965; Weathers and White 1971; White 1973; Grigg and Alchin 1976; Smith 1976, 1979; Smith and Adams 1978; Smith et al. 1978, 1984; Grigg et al. 1979; Robertson and Smith 1981; Grigg and Seebacher 1999; Seebacher 2000; Seebacher and Franklin 2007). However, if subjected to heat stress, the reptile can use "reverse hysteresis" to deliver extra blood to the skin for dumping excess heat to heat sinks (shaded parts of the body, parts exposed to the wind or a cool substrate: White 1973; Grigg and Seebacher 1999). Control of blood flow to/from the body surface is also an important component of physiological thermoregulation in endotherms, and may be especially significant in large-bodied mammals (Phillips and Heath 1995; Mortola and Lanthier 2004).

Thermal exchange (whether gain or loss) with the environment can be modulated by controlling blood flow to "appendages" that have higher surface: volume ratios than the animal's body core. Appendages in this sense include the limbs of lizards and turtles (Hochscheid et al. 2002;



**Fig. 12** Thermal imaging of basking caimans (*Caiman latirostris*). The animals were captives kept outdoors at São Paulo State University (UNESP), Rio Claro, Brazil. The pictures were taken 26 June 2005. The weather was clear, with intense solar radiation; air temperature at the time the picture of the animal in (a) was taken was

approximately 16°C (early morning), and air temperature at the time the picture of the animal in (b) was taken was approximately 25°C. In both images the colour was scaled to maximize contrasting temperatures, with background temperatures being the coldest temperature in each image

Dzialowski and O'Connor 2004); the limbs, toes, neck, beak, wings (in *Struthio*), and (in *Casuarius*) casque of ratites (Phillips and Sanborn 1994), duck bills (Hagan and Heath 1980), toucan bills (Tattersall et al. 2009) and (depending on species) the feet, ears, and horns of mammals (Taylor 1966; Buss and Estes 1971; Wright 1984; Phillips and Heath 1992, 2001; Picard et al. 1996, 1999; Hoefs 2000).

#### Function of thyreophoran osteoderms

Viewed in a phylogenetic context (Colbert 1981; Galton and Upchurch 2004; Main et al. 2005; Maidment et al. 2008; Mateus et al. 2009), thyreophoran osteoderms probably initially functioned as passive armor (as in crocodylians) and possibly for stiffening the back, functions that were probably retained to varying degrees throughout the evolution of the group, particularly in ankylosaurs (Scheyer and Sander 2004). Stegosaur spikes and ankylosaur tail clubs were undoubtedly less passive and more aggressive weaponry, being employed against conspecifics, predators, or both. The variety of osteoderm shapes and deployments in stegosaurs strongly suggests that these features also operated as species recognition devices (Main et al. 2005). By analogy with the osteoderms of extant modern crocodylians, however, other, less obvious osteoderm functions may have operated more quietly in the background of thyreophoran evolution.

A continuous blood supply would have been necessary for maintenance and repair of thyreophoran osteoderms, and is evidenced by the external appearance and the bone histology of these features (Farlow et al. 1976; Buffrénil et al. 1986; Scheyer and Sander 2004; Main et al. 2005;

Hayashi et al. 2009, 2010), as well as by our CT scans. It is plausible, therefore, that osteoderms of all thyreophorans played at least a minor role in thermoregulation, not because they had evolved specifically for that function, but rather because they were simply part of the integument, which was likely involved in heat exchange with the environment, just as it is in extant amniotes.

In *Stegosaurus* the thermoregulatory role of the plates was possibly greater than in other thyreophorans (an exaptation; Gould and Vrba 1982), by virtue of their size, dorsal position (which would have placed them in wind currents), and staggered arrangement along the animal's back (Farlow et al. 1976; O'Connor and Dodson 1999). If the plates did indeed play a significant role in heat exchange with the environment, blood vessels on the plate surface may have been more important than internal blood flows, but the thin cross sections of plates above their bases would have facilitated heat exchange between an osteoderm's interior and exterior by conduction, regardless of the extent to which blood flow to the plate interior communicated with blood flow to the osteoderm's external surface. *Stegosaurus* plates might be viewed as the equivalents of an alternating array of bovid horns shaped like elephant ears. This does not prove that big-plated stegosaurs did in fact use their plates for thermoregulation, but the potential does seem to have been there.

Our observations on plate vascularity say nothing about whether heat exchange with the environment primarily involved heat gain or loss. However, the experiments of Farlow et al. (1976) suggest that the alternating arrangement of *Stegosaurus* plates was best suited for shedding heat to breezes via forced convection.

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