

## Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior

Mark B. Goodwin and John R. Horner

**Abstract.**—Modern histological techniques allow paleontologists to investigate the internal microstructure of bone tissue. We apply high resolution images of histological thin sections from an ontogenetic series (not conspecific) of pachycephalosaurid frontoparietal domes to test the hypothesis that these Late Cretaceous dinosaurs used their heads as battering rams, analogous to the behavior of the bighorn sheep, *Ovis canadensis*, or as a thermoregulatory device. Our analysis reveals that the internal structure of the pachycephalosaur dome is a dynamic tissue that reflects the changeable expansion and vascularity of the dome throughout ontogeny. The *radiating structures* within the frontoparietal dome, used previously to support “head-butting” hypotheses, are unexpectedly transitory, diminishing in mature individuals and nearly absent in adult skulls where head-butting behavior is presumed to occur. The unique architecture of the pachycephalosaurid dome is dividable into three distinct Zones. We demonstrate that the relative vascularity, associated tissue structures, and orientation and density of Sharpey’s fibers within these Zones are modified during growth. Evidence for an external dome covering in vivo precludes the determination of the final shape of the pachycephalosaur skull. On the basis of these new observations, we propose that cranial display in support of species recognition and communication is a more parsimonious interpretation of the function of the pachycephalosaurid dome. Sexual display behaviors were probably secondary.

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### Introduction

Pachycephalosaurs (Ornithischia: Marginocephalia), popularly known as dome-headed dinosaurs, are a group of bipedal ornithischian dinosaurs characterized by their distinctive greatly thickened dome above their braincase (Sues and Galton 1987). The majority of Late Cretaceous species occur in the Western Interior of North America and central Asia (Sues 1997). The pachycephalosaurid dome is made up of the fused paired frontals and parietal bones (Fig. 1). The degree of inflation or dome thickness, shape of the dome, and incorporation of the squamosal and lateral cranial elements into the dome have all been used as (1) diagnostic characters of the group (Maryańska and Osmólska 1974; Sereno 1986; Sues and Galton 1987; Maryańska 1990; Sullivan 2000, 2003; Williamson and Carr 2002); (2) support for recognizing sexual dimorphism (Chapman et al. 1981); and (3) relative age assignment of individual specimens (Giffin

1989; Goodwin et al. 1998; Williamson and Carr 2002).

The function of the domed skull of pachycephalosaurid dinosaurs has puzzled paleontologists for decades and continues to stimulate debate on the topic (Carpenter 1997; Horner and Goodwin 1998). Previous studies form the basis for the paleobiological interpretation that internal cranial features in the thickened pachycephalosaurid dome supported head-butting behavior.

What bones in the skull contribute to the pachycephalosaurid dome? This was a question Brown and Schlaikjer asked in their 1943 study describing a new assemblage of pachycephalosaurid dinosaurs (known then as troödonts) from the Western Interior of North America. Brown and Schlaikjer (1943: p.145) confirmed the absence of fused dermal ossifications over the skull roof (contra Gilmore 1931: p. 3) and demonstrated that the pachycephalosaurid dome was made up of the fused

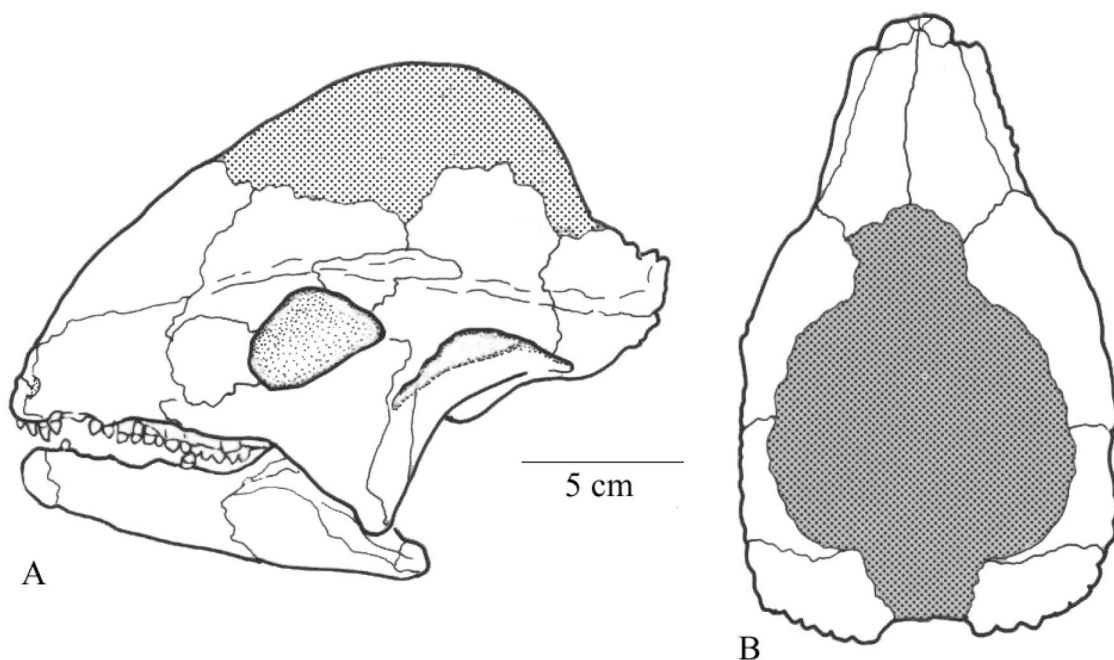


FIGURE 1. The pachycephalosaurid frontoparietal (fp) dome is shown in the stippled portion of this illustration of the skull of *Stegoceras validum* (UA 2) in left lateral view (A) and dorsal view (B). The fused paired frontals and the parietal coalesce and inflate during ontogeny to form the fp dome in pachycephalosaurid dinosaurs.

frontals and parietal bones. In addition, they recognized the variable density in the internal composition of the dome and described the interior of the dome as having a "radiating structure." This variability in dome density was also noted earlier by Lambe (1918: p. 24) who described the inner organization of the dome as possessing a "columnar structure."

Colbert (1955: p. 195) first suggested, "Perhaps (as a very wild surmise) the skull was used as a sort of battering ram." L. Sprague de Camp (1956: p. 17) popularized this idea a year later in his science fiction story "A Gun for Dinosaur," writing that "the males butt each other with these heads in fighting over the females." Galton (1970: p. 23) referred to pachycephalosaurids as "Dinosaurian Battering Rams" in the title of his 1970 study and proposed that the thick pachycephalosaurid dome was used in the same mode as the horns of fighting rams in the mountain sheep, *Ovis canadensis*. Galton (1970: p. 31) described the internal texture of the pachycephalosaurid dome as "a radiating series of trabeculae or bony fibers, each of which is perpendicular to the outer surface of the dome" (sensu Brown

and Schlaikjer 1943) and suggested that the dome was used for head-butting, acknowledging L. Sprague de Camp's short story. Galton (1971: p. 45) went on to claim "this arrangement is ideal for resisting a force applied against the top of the dome" without further quantification. In a follow-up study of the pachycephalosaurid dome using photoelastic analysis, Sues (1978) stressed a piece of plexiglass in the shape of a pachycephalosaurid dome. This produced a radiating pattern similar to the radiating structure in the coronal-sectioned pachycephalosaurid dome described and figured earlier by Brown and Schlaikjer (1943: p. 143). Sues (1978: p. 465) concluded, "The radiating pattern of the trabeculae and the fact that the trabeculae are oriented in a perpendicular fashion to the dorsal surface of the frontoparietal invite a functional explanation. Working with the trajectorial theory of bone architecture, the trabeculae could be considered to be compressive resistant." According to Alexander (1997: p. 423), "the bone of the pachycephalosaur dome seems to have had a spongy texture, so it probably deformed enough in an impact to

provide useful cushioning.” Rigby et al. (1987), Landry (1995), and Reid (1996) suggested that the internal “radiating structures” of the pachycephalosaur dome indicated the dome was more suitable as a heat-exchange organ than for head-butting.

In our preliminary study (Horner and Goodwin 1998) and in this more comprehensive cranial histological analysis, we confirm that these *radiating trabeculae* occur in some pachycephalosaurid domes. Our observation, however, does not end there. We also have determined that these internal features of the skull are, in fact, transitory and limited to an early stage of ontogeny. During growth of the skull, these radiating structures within the dome are transformed and later lost as the frontoparietal dome fully develops in adult individuals, where head-butting behavior is presumed to occur.

### Materials and Methods

**Institutional Abbreviations.**—CM = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMN = Canadian Museum of Nature, formerly GSC = Geological Survey of Canada and NMC = National Museum of Canada, Ottawa; MOR = Museum of the Rockies, Montana State University, Bozeman; UCMP = University of California Museum of Paleontology, Berkeley; VRD = Sierra College, Rocklin, California.

Seven pachycephalosaurid frontoparietal domes (not con-specific) were sectioned with an Isomet diamond saw. The samples were embedded in Silmar-40 polyester resin prior to cutting and mounted to glass slides with epoxy resin. Sagittal, coronal, and transverse cuts were made. Our use of an ultra-thin (0.012-inch) diamond saw blade results in a minimal loss of fossil material for study. Archival casts were made of the specimens before cutting and are cataloged in the collections of the MOR and UCMP. The thin-sections were ground on a Buehler Ecomet grinder and sections were studied by light microscopy under normal and polarized light. Histological sections from this study are cataloged into the slide libraries of the MOR and UCMP.

The specimens are as follows: UCMP 130049, *Stegoceras* sp., frontoparietal dome, Ju-

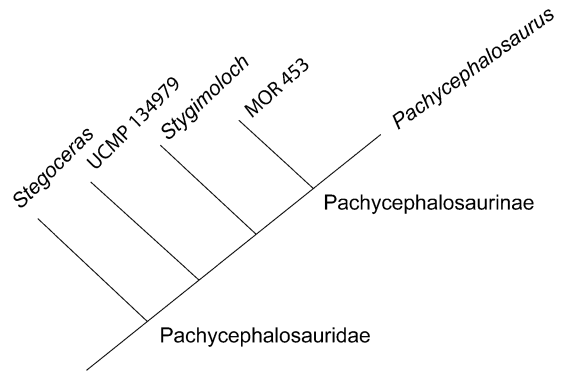


FIGURE 2. Phylogenetic placement of *Pachycephalosaurus*, *Stegoceras*, *Stygimoloch*, and MOR 453 and UCMP 134979. Cladistic relationships from Sereno 1986. MOR 453 is a full-domed taxon with the frontoparietal dome expanded posteriorly. The lateral cranial sutures indicate that the fp dome incorporates the postorbitals and squamosals, synapomorphies for the Pachycephalosaurinae of Sereno (1986).

dith River Formation; MOR 295, *Stegoceras validum*, unfused left and right frontals, Judith River Formation; UCMP 134979, pachycephalosaurid indet., frontoparietal dome, Hell Creek Formation; MOR 1179, *Stegoceras validum*, frontoparietal dome, Judith River Formation; UCMP 128383, *Stygimoloch spinifer*, Hell Creek Formation; MOR 453, pachycephalosaurid indet. (full-domed taxon), frontoparietal dome, Two Medicine Formation; VRD 13, *Pachycephalosaurus wyomingensis* (sensu Sues and Galton 1987), partial skull, Hell Creek Formation.

### Assessing Ontogeny

The seven pachycephalosaurid frontoparietal domes selected for histological analysis comprise a size gradient among phylogenetically closely related taxa (Fig. 2). They were all collected from the coeval Judith River and Two Medicine Formations, and the slightly younger Hell Creek Formation, all part of the Upper Cretaceous sequence of fossil-bearing sediments, Montana. Prior to sectioning, each specimen was: (1) identified to genus following the classification of Sereno (1986) and Sues and Galton (1987) and (2) assigned a relative ontogenetic stage (juvenile, subadult, adult) according to their phylogenetic relationships, total length and inflation of the frontoparietal, and sutural morphology. Using these results,

TABLE 1. Prior to histological sectioning, each of the seven pachycephalosaurid frontoparietal domes was identified to genus. Their phylogenetic relationships, comparative dome thickness, and length of the frontoparietal (fp) were used to support their relative age assignment from youngest (top) to oldest (bottom). Cranial histological characters provided additional criteria after sectioning that indicated UCMP 134979 was "older" than MOR 1179, despite having a significantly less inflated and smaller frontoparietal dome.

Specimen no.	Taxon	Age	Dome thickness from roof of the braincase to apex of the fp dome (mm)		Length of fp dome (mm)
UCMP 130049	<i>Stegoceras</i> sp.	Campanian	18.6	youngest	61.0
MOR 295	<i>Stegoceras validum</i>	Campanian	31.4		65.0 est.
UCMP 134979	Pachycephalosauridae indet.	Maastrichtian	23.5		52.5
MOR 1179	<i>Stegoceras validum</i>	Campanian	43.4		80.6
UCMP 128383	<i>Stygomoloch spinifer</i>	Maastrichtian	56.2		135.0 est.
MOR 453	Pachycephalosauridae indet.	Latest Campanian	104.0		180.0
VRD 13	<i>Pachycephalosaurius wyomingensis</i>	Maastrichtian	138.0	oldest	267.0

we placed the specimens in a presumed ontogenetic sequence from youngest to oldest (Table 1).

The degree of sutural fusion between cranial elements in the skulls of dinosaurs is often used as a measure of the relative age of the individual. Timing of fusion is variable among the Marginocephalia (Ceratopsids + Pachycephalosaurids). For instance, the frill (= parietal and squamosal bones) and associated cranial elements in one of the largest and presumed adult *Triceratops* skulls (UCMP 113697) remain unfused (Forster 1996). In juvenile and subadult pachycephalosaurid skulls, however, the degree of sutural fusion medially between the paired frontals and transversely between the frontals and the parietal, combined with dome size and shape, degree of closure of the supratemporal fenestrae, and dorsal surface texture of the dome, appears to constitute a reliable suite of characters for determining relative age (Goodwin et al. 1998; Williamson and Carr 2002). This is supported in the fossil record by the occurrence of unfused, thick, undomed frontals (Galton and Sues 1983: Fig. 1C–F,G–J) and thick but uninflated parietals with large, open supratemporal fenestrae (Goodwin 1990: Fig. 14.11, G–I; Sullivan 2003: Fig. 1C,D) in juvenile skulls of *Stegoceras*. We concur with Williamson and Carr (2002) and Sullivan (2003) that these specimens, previously described as *Ornatolithus* (Wall and Galton 1979; Galton and Sues 1983) are best reinterpreted as juvenile members of *Stegoceras*. Low-domed frontals, some unfused along the

midline frontal suture (Goodwin 1990: Fig. 14.11, A–C), also represent juveniles of *Stegoceras*. In the subadult stage of frontoparietal dome development, the frontals progress from thick and flat to slightly inflated and dome-forming whereas the parietal remains uninflated (Lambe 1902: Pl. XXI Figs. 1, 2; Lambe 1918: Pl. I, II; Sullivan 2003: Fig. 2D–I). The two supratemporal fenestrae begin to close, getting smaller, sometimes asymmetrically. In progressively more adult pachycephalosaurid specimens, the paired frontals fuse and coalesce with the increasingly inflated parietal to form a dorsally round, vaulted frontoparietal dome as the supratemporal fenestrae close further or entirely (Gilmore 1924: Pl. I–III; Brown and Schlaikjer 1943: Pl. 38). In juvenile and some subadult pachycephalosaurids, particularly *Stegoceras* and *Stygomoloch*, the frontal-parietal suture may be visible and remain open on the dorsal surface of the skull (Gilmore 1924: Pl. VII, Figs. 3, 4; Sues and Galton 1987: Pl. I, Figs. 1, 2; Goodwin et al. 1998: Fig. 10). Juvenile and subadult cranial records of *Pachycephalosaurius* are lacking.

UCMP 130049, a low-domed, fused frontoparietal, is hypothesized on the basis of its incipient doming and large brain case relative to frontoparietal length, to represent a juvenile *Stegoceras* and forms the starting point in our growth series. A pair of unfused frontals, MOR 295, and an equal sized but fused articulated frontoparietal dome, MOR 1179, represent a second and third juvenile of *Stegoceras*



*validum*, judging from their relative size, sutural contacts, and deeply sculptured dorsal surfaces of their domes. Three intermediate-sized domes, UCMP 134979, UCMP 128383, and MOR 453 represent a subadult stage of ontogeny. Prior to sectioning, UCMP 134979 was hypothesized to represent a juvenile *Pachycephalosaurus* on the basis of its similarity to the regular, round shape of the frontoparietal dome in some adult *Pachycephalosaurus* skulls. UCMP 134979 compares very well to the *Pachycephalosaurus* “morphotype” of CM 3180 described by Gilmore (1936: p. 110). UCMP 128383, on the basis of size and cranial and postcranial morphology, represents a subadult *Stygimoloch spinifer*. MOR 453, a new taxon from the Two Medicine Formation (see Horner et al. 1992), is the largest frontoparietal dome known from Campanian Age sediments in North America. VRD 13, the largest specimen in our sample set, possesses diagnostic characters consistent with *Pachycephalosaurus wyomingensis* and is considered to be an adult on the basis of its relative size, a fully developed frontoparietal dome, and parietosquamosal ornamentation. This skull provides the endpoint for the hypothesized adult condition.

## Results and Discussion

In this study, we recognize three distinctive histological zones, formalized as Zones I, II, and III, directly above the roof of the braincase and continuing outward to the dorsal surface of the frontoparietal dome (Fig. 3). A brief description of each Zone is given here, followed by examples using the sectioned frontoparietal domes described in the previous section.

Zone I is a blend of deformed, stretched-out, and ropey-looking primary and secondary osteons. These features are characteristic of “typical” bone of endochondral origin. Sharpey’s fibers occur, mainly along the roof of the braincase. The histological features and thickness of Zone I remain relatively constant throughout ontogeny, regardless of the height of the overlying dome.

Zones II is the vascular portion of the dome and its thickness decreases during ontogeny. When Zone II is extensive, long bony struts reveal abundant osteocyte lacunae and bundles

of radiating Sharpey’s fibers—collagen fibers originating in the periosteum and extending into peripheral lamellar bone, anchoring some form of external covering over the dome. These fibers become buried within the bone matrix as new subperiosteal bone is formed (Martin et al. 1998). Sharpey’s fibers are a micron-scale constituent of the hydroxyapatite tissue of the dome, not the macroscopic hydroxyapatite “columns” or “bony fibers” observed along sutural or broken surfaces (contra Sullivan 2003). Alternating between the bony struts are long, tubelike, radial vascular spaces that illustrate the spongy texture originally described by Brown and Schlaikjer (1943: p. 145).

Zone III consists of a relatively dense, sparsely vascularized layer of bone sandwiched between the vascular bone of Zone II and the exterior, periosteal surface of the frontoparietal dome. The thickness of Zone III increases during ontogeny. Sharpey’s fibers are very common at the periosteal surface of the dome but are patchy, occurring as islands within the deeper tissues of the skull in Zones II and III. Specific regions of Zone III are devoid of osteocyte lacunae in some specimens.

In Figure 4, five of the seven sectioned specimens illustrate the relative size difference between the smallest (UCMP 130049; Fig. 4A) and the largest (VRD 13; Fig. 4E) specimens. UCMP 130049 (Fig. 4A), MOR 295 (Fig. 4B), and MOR 1179 (Fig. 4C) represent juveniles of *Stegoceras validum*. MOR 453 (Fig. 4D) and VRD 13 (Fig. 4E) represent a new full-domed taxon and an adult *Pachycephalosaurus*, or alternatively a subadult and adult *Pachycephalosaurus*, respectively.

UCMP 130049 possesses an extensive Zone II, with only a thin veneer of bone representing Zone III visible in Figures 4A and 5B. Zone I is composed of mature primary osteons intermixed with a small number of secondary osteons. Zone II is extremely vascularized with long radially oriented canals forming a very spongy-looking bone matrix. The bony struts between radial canals contain abundant osteocyte lacunae and occasional bundles of Sharpey’s fibers.

MOR 295 (Fig. 4B), a right frontal, and MOR 1179 (Fig. 4C), a coalesced frontoparietal

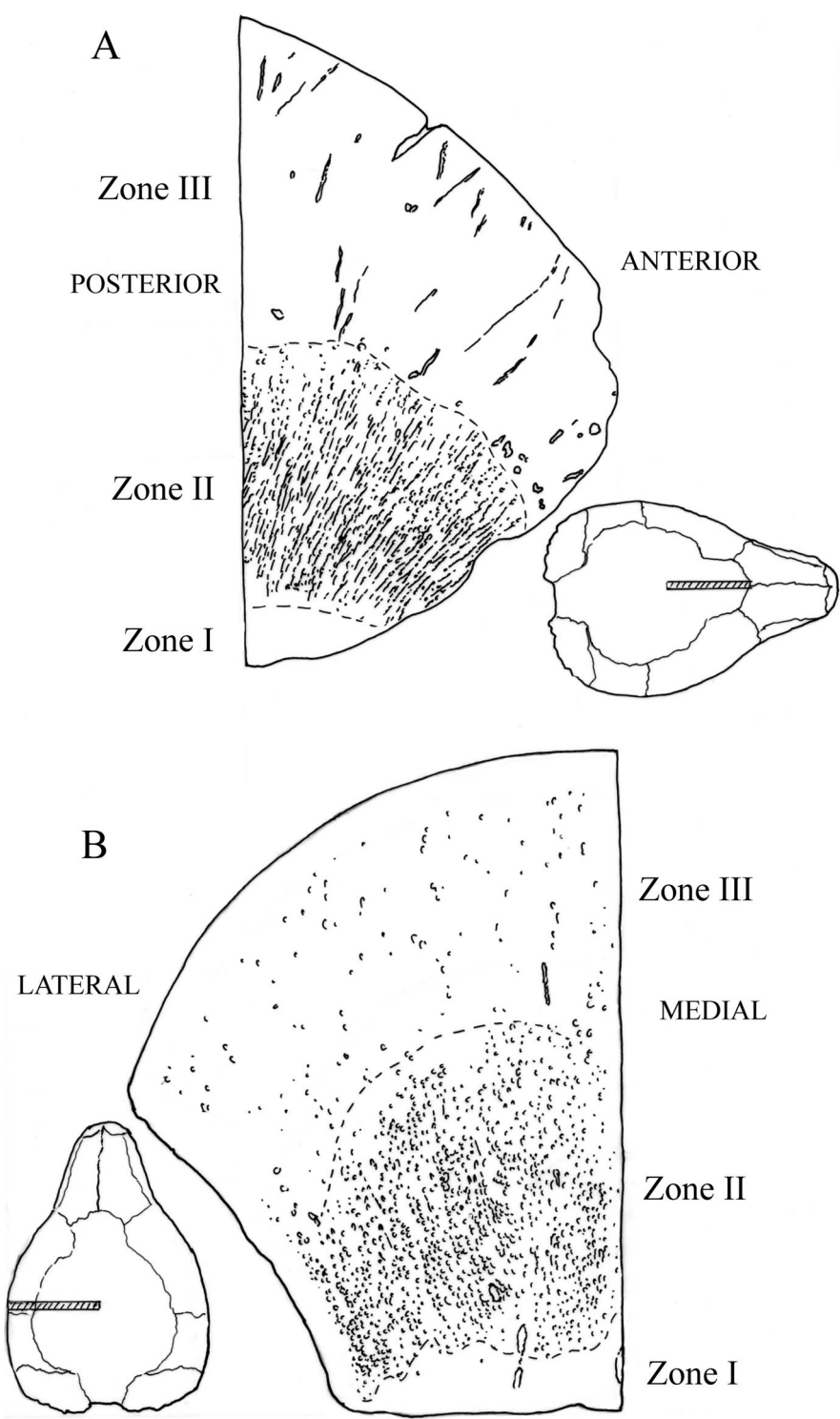


FIGURE 3. This is an illustration of the three histological zones observed in the subadult domed pachycephalosaurid (MOR 453) from the Two Medicine Formation, Montana, Gen. and sp. nov. Cranial histological Zones I, II, and III, defined in this study, are shown in right lateral (A) and transverse (B) views.

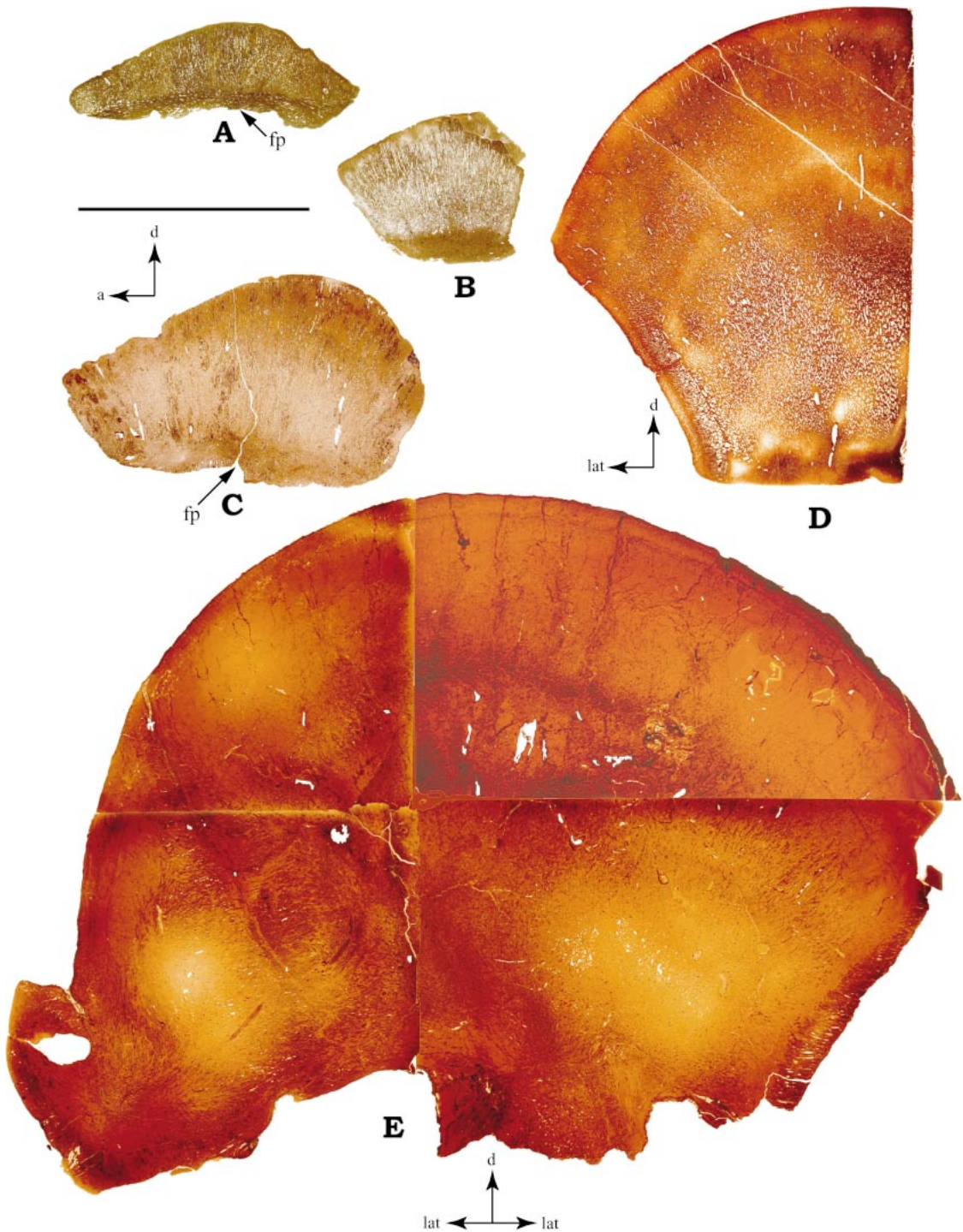


FIGURE 4. Histological thin sections of five of the seven pachycephalosaurid specimens comparing their relative sizes and their cranial vascularity. A, Frontoparietal dome of a juvenile *Stegoceras validum* (UCMP 130049) in sagittal section, left lateral view. B, Right unfused frontal of a juvenile *Stegoceras validum* (MOR 295) in sagittal section, left medial view. C, Frontoparietal dome of *Stegoceras validum* (MOR 1179) in sagittal section, left lateral view. The frontal-parietal (fp) suture is visible on the roof of the braincase and denoted by the arrow in A and C. D, Frontoparietal dome of a subadult full-domed pachycephalosaurid, Gen. et sp. nov. (MOR 453) in coronal section showing the right half of the skull. E, Frontoparietal dome of an adult *Pachycephalosaurus wyomingensis* (VRD 13) in coronal section from "ear to ear." Abbreviations: Orientation arrows denote anterior (a) and dorsal (d) for A–C; lateral (lat) and dorsal (d) for D and E. Scale bar, 5 cm.



dome, represent individuals of nearly identical size, histological tissue structure, and stage of ontogeny. In both specimens, Zone II tissue within the frontals is exceptionally vascular with an overlying thin veneer of bone at the dorsal surface representing Zone III (Fig. 5C). In MOR 1179, Zone II of the parietal and Zone II of the frontal both share a common spongy texture (Fig. 4C). The frontoparietal suture is clearly visible between the frontal and parietal, traceable from the roof of the braincase to the dorsal surface of the dome (Fig. 4C). The parietal portion of the dome in MOR 1179 also possesses a significant development of Zone III (see Fig. 5D). The juvenile *Stegoceras* frontoparietal dome (CMN 1108) sectioned by Brown and Schlaikjer (1943: p. 129) is approximately the same size (length, width, and height above the roof of the braincase) as the *Stegoceras* dome, MOR 1179 (Fig. 4C), and reveals an internal tissue arrangement that matches our Zones I–III. The coronal section of Brown and Schlaikjer (1943: Pl. 43, Fig. 1) shows an expansive Zone II overlain by a relatively thinner but identifiable Zone III through the frontoparietal.

MOR 453 is a robust, highly inflated frontoparietal dome. The dorsal surface is smooth, a feature common in some of the largest pachycephalosaurid skulls (Gilmore 1936: Fig. 2; Brown and Schlaikjer 1943: Pl. 42). We think this may occur late in ontogeny when the underlying bone becomes less sculptured as the keratinous covering enlarges with continued growth into adulthood. The dorsal surface of smaller domes has a contrasting sculptured appearance produced by numerous octagonal sulci (Brown and Schlaikjer 1943: Pl. 43, Fig. 4; Williamson and Carr 2002: Fig. 10). We hypothesize that the sulci are scale margins. As the dome covering grows, these separate octagonal scales join together and form a more uniform structure with age. The sulci become less distinct as the bone beneath the expanded,

thicker covering is remodeled and becomes smoother.

MOR 453 reveals a reduced Zone II and a relatively thicker Zone III (see Fig. 4D). The shape of the vascular spaces of Zone II is for the most part less elongated compared with the younger specimens in Fig. 4A–C and in the juvenile *Stegoceras* figured by Brown and Schlaikjer (1943: Pl. 43, Fig. 1). Although post-mortem bacterial invasion obscures most of the tissue structure of Zone III, much of the bone is interlaced with bundles of Sharpey's fibers. Some regions of Zone III appear to be acellular.

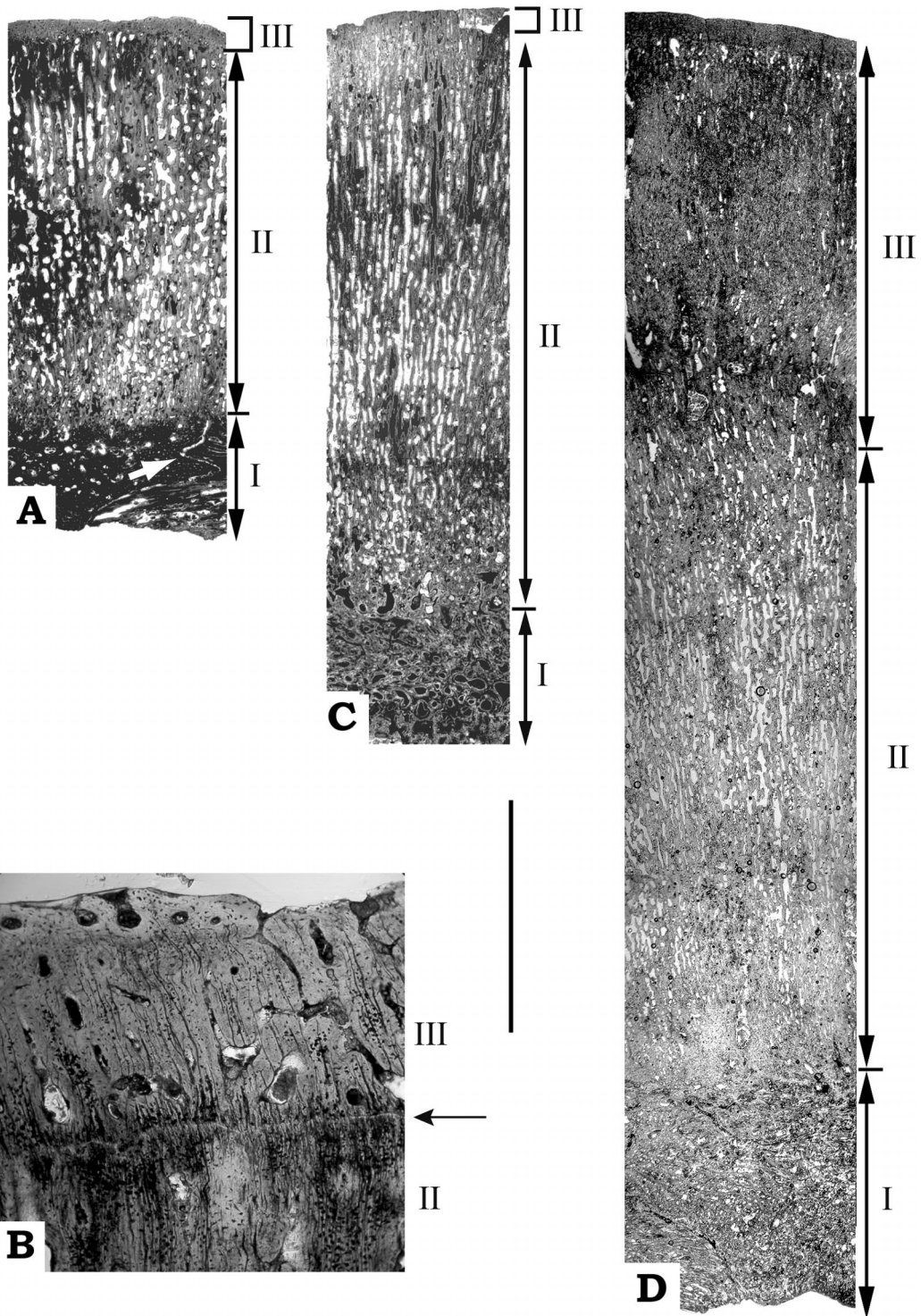
VRD 13 (Fig. 4E), a nearly complete adult skull of *Pachycephalosaurus* and the largest specimen in our sample, is devoid of elongated vascular spaces so characteristic of Zone II (Fig. 6A–D). Here, the minimal vascularity that does exist is restricted to two very small pockets deep within the dome (Fig. 6B), which we interpret to be the remaining trace of Zone II. Zone I contains an abundance of deformed Haversian canals (Fig. 6D), and limited Sharpey's fibers. In several areas of Zone III, Sharpey's fibers are common between small vascular canals in a tissue complex that can be either cellular (Fig. 6C) or acellular (Fig. 7D). This combination of Sharpey's fibers and acellular bone tissue is very unusual. These local "islands" of metaplastic bone (see Haines and Mohiuddin 1968) lack canaliculi in VRD 13 and mature pachycephalosaurid domes. These tissues can theoretically be identified from very small samples, such as fragments in dinosaur coprolites (Chin et al. 2003).

Prior to thin-sectioning, UCMP 128383 (Fig. 7A) and UCMP 134979 (Fig. 7B), two intermediate-sized domes, were originally hypothesized to represent a subadult *Stygimoloch* and a juvenile *Pachycephalosaurus* respectively (see Table 1). The histological profile we obtained provides additional data to both substantiate and challenge our original hypotheses of on-

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FIGURE 5. Sagittal sections through the juvenile domes of *Stegoceras validum* illustrate the relative proportions of Zones I–III preserved. A, Posterior region of the frontal (UCMP 130049) showing a dark basal Zone I and an extensive Zone II with only a thin veneer of Zone III at the dorsal surface. The frontal-parietal suture, shown by the white arrow, is clearly visible and bisects the basal region of Zone I. B, Highly magnified view of Zone III, fron-





toparietal dome (UCMP 130049) showing the interface between Zone II below the arrow and Zone III above the arrow. Note the dense accumulation of abundant Sharpey's fibers in the darker area near the interface in the upper region of Zone II. C, Midsection of right frontal (MOR 295) with an extensive Zone II and a very minimal Zone III. D, Midsection of parietal (MOR 1179) reveals the enhanced development of Zone III compared with A and C. Scale bar, 10 mm for A, C, D; 1 mm for B.



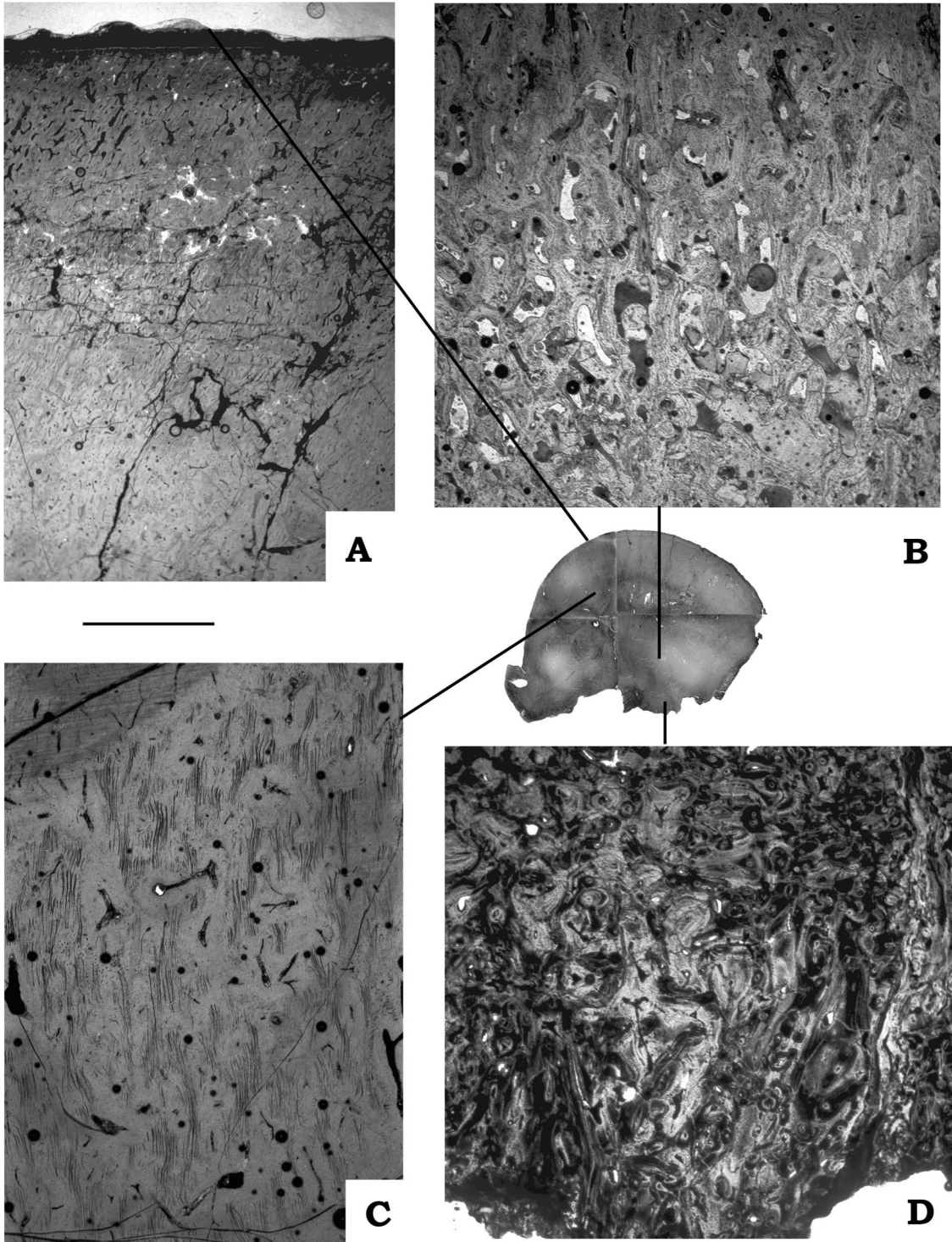


FIGURE 6. Selected histological thin-sections from the coronal section of *Pachycephalosaurus wyomingensis* (VRD 13). A, Bone tissues of Zone III near the exterior surface of the dome reveals that most vascular-rich tissue is restricted to an area near the periosteal surface. B, A small island of vascular tissue deep within the dome is interpreted as last remaining remnant of Zone II. C, An area deep within Zone III shows bundles of Sharpey's fibers in a matrix of low vascularity. D, Zone I at the base of the frontoparietal dome showing the ropey texture with distorted osteons. Scale bar, 4 cm for A; 1 cm for B-D.

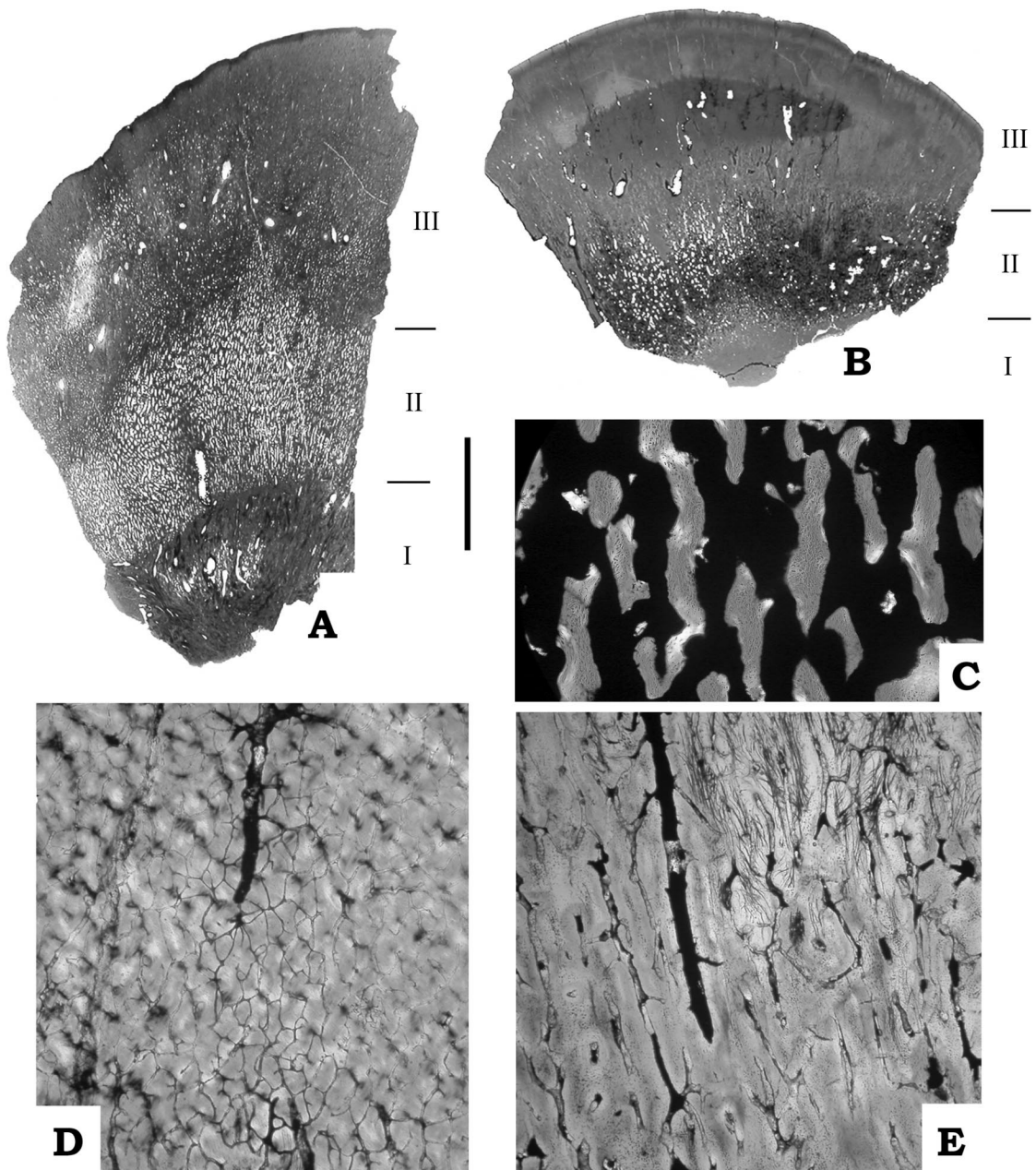


FIGURE 7. Histological sections from two pachycephalosaurid frontoparietal domes, UCMP 128383 in A and UCMP 134979 in B, show the variable bone tissue reflecting different degrees of maturity. A, A coronal section through the parietal of *Stygimoloch* (UCMP 128383) shows a moderately developed Zone III underlain by a highly vascularized Zone II, indicating that this is a relatively younger, subadult. B, A sagittal section of a low domed pachycephalosaur frontoparietal (UCMP 134979) shows a significant reduction in Zone II with a well-developed, overlying Zone III, indicating that this is an older, more mature individual. C, Magnified region of Zone II (UCMP 134979) shows the filled-in vascular spaces (black) and struts of bone with abundant osteocyte lacunae. D, Magnified region of Zone III (UCMP 134979) reveals a 3-D network of vessels in an acellular bone tissue. E, Cellular region of Zone III (UCMP 134979) with an island patch of Sharpey's fibers (upper right corner). Scale bar, 12 mm for A and B; 1 mm for C–E.



togenetic stage assignments to these two specimens.

UCMP 128383, the presumed subadult *Stygimoloch*, possesses a relatively thickened Zone I above the roof of the braincase, a highly porous Zone II, and an overlying, moderately thickened Zone III (Fig. 7A). The vascular spaces of Zone II are generally round and shortened in their radial direction. The accompanying bony struts contain abundant osteocytes and Sharpey's fibers. The bone of Zone III is relatively thicker than the underlying zones and contains abundant Sharpey's fibers, particularly near the periosteal surface. The histological architecture of UCMP 128383 confirms its status as a subadult individual, and this assignment is also supported by the preservation of associated unfused vertebral neural spines and immature epiphyses on the tibia and femur found with the partial skull (Goodwin et al. 1998).

Prior to sectioning, UCMP 134979 (Fig. 7B) was considered a potential candidate for a juvenile *Pachycephalosaurus* on the basis of the overall size and shape of the frontoparietal. Although most of Zone I is missing because of damage to the specimen, a small projection at the base of the slide reveals a portion of the uppermost layers of Zone I (see Fig. 7B), allowing a measurement of the thickness of Zones II and III. The porous bone that is characteristic of Zone II is much reduced, and nearly all of the accompanying vascular spaces are rounded or radially shortened in shape. Zone III is extensive in this frontoparietal dome and reveals a highly modified bone tissue, with large areas devoid of osteocytes (Fig. 7D). Masses of Sharpey's fibers (Fig. 7E), some perpendicular to one another, exist in many regions of Zone III, particularly where osteocytes occur. Through high-resolution imaging of UCMP 134979, the excellent preservation of the microstructure reveals the vascular networks preserved within the clear bone tissue of Zones II (Fig. 7D) and III (Fig. 7E). Overall, the histological architecture reveals a mature tissue, characteristic of an older subadult / younger adult individual. This falsifies the earlier identification of this specimen as a juvenile *Pachycephalosaurus*. UCMP 134979 most likely represents a new low-domed pachyce-

phalosaur species from the Hell Creek Formation, Montana.

The three small frontoparietal domes (Fig. 4A–C) referable to *Stegoceras* possess the largest proportional thickness of the highly vascularized Zone II with only a thin veneer of Zone III overlying the frontal region. In MOR 1179 (Fig. 4C) Zone III is thickest in the middle of the posterior portion of the dome formed by the parietal. Two of the intermediate domes, MOR 453 (Fig. 4D) and UCMP 128383 (Fig. 7A), possess a more extensive Zone III and a reduced Zone II compared with the presumed younger specimens of *Stegoceras*. Also, the vascular spaces of Zone II in the intermediate-sized MOR 453 and UCMP 128383 are much less elongated than in the three smaller specimens of *Stegoceras*. The largest specimen, referred to *Pachycephalosaurus wyomingensis*, possesses a very solid robust dome composed of bone tissues representing Zones I and III, with almost no remaining evidence of Zone II.

Brown and Schlaikjer (1943: p. 145) noted that the specimen they sectioned was a juvenile, and we concur. The "radiating trabeculae" they described within the frontoparietal dome, and subsequently noted by Galton (1970, 1971) and Sues (1978) as evidence for a compression-resistant capability valuable in head butting, is actually an expression of the growth mechanism that produced the doming of the pachycephalosaurid skull during ontogeny. Francillon-Vieillot et al. (1990: p. 512) describe radiating fibro-lamellar bone tissue as being "functionally associated with very fast deposition of relatively modest amounts of new compact bone." These "radiating trabeculae" are transitory growth structures and are absent in adult pachycephalosaurs. The consequent reduction of vascularization in adults negates the dome's utility as a heat-exchange organ proposed by Rigby et al. (1987), Landry (1995), and Reid (1996).

One of the more interesting discoveries resulting from this study is the nature of Zone III in adult individuals. The bone tissue of well-preserved individuals reveals some regions that are acellular adjacent to areas that are highly cellular, and other areas where masses of Sharpey's fibers are adjacent to areas where none exist. In addition, there are ar-



eas where bundles of Sharpey's fibers are perpendicular to one another. In some individual domes, including the juveniles, bundles of Sharpey's fibers are bent as though the angle of attachment may have shifted during growth. The unpredictability of these highly differentiated regions suggests that whatever type of epidermal layer may have been attached to the surface of the dome, it was extremely pliable, and may have changed shape dramatically during ontogeny.

### Conclusion

The focus of this study is to test the previously held hypotheses proposing that the pachycephalosaurid frontoparietal dome was utilized either for head butting or as a heat-exchange organ. Our results dispute both hypotheses by demonstrating that the spongy, highly vascular bone structures (or "*radiating trabeculae*"), described by previous researchers and presented as evidence in support of their behavioral and functional hypotheses, are fundamentally an ephemeral ontogenetic stage of dome growth. Three histological zones, Zones I, II, and III, are described and mapped ontogenetically. The degree of vascularity within Zone II is highly variable and the radiating structures associated with it are transitory with growth and increasing age of the individual. The dense layer of Sharpey's fibers on the outer margin of Zone III indicates that the frontoparietal dome possessed an external covering present during the life of these dinosaurs. Consequently, we cannot be certain of the final shape of the pachycephalosaurid dome.

North American pachycephalosaurid taxa are differentiated by the relative size and shape of their frontoparietal domes and accompanying cranial ornamentation consisting of tubercles, nodes, and horns (Maryńska 1990; Williamson and Carr 2002; Sullivan 2003). Their ornamented dome may have served as a communication system that was primarily visual within species, analogous to the crests, horns, and frills of ceratopsid dinosaurs (Sampson and Forster 2001). In the modern African bovid sister group Alcelaphini-Aepycerotini, horn morphology and orientation are also important in species recognition

(Vrba 1984). We propose that the frontoparietal dome and accompanying cranial ornaments may also have created a unique species recognition system in pachycephalosaurids.

Did color play an additional role in visual communication among pachycephalosaurids? We have evidence for an external covering, however we do not know if it generated color. A diverse assortment of extant birds, including velvet asities (Eurylaimidae), cassowaries (Casuariidae), peafowls (Numididae), and toucans (Ramphastidae), have bright integumental colors around the face and head for visual communication (Prum et al. 1994, 1999). Colors arise from the scattering of light by collagen fibers. These tissues have substantial reflection in the near-ultraviolet spectrum visible to birds but not to humans, suggesting their role in avian communication. Following these lines of evidence, it is reasonable to consider that the external covering over the frontoparietal dome in pachycephalosaurs may have also been brightly colored, or subject to color change seasonally.

Sexual dimorphism in pachycephalosaurids is not easily tested. Associated skeletons are relatively rare (Maryńska 1990). Pachycephalosaurid cranial characters are extremely variable (Williamson and Carr 2002; Sullivan 2003). Chapman et al.'s (1981) morphometric analysis of the cranium of *Stegoceras* recognized two distinct phenons as males and females. We can now demonstrate that their sample was composed primarily of juveniles and subadults. As a consequence, their gender assignment of males to individuals with larger and thicker domes is not supported. We propose that cranial display in support of species recognition is a more parsimonious interpretation of the function of the pachycephalosaurid dome. If sexual display between pachycephalosaurs also employed a strong visual component using the frontoparietal dome, these behaviors were probably secondary, judging from the apparent late ontogenetic development of the frontoparietal dome and absence of sexual dimorphism expressed in the group so far.

Individual variation in the morphology of the skull is high (Maryńska 1990; Forster and

Sereno 1997) and we show that using external cranial morphology alone may not provide enough data to identify each of the taxa to the generic level. Overall, the tissue character is remarkably variable and localized particularly in the more mature domes. Adult skulls require further study to determine all of the different tissue types within the dome.

Aspects of cranial morphology, paired with histological information using modern histological techniques and an improved fossil record, provide a more powerful assessment of behavioral hypotheses, ontogeny, and taxonomic affinity of these enigmatic and unique dinosaurs.

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### Literature Cited

- Alexander, R. M. 1997. Engineering a dinosaur. Pp. 414–425 in J. O. Farlow and M. K. Brett-Surman, eds. *The complete dinosaur*. Indiana University Press, Indianapolis.
- Brown, B., and S. M. Schlaikjer. 1943. A study of the Troödont dinosaurs with the description of a new genus and four new species. *Bulletin of the American Museum of Natural History* 82:115–150.
- Carpenter, K. 1997. Agonistic behavior in pachycephalosaurs (Ornithischia: Dinosauria): a new look at head-butting behavior. *Contributions to Geology* 32:19–25.
- Chapman, R. E., P. M. Galton, J. J. Sepkoski Jr., and W. P. Wall. 1981. A morphometric study of the cranium of the pachycephalosaur dinosaur *Stegoceras*. *Journal of Paleontology* 55:608–618.
- Chin, K., D. A. Eberth, M. H. Schweitzer, T. A. Rando, W. J. Sloboda, and J. R. Horner. 2003. Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite from Alberta, Canada. *Palaio* 18:287–293.
- Colbert, E. H. 1955. *Evolution of the vertebrates*. Wiley, New York.
- de Camp, L. S. 1956. A gun for dinosaur. *Galaxy Science Fiction* 11:56–49.
- Forster, C. A. 1996. New information on the skull of *Triceratops*. *Journal of Vertebrate Paleontology* 16:246–258.
- Forster, C. A., and P. C. Sereno. 1997. Marginocephalians. Pp. 317–329 in J. O. Farlow and M. K. Brett-Surman, eds. *The complete dinosaur*. Indiana University Press, Indianapolis.
- Francillon-Vieillot, H., V. de Buffrénil, J. Castanet, J. Gaudie, F. J. Meunier, J. Y. Sire, L. Zylberberg, and A. de Ricqlès. 1990. Microstructure and mineralization of vertebrate skeletal tissues. Pp. 471–548 in J. G. Carter, ed. *Skeletal biomineralization: patterns, processes and evolutionary trends*, Vol. 1. Van Nostrand Reinhold, New York.
- Galton, P. M. 1970. Pachycephalosaurids: dinosaurian battering rams. *Discovery* 6:22–32.
- . 1971. A primitive dome-headed dinosaur (Ornithischia: Pachycephalosauridae) from the lower Cretaceous of England and the function of the dome of pachycephalosaurids. *Journal of Paleontology* 45:40–47.
- Galton, P. M., and H.-D. Sues. 1983. New data on pachycephalosaurid dinosaurs (Reptilia: Ornithischia) from North America. *Canadian Journal of Earth Sciences* 20:462–472.
- Giffin, E. B. 1989. Notes on pachycephalosaurs (Ornithischia). *Journal of Paleontology* 63:525–529.
- Gilmore, C. W. 1924. On *Troodon validus*, an orthopodous dinosaur from the Belly River Cretaceous of Alberta, Canada. *University of Alberta Bulletin* 1:1–43.
- . 1931. A new species of Troödont dinosaur from the Lance Formation of Wyoming. *Proceedings United States National Museum* 79(9):1–6.
- . 1936. Remarks on the skull cap of the genus *Troödon*. *Annals of the Carnegie Museum* 25:109–112.
- Goodwin, M. B. 1990. Morphometric landmarks of pachycephalosaurid cranial material from the Judith River Formation of northcentral Montana. Pp. 189–201 in K. Carpenter and P. Currie, eds. *Dinosaur systematics: perspectives and approaches*. Cambridge University Press, London.
- Goodwin, M. B., E. A. Buchholtz, and R. E. Johnson. 1998. Cranial anatomy and diagnosis of *Stygimoloch spinifer* (Ornithischia: Pachycephalosauria) with comments on cranial display structures in agonistic behavior. *Journal of Vertebrate Paleontology* 18:363–375.
- Haines, R. W., and A. Mohuiddin. 1968. Metaplastic bone. *Journal of Anatomy* 103:527–538.
- Horner, J. R., D. J. Varrichio, and M. B. Goodwin. 1992. Marine transgressions and the evolution of Cretaceous dinosaurs. *Nature* 358:59–61.
- Horner, J. R., and M. B. Goodwin. 1998. Did *Pachycephalosaurs* really head-butt? An osteohistogenic cranial analysis. *Journal of Vertebrate Paleontology* 18(Suppl. to No. 3):52A.
- Lambe, L. M. 1902. New genera and species from the Belly River series (Mid-Cretaceous). *Contributions to Canadian Palaeontology*, Geological Survey of Canada 3:25–81.
- . 1918. The Cretaceous genus *Stegoceras* typifying a new family referred provisionally to the Stegosauria. *Transactions of the Royal Society of Canada* 12:23–36.
- Landry, S. O. 1995. *Stegoceras* not a head-butter. *American Zoologist* 35:560A.
- Martin, R. B., D. B. Burr, and N. A. Sharkey. 1998. *Skeletal tissue mechanics*. Springer, New York.

- Maryańska, T. 1990. Pachycephalosauria. Pp. 564–577 in D. B. Weishampel, P. Dodson, and H. Osmólska, eds. *The Dinosauria*. University of California Press, Berkeley.
- Maryańska, T., and H. Osmólska. 1974. Pachycephalosauria, a new suborder of ornithischian dinosaurs. *Palaeontologia Polonica* 30:45–102.
- Prum, R. O., R. L. Morrison, and G. R. Ten Eyck. 1994. Structural color production by constructive reflection from ordered collagen arrays in a bird (*Philepitta castanea*: Eurylaimidae). *Journal of Morphology* 222:61–72.
- Prum, R. O., R. Torres, C. Kovach, S. Williamson, and S. M. Goodman. 1999. Coherent light scattering by nanostructured collagen arrays in the caruncles of the Malagasy asities (Eurylaimidae: Aves). *Journal of Experimental Biology* 202:3507–3522.
- Reid, R. E. H. 1996. Bone histology of the Cleveland-Lloyd dinosaurs and of dinosaurs in general, Part I. Introduction: introduction to bone tissues. In B. J. Kowallis and K. Seely, eds. *Brigham Young University Geology Studies* 41:25–72. Provo, Utah.
- Rigby, J. K., Jr., A. Rice, and P. J. Currie. 1987. Dinosaur thermoregulatory Cretaceous/Tertiary survival strategies. *Geological Society of America Abstracts with Programs* 19(7):820.
- Sampson, S. D., and C. Forster. 2001. Parallel evolution in hadrosaurid and ceratopsid dinosaurs. *Journal of Vertebrate Paleontology* 21(Suppl. to No. 3):96A.
- Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research* 2:234–256.
- Sues, H.-D. 1978. Functional morphology of the dome in pachycephalosaurid dinosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Monatsheft* 1978:459–472.
- . 1997. Pachycephalosauria. Pp. 511–513 in P. J. Currie and K. Padian, eds. *Encyclopedia of dinosaurs*. Academic Press, San Diego.
- Sues, H.-D., and P. M. Galton. 1987. Anatomy and classification of the North American Pachycephalosauria (Dinosauria: Ornithischia). *Palaeontographica, Abteilung A* 198:1–40.
- Sullivan, R. M. 2000. *Prenocephale edmontonensis* (Brown and Schlaikjer) new comb. and *P. brevis* (Lambe) new comb. (Dinosauria: Ornithischia: Pachycephalosauria) from the Upper Cretaceous of North America. *New Mexico Museum of Natural History and Science Bulletin* 17:105–108.
- . 2003. Revision of the dinosaur *Stegoceras* Lambe (Ornithischia, Pachycephalosauridae). *Journal of Vertebrate Paleontology* 23:181–207.
- Vrba, E. S. 1984. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammalia: Bovidae). Pp. 62–79 in N. Eldredge and S. M. Stanley, eds. *Living fossils*. Springer, New York.
- Wall, W. P., and P. M. Galton. 1979. Notes on pachycephalosaurid dinosaurs (Reptilia: Ornithischia) from North America, with comments on their status as ornithopods. *Canadian Journal of Earth Sciences* 16:1176–1186.
- Williamson, T. E., and T. D. Carr. 2002. A new genus of derived pachycephalosaurian from western North America. *Journal of Vertebrate Paleontology* 22:779–801.