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Function and evolution of ankylosaur dermal armor

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Ankylosaurs have spike-, plate-, and club-shaped osteoderms probably used as defensive and/or offensive weapons. Previous studies have proposed the evolution and function of small ankylosaur osteoderms, but histological variations in their defensive weapons are little known. Here, we provide comparisons of the internal structures in defensive weapons of ankylosaurs, which shed light on understanding their evolutionary history and function. Histological features of spikes, plates, and clubs are similar to those of small osteoderms in having thin compact bone, thick cancellous bone with large vascular canals, and abundant collagen fibers. A previous study demonstrated that each of the three groups of ankylosaurs (the Polacanthidae, Nodosauridae, and Ankylosauridae) have distinct arrangements of collagen fibers in small osteoderms. This study shows that spikes and clubs of ankylosaurs maintain the same characteristic features for each group despite the differences in shapes and sizes. These histological similarities suggest that various types of osteoderms in ankylosaurs retained the thin compact bone and abundant fiber structures of the small osteoderms during their evolution. Polacanthid spikes show thin compact bone, with less collagen fibers than in spikes of nodosaurids and spikes and clubs of ankylosaurids. Also, ankylosaurid plates with hollow bases are very thin in morphology and show thin compact bone. These results imply that the bone strengths of polacanthid spikes and ankylosaurid plates are lower than spikes and clubs of other ankylosaurs, indicating that they may be used more probably as display and/or thermoregulation rather than as weapons. It is thus probable that ankylosaur armor in general played more than just a defensive role.

Key words: Ankylosauria, Thyreophora, dermal armor, bone histology, evolution, growth, function.

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Introduction

Ankylosaurs possess an impressive osteoderm covering, including cervical half-rings and small osteoderms along the neck and body, thoracic spikes, caudal plates, and/or a tail club (e.g., Coombs 1978a; Blows 1987, 2001; Ford 2000). Because of this notable variation in osteoderm shape, previous studies have discussed their possible functions based on the external morphologies: cervical half-rings and small osteoderms for protective armor (Blows 2001); spikes for weapons and/or display (Bakker 1986; Carpenter 1997); plates for thermoregulation and defensive weapons (Blows 2001) or display (Carpenter 1997); and tail clubs as weapons (Coombs 1979) or display (Thulborn 1993).

Recently, ankylosaur osteoderms have been studied using a histological approach. For example, Scheyer and Sander

(2004) revealed that unique structures of collagen fibers in small osteoderms possibly provided strength for their use as armor. Furthermore, they demonstrated that the density and arrangements of these collagen fibers differ in each of three groups of ankylosaurs, the polacanthids, nodosaurids, and ankylosaurids. Main et al. (2005) studied the evolution of ankylosaur osteoderms based on the histology of small osteoderms of an ankylosaur and basal thyreophorans, and suggested that the morphology of ankylosaur osteoderms developed from the lateral expansion of basal thyreophoran osteoderms. Previous studies have explored the evolution and function of ankylosaur osteoderms, but with little attention paid to bone histology of different types of osteoderms such as spikes, plates, and clubs. Histological variation in compact bone thickness of different-shaped osteoderms (plates and spikes) has been described in *Stegosaurus*, and functional variations

have been suggested, such as plates for display (Hayashi et al. 2009), and spikes for weapons (Carpenter 1998; Carpenter et al. 2005; Hayashi and Carpenter 2006). Therefore, comparisons among different-shaped osteoderms might be useful for elucidating the function of ankylosaur osteoderms and their biology. Also, histological examinations from a phylogenetic perspective would address the question how those variations of osteoderms have evolved.

To understand histological variations of ankylosaur osteoderms among various taxa and different-shaped osteoderms (small osteoderms, spikes, plates, and clubs), this study (1) examines variation of compact bone thicknesses and collagen fiber arrangement of their defensive weapons, using CT images and thin-sections from six ankylosaur taxa and (2) discusses the function and evolution of osteoderms.

Institutional abbreviations.—DMNH, Denver Museum of Nature and Science, Denver, USA; MPD, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; TMP, Royal Tyrell Museum of Paleontology, Drumheller, Canada.

Other abbreviation.—LAG, line of arrested growth.

Materials

Nineteen osteoderms were examined from six ankylosaur taxa (*Edmontonia* sp., *Gargoylesaurus parkpini*, *Gastonia* sp., *Saichania chulsanensis*, *Sauropelta* sp., and Ankylosauridae indet. from Canada) for this study (Table 1). Identifications of most materials were based on published information (Coombs 1971, 1978a, b, 1979, 1986, 1995; Carpenter 1982, 2004; Carpenter and Breithaupt 1986; Coombs and Maryańska 1990; Carpenter et al. 1998; Vickaryous et al. 2004; Kilbourne and Carpenter 2005). Some specimens (TMP 2000.57.03 and TMP 85.36.218/1) were identified only to Ankylosauridae indet., because generic and specific assignment based on isolated osteoderms is difficult for some ankylosaurs. Most speci-

mens were examined using both diagnostic CT scanning (medical CT) and thin-sectioning to observe their compact bone thickness and collagen fiber arrangement, but some materials were examined only by CT scanning (for MPD 100/1305) or thin-sectioning (for TMP 85.36.218/1).

Four small osteoderms and a spike were obtained from two polacanthids, *Gastonia* sp. (DMNH 49754) and *Gargoylesaurus parkpini* (DMNH 27726). The materials of a spike and three osteoderms of *Gastonia* sp. (DMNH 49754) were excavated from the Lower Cretaceous Cedar Mountain Formation, Utah, USA. An osteoderm of *Gargoylesaurus parkpini* (DMNH 27726) was sampled from the type specimen, which was found in the Upper Jurassic Morrison Formation, Utah, USA (Carpenter et al. 1998; Kilbourne and Carpenter 2005).

Four osteoderms of nodosaurids, two osteoderms of *Sauropelta* sp. (DMNH 18203) and a spike and an osteoderm of *Edmontonia* sp. (TMP 1979.147.94 and DMNH 2452), were obtained for this study. *Sauropelta* materials (DMNH 18203) are from the Lower Cretaceous Cloverly Formation, Wyoming, USA. The *Edmontonia* spike (TMP 1979.147.94) was collected from the Upper Cretaceous Dinosaur Park Formation of Dinosaur Provincial Park, Alberta, Canada, while the osteoderm of *Edmontonia* (DMNH 2452) was from the Upper Cretaceous Hell Creek Formation of South Dakota, USA.

Two tail clubs, six plates, and two osteoderms were sampled from two ankylosaurids, *Saichania chulsanensis* (MPD 100/1305) and Ankylosauridae indet. (TMP 2000.57.03). Osteoderms from *Saichania chulsanensis* (MPD 100/1305) belong to a complete skeleton from the Upper Cretaceous Barun Goyot Formation, Khulsan, Mongolia (KC personal observation). A club from Ankylosauridae indet. (TMP 2000.57.03) was collected from the Upper Cretaceous Dinosaur Park Formation of Dinosaur Provincial Park, Alberta, Canada. Additionally, an isolated osteoderm of Ankylosauridae indet. (TMP 85.36.218/1) from Canada, previously described by Scheyer and Sander (2004), was reexamined.

Table 1. Material sectioned for this study, including taxa names, specimen numbers, short notes on general morphologies, and specimen localities.

Sampled taxa	Specimen no.	General morphology	Locality
<i>Gastonia</i> sp.	DMNH 49754-1	Roughly oval osteoderm with apex	Cedar Mountain Formation
<i>Gastonia</i> sp.	DMNH 49754-2	Roughly oval osteoderm with apex	Cedar Mountain Formation
<i>Gastonia</i> sp.	DMNH 49754-3	Roughly oval osteoderm with apex	Cedar Mountain Formation
<i>Gastonia</i> sp.	DMNH 49754-4	Spike	Cedar Mountain Formation
<i>Gargoylesaurus parkpini</i>	DMNH 27726	Pup-tent shaped osteoderm	Morrison Formation
<i>Sauropelta</i> sp.	DMNH 18206-1	Pup-tent shaped osteoderm	Cloverly Formation
<i>Sauropelta</i> sp.	DMNH 18206-2	Keeled oval osteoderm	Cloverly Formation
<i>Edmontonia</i> sp.	DMNH 2452	Pup-tent shaped osteoderm	Hell Creek Formation
<i>Edmontonia</i> sp.	TMP 1979.147.94	Spike	Dinosaur Park Formation
Ankylosauridae indet.	TMP 2000.57.03	Club	Dinosaur Park Formation
Ankylosauridae indet.	TMP 85.36.218/1	Pup-tent shaped osteoderm	Dinosaur Park Formation
<i>Saichania chulsanensis</i>	MPD 100/1305-1	Pup-tent shaped osteoderm	Barun Goyot Formation
<i>Saichania chulsanensis</i>	MPD 100/1305-2	Articulated six plates and club	Barun Goyot Formation

Table 2. The measurements of ratios of compact bone area versus total area in cross-section. In polacanthids, the ratio of a spike is less than that of a small osteoderm. In nodosaurids, the ratio of a small osteoderm is almost the same as that of a large sized spike. On the other hand, the ratio of ankylosaurid tail clubs is greater than in a small osteoderm. The average compact bone thickness in thin-section is shown in the parentheses.

Family	Sampled taxa	Specimen no.	Small osteoderm	Spike	Club
Polacanthidae	<i>Gastonia</i> sp.	DMNH 49754	38.3% (2.16 mm)	24.7% (2.30 mm)	–
Polacanthidae	<i>Gargoylesaurus parkpini</i>	DMNH 27726	36.3% (2.32 mm)	–	–
Nodosauridae	<i>Edmontonia</i> sp.	TMP 1979.147.94	–	36.8% (3.28 mm)	–
Nodosauridae	<i>Edmontonia</i> sp.	DMNH 2452	36.4% (6.86 mm)	–	–
Nodosauridae	<i>Sauropelta</i> sp.	DMNH 18206	36.3% (2.76 mm)	–	–
Ankylosauridae	Ankylosauridae indet.	TMP 2000.57.03	–	–	22.8% (8.81 mm)
Ankylosauridae	Ankylosauridae indet.	TMP 85.36.218/1	13.9% (0.64 mm)	–	–

Most of the specimens in this study (DMNH27726, 49754, TMP 1979.147.94, 2000.57.03, MPD 100/1305) probably belong to either subadults or adults based on the size of the osteoderm and/or the fusion of neurocentral sutures of the body skeleton. The ontogenetic stage for some small osteoderms (DMNH 2452, 18206, TMP 85.36.218/1) is uncertain, as these are isolated materials. Variations in osteoderm histology linked to the position of the osteoderm within the armor (dorsal, ventral, or tail regions) cannot be ruled out in all sampled ankylosaurs. However, there are no regional variations among osteoderms sampled from a *Saichania* skeleton (MPD 100/1305). We believe that neither of these factors influenced our results significantly, simply because major variation in histology is seen between the sampled taxa, not within taxa. In addition, most samples except *Saichania* (MPD 100/1305) and *Gargoylesaurus* (DMNH 27726) can be viewed as random with regard to anatomical position because these attributes were not known and thus not actively selected for in the specimens we studied.

Whereas several studies have recovered a monophyletic Polacanthinae or Polacanthidae (e.g., Kirkland 1998; Carpenter 2001; see also discussion in Kilbourne and Carpenter 2005), others have found the “polacanthid” taxa to represent a paraphyletic grade among Ankylosauridae (e.g., Pisani 2002; Hill et al. 2003; Vickaryous et al. 2004). However, as will be shown later, our results support monophyly of the group, thus we tentatively adopt Polacanthidae in the present study.

Methods

Histological sampling was carried out using standard thin-sectioning methods (Sander 2000; Klein and Sander 2007). Before sectioning, all specimens were photographed and standard measurements were taken, because sectioning is a destructive method. Thin-sections were taken at the base, middle, and apex in the spikes. A thin-section was cut along the sagittal axis in a club and parallel to the ridge in each osteoderm because the histology of dinosaur osteoderms varies from the base to the apex (Buffrénil et al. 1986). After cutting, both sides of the slice were impregnated in a synthetic epoxy resin, finely ground, and polished to a high gloss. The

thin-sections were examined using polarized light microscopy. Images of each thin-section were captured with a digital camera. Bone microstructures were diagnosed based on the nomenclature and definitions of Francillon-Vieillot et al. (1990) and Castanet et al. (1993). Ratios of compact bone area versus total area in cross-section were measured using NIH Image J (NIH, Bethesda, MD) and compared among these elements (Table 2).

We use the terms “base” for the most proximal region of an osteoderm and “apex” for the most distal part (or apical region) of an osteoderm. “Middle” is used for the mid-region between base and apex. “External” refers to the side facing away from the body surface of the animal. Additionally, we refer to Coombs (1995) for the terminology of tail clubs.

All materials were also examined using a diagnostic CT scanner (CT-W2000, Hitachi Medical Corporation, 1 mm slice thickness, 120 kV, 175 mA at Hokkaido University) to observe the compact bone three-dimensionally, and internal structures were analyzed using three-dimensional reconstructions created in VG Studio Max (Volume Graphics).

Results

All ankylosaur osteoderms are composed of an outer thin cortical bone of variable thickness and inner thick cancellous bone. Ankylosaur osteoderms may be homologous to crocodilian osteoderms (Main et al. 2005; Vickaryous and Hall 2008; Vickaryous and Sire 2009) and were probably covered with skin and keratin.

Polacanthidae

All osteoderms are composed of well-developed compact bone and thick cancellous bone, whereas the spike exhibits poorly developed compact bone with thick cancellous bone (Figs. 1, 2). All specimens show woven fibers on the basal surfaces and on the margins. These fibers are visible macroscopically (Barrett et al. 2002; Scheyer and Sander 2004).

***Gastonia* sp.**—Three osteoderms of DMNH 49754-1, 49754-2, and 49754-3 are small (4 to 6 cm in maximum length: Fig. 1), oval osteoderms and have an apex. Bone sur-

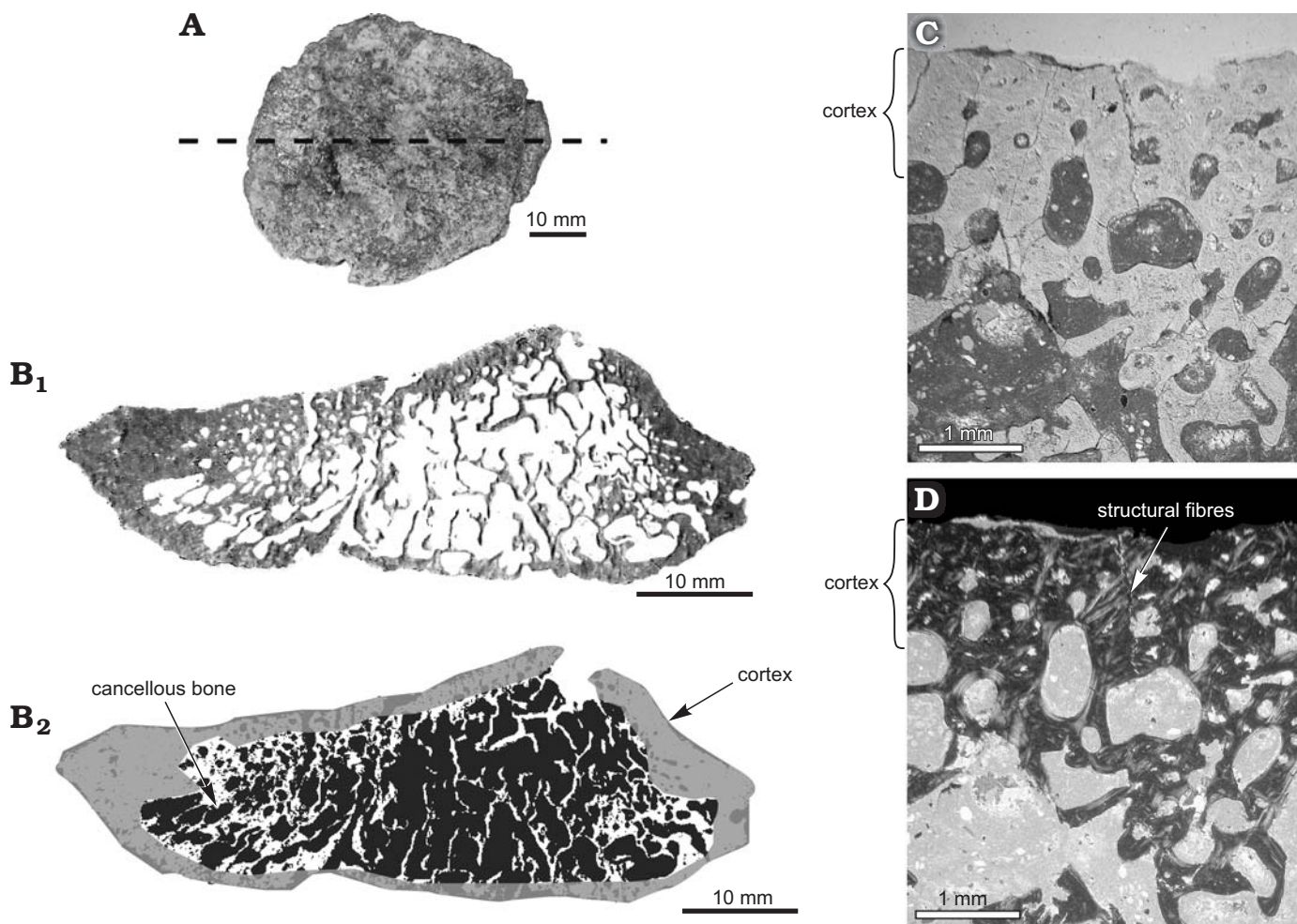


Fig. 1. An osteoderm from the polacanthid *Gastonia* (DMNH 49754-1) from the Lower Cretaceous Cedar Mountain Formation of Utah. **A**. Photograph of the external surface of the specimen. **B**. Thin-section, cut along plane indicated by dashed line in A. The thin-section was cut parallel to the ridge of the osteoderm; photograph (**B₁**) and interpretive drawing (**B₂**). The cortex completely surrounds the inner cancellous bone: dark gray, cortical bone consisting of woven or structural fiber bone; white, cancellous bone built up of bone trabeculae which show primary bone tissue in most parts. **C**, **D**. Cortical bone tissue of the osteoderm. Detail of the cortex and inner trabecular bone in normal (**C**) and polarized light (**D**); external surface is to the top. Many structural fiber bundles occur within the cortex.

faces are pierced by pits and striated. Pits are mainly seen on the basal surfaces, and striations are present on the margins. While the external surface rises continuously toward the off-centered apex, the planar basal surface is slightly undulating. The spike of DMNH 49754-4 is a large, compressed, triangular osteoderm (24 cm in maximum length; Fig. 2). Its external surface is characterized by striations developed on the apical side. Most of the basal surface is damaged, but what remains shows many large pits with woven fibers and exhibits a pustulate or lumpy morphology.

Cavities between trabeculae in the cancellous bone are distinctly proportionally larger than those of ankylosaurids and nodosaurids because diameters of the trabeculae are thinner (average 0.38 mm for DMNH 49754-1 and 0.35 mm for DMNH 49754-4) than those of other ankylosaurs (Figs. 1B, 2B). The bone histology between small osteoderms and the spike differs in the area and distribution of the compact bone (Table 2), but the two types are similar in distribution and arrangement of collagen fibers. Osteoderms have a well-devel-

oped layer of compact bone on all surfaces, but the spike exhibits a poorly developed layer of compact bone that is only on the external surfaces.

The compact bone of all osteoderms is primary woven or structural fiber bone tissue composed of numerous fibers, lacking lines of arrested growth (LAGs). In their outermost cortex, the vascular canals are large and open to the surface, indicating active growth at the time of death (Curry 1999; Sander et al. 2006). Notably, the compact bone shows a high content of collagen fiber bundles (Figs. 1D, 2F). Most of these appear to be similar to Sharpey's fibers; however, because they cannot generally be linked to the insertion of connective tissue such as tendons, ligaments, or muscle attachments (e.g., Francillon-Vieillot et al. 1990; Suzuki et al. 2002, 2003), but appear to be structural reinforcement of the osteoderms, we use the purely descriptive term "structural fibers" here (*sensu* Scheyer and Sander 2004). Also, these fibers are present in the trabeculae of the cancellous bone, but their density is less than that in the compact bone. Secondary osteons are very rare in

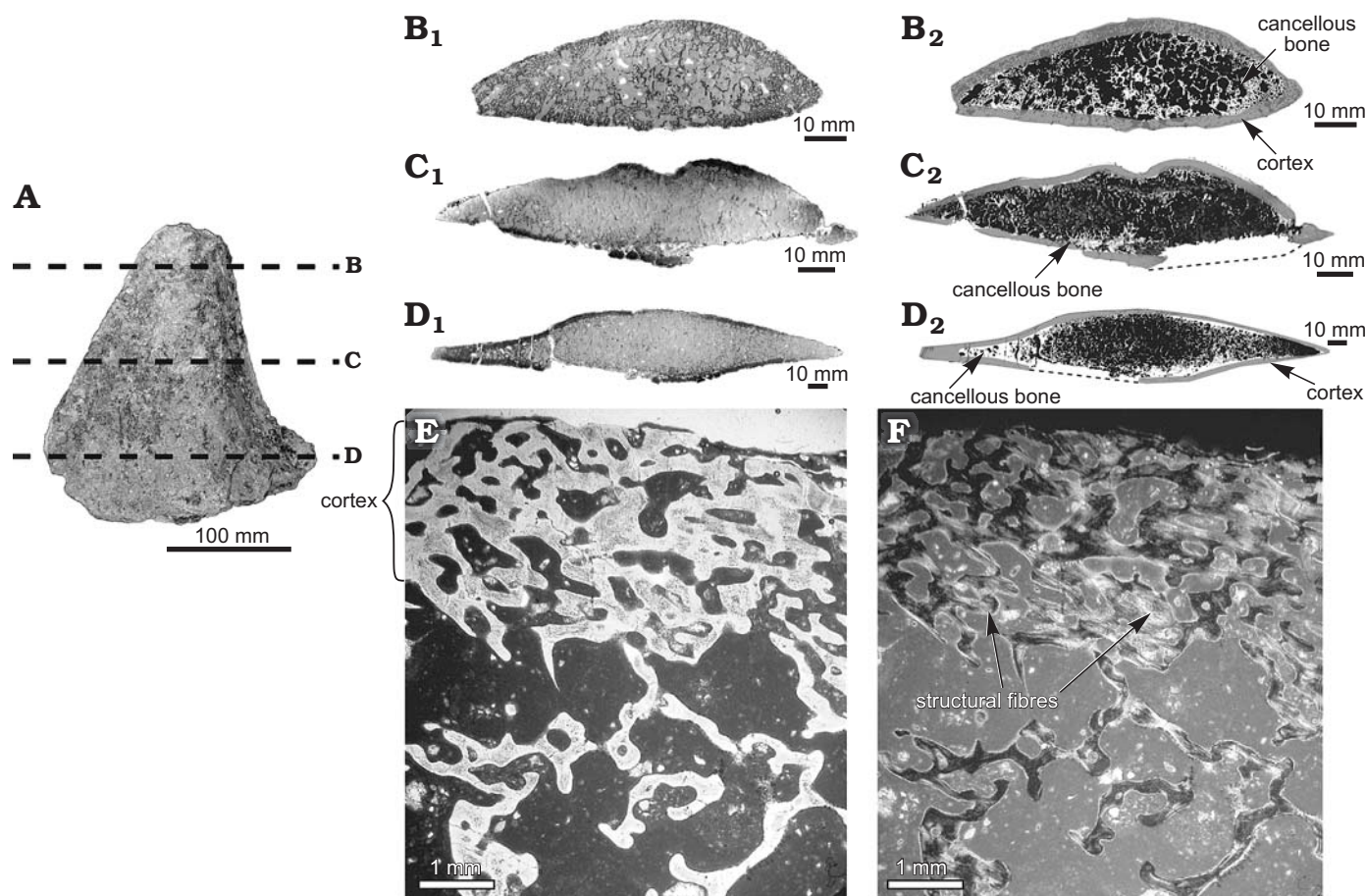


Fig. 2. A spike from the polacanthid *Gastonia* (DMNH 49754-4) from the Lower Cretaceous Cedar Mountain Formation of Utah. **A**. External surface photograph of specimen. **B–D**. Thin-section of a spike, dashed lines in **A** indicate cutting planes. The cortex in the sections is relatively thin. Note that cavities between trabeculae in the cancellous bone are proportionally larger than those of ankylosaurid and nodosaurid cancellous bone: dark gray, cortical bone showing woven or structural fiber bone; white, cancellous bone built up of bone trabeculae that show primary bone tissue in most parts; photographs (**B₁–D₁**), interpretive drawings (**B₂–D₂**). **E**, **F**. Cortical bone tissue of the spike. Detail of the cortex and inner trabecular bone of *Gastonia* spike in normal (**E**) and polarized (**F**) light; external surface is to the top. Many structural fiber bundles are oriented perpendicular to the bone surface within the cortex.

both the compact bone and cancellous bone, but are seen within the deeper layers of the compacta.

***Gargyleosaurus parkpini*.**—DMNH 27726 is an asymmetrical pup-tent shaped osteoderm (6.5 cm in maximum length) from a partial skeleton (Carpenter et al. 1998; Kilbourne and Carpenter 2005). The external surface is smooth with sparse pits, while the basal side is concave with a rough surface. The specimen has a rounded ridge extending from anterior to posterior, ending in a posteriorly situated, off-center apex (Fig. 3).

The histology of the osteoderm is characterized by a central area of cancellous bone that is completely mantled by a well-developed compact bone layer (Fig. 3B). In the external cortex, primary bone tissue shows woven or structural fiber bone tissue without LAGs. Structural fibers are distributed throughout the whole osteoderm, but are mainly developed in the compact bone (Fig. 3D). Secondary reconstruction has occurred at the deep part of the cortical bone and the cancellous bone, although not extensively. Diameters of the trabeculae are thinner (average 0.45 mm) than those of other ankylosaurs (Fig. 3B), and cavities between

trabeculae are relatively large, such as those of *Gastonia* (DMNH 49754).

Nodosauridae

The osteoderms possess a well-developed cortical layer on the external surface but lack this layer on the basal surface. Highly ordered structural fibers are present in these osteoderms as suggested by a previous study (Scheyer and Sander 2004).

***Edmontonia* sp.**—The sectioned osteoderm DMNH 2452 is a large pup-tent shaped osteoderm with an off-center apex (17.5 cm in maximum length; Fig. 4). The surface of the flat base shows a woven pattern of ordered collagen fibers. The basal and external sides have pits. There are some grooves from the apex to margin. The most prominent feature of the osteoderm is its large canals on the basal surfaces, which are similar to the “pipe”-like large vascular canals of *Stegosaurus* plates (Buffrénil et al. 1986; Main et al. 2005). The canals are observable both in section and CT images and make a

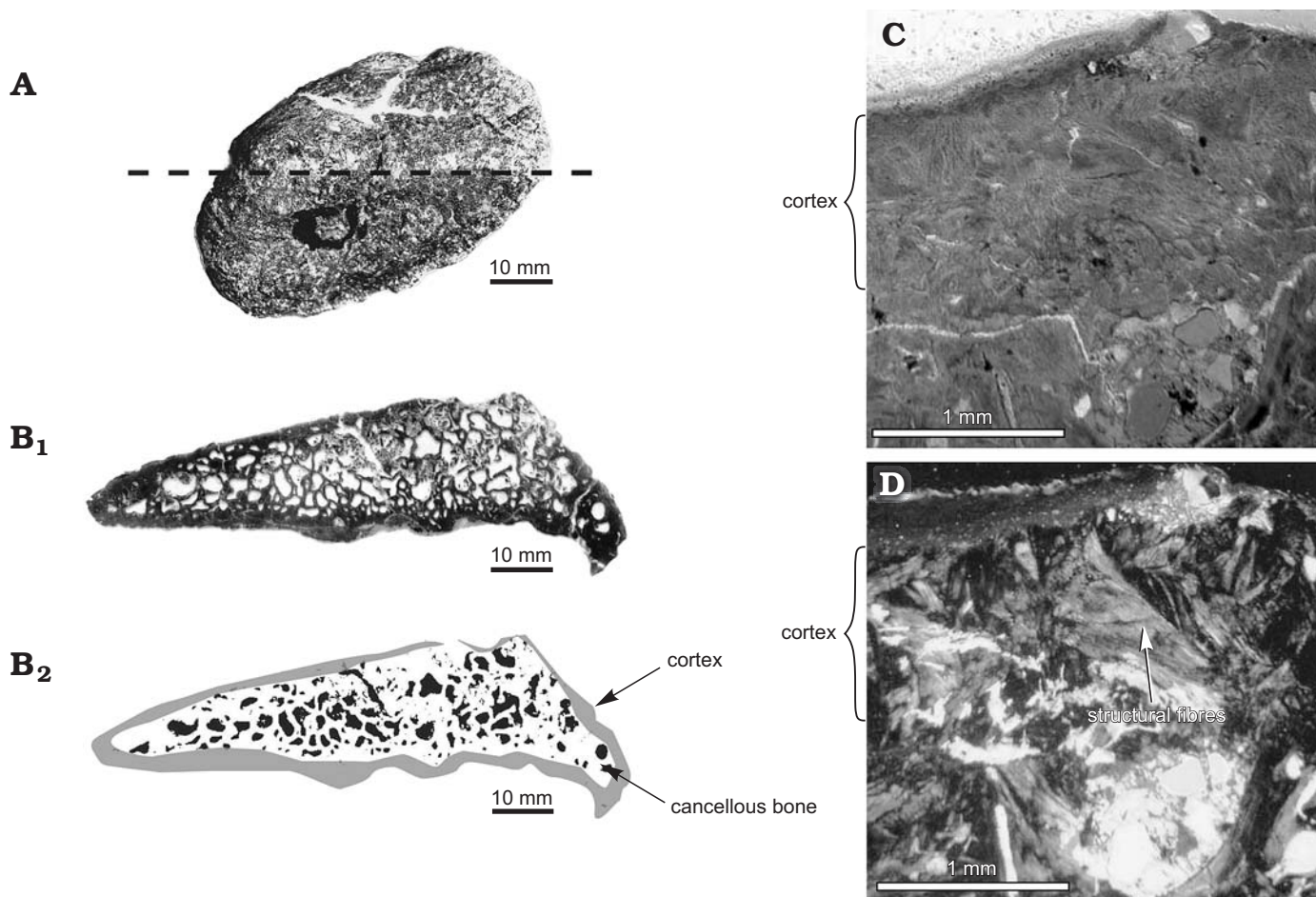


Fig. 3. An osteoderm from the polacanthid *Gargoylesaurus parkpini* (DMNH 27726) from the Upper Jurassic Morrison Formation of Utah. **A**. Photograph of the external surface of the specimen. **B**. Thin-section of an osteoderm, cut along indicated by dashed line in **A**. The thin-section was cut parallel to the ridge of the osteoderm; photograph (**B**₁) and interpretive drawing (**B**₂). The cortex in the section completely surrounds the inner cancellous bone; dark gray, cortical bone consisting of woven or structural fiber bone; white, cancellous bone. **C**, **D**. Cortical bone tissue of the osteoderm. Detail of the cortex and inner trabecular bone in normal (**C**) and polarized (**D**) light; external surface is to the top. Many structural fiber bundles occur within the cortex.

complex network of interconnected tubes, connecting pits on the basal surface and grooves on the external surface (Fig. 4B₁).

Specimen TMP 1979.147.94 is a thoracic spike (25 cm in maximum length; Fig. 5). The flat basal surface is characterized by the presence of extensive fiber bundles and pits. The external surface is generally smooth with some pits and grooves. Grooves mainly develop at the apical region. A large vascular canal is present at the apex, and the thin-sections and CT images of the spike show that this canal connects to the basal pits, as in the osteoderm (DMNH 2452).

Despite distinct different morphological forms of these osteoderms, they are identical in their bone histology. These are composed of a well-developed external layer of compact bone and a basal layer of cancellous bone (Figs. 4, 5). The trabeculae in the cancellous bone (Figs. 4B, 5B–E) are generally thicker (average 1.02 mm for DMNH 2452 and 0.86 mm for TMP 1979.147.94.) than those of other ankylosaurs. The osteoderms have poorly developed cortices on their basal surface. Also, the area of the compact bone between the osteoderm and spike is almost identical (Table 2). Their superficial

cortex is composed of woven or structural fiber bone tissue without LAGs. Notably, the number of structural fibers in the cortical layer is higher than that of polacanthid osteoderms (Figs. 4D, 5G). Structural fibers extend from the compact bone to cancellous bone, but they are abundant in compact bone. Two differently arranged sets of these fibers can be observed. Therefore, the structural fibers are highly ordered and make a fibrous meshwork inside the cortex. Vascular canals in the outmost cortex open to the surface, and secondary osteons develop only at the deeper layers of the cortex.

Sauropelta sp.—The pup-tent shaped osteoderm (DMNH 18206-1: 10 cm in maximum length) shows a smooth external surface pierced by some pits, and concave base with a rough surface texture (Fig. 6A). In the oval small osteoderm (DMNH 18206-2: 4 cm in maximum length), the basal and external sides show rugose surface textures, and the rugosity increases externally from the apex toward the outer margins of the osteoderm (Fig. 6B).

The osteoderms are both very similar in their bone histology in spite of their distinct difference in size. The histology

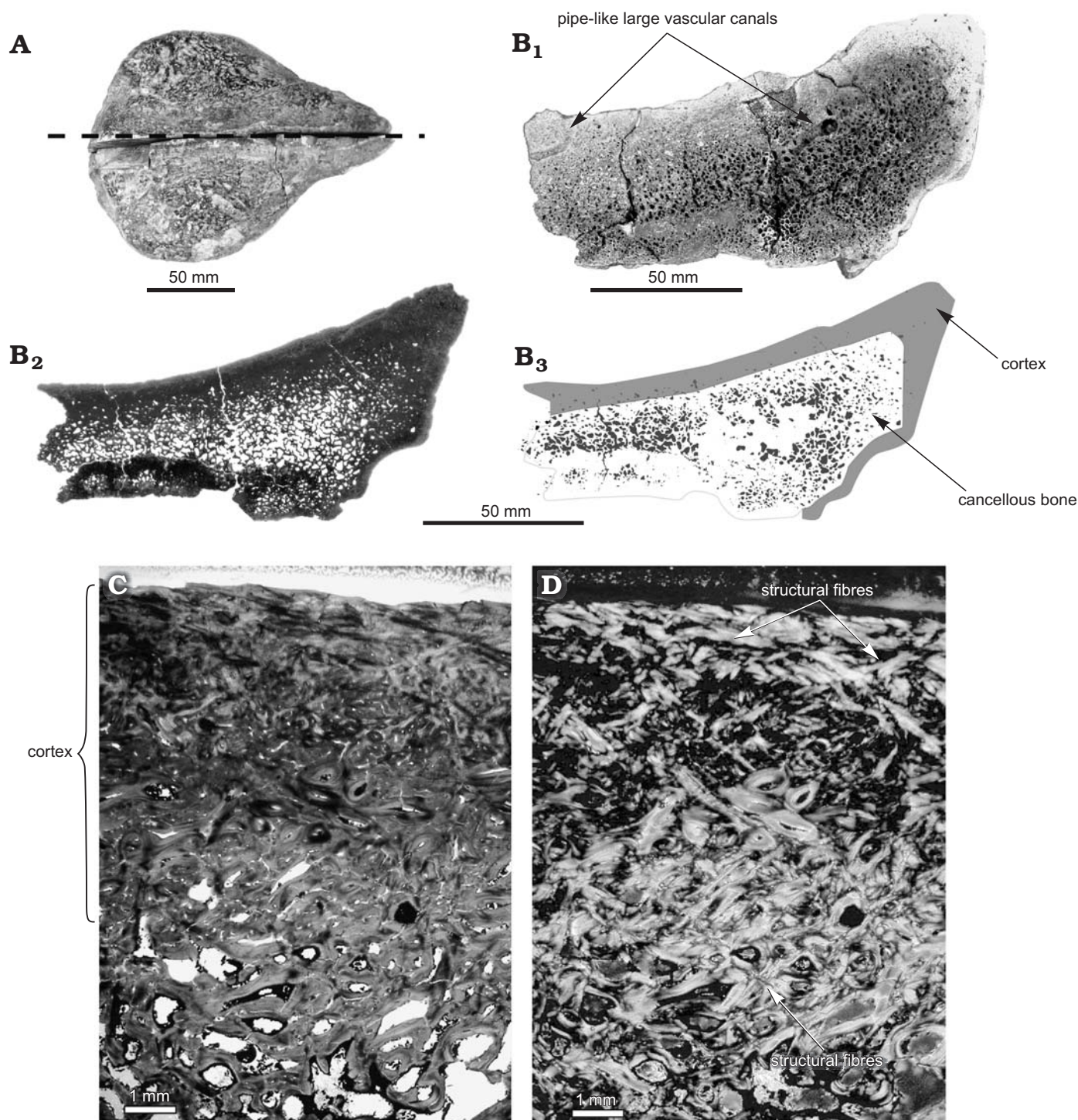


Fig. 4. An osteoderm from the nodosaurid *Edmontonia* (DMNH 2452) from the Upper Cretaceous Hell Creek Formation of South Dakota. **A**. Photograph of the external surface of the specimen. **B**. Section and thin-section of an osteoderm, cut along indicated by dashed line in **A**. The thin-section was cut parallel to the ridge of the osteoderm. Pipe-like large vascular canals are extensively developed in the cancellous bone. An external cortex layer (dark gray) and an internal region (white) of cancellous bone can be seen. Photographs (**B**₁, **B**₂) and interpretive drawing (**B**₃). **C**, **D**. Cortical bone tissue of the osteoderm. Detail of the cortex and inner trabecular bone in normal (**C**) and polarized (**D**) light; external surface is to the top. Many structural fiber bundles oriented perpendicular and parallel to the osteoderm surface occur within the cortex.

of these osteoderms is differentiated into an external cortical layer and a basal layer of cancellous bone (Fig. 6C, D). The trabeculae in the cancellous bone are thick (average 0.68 mm for DMNH 18206-1 and 0.69 mm for DMNH 18206-2), but

slightly less than in those of *Edmontonia* (DMNH 2452, TMP 1979.147.94.). Well-developed compact bone is not seen on the basal side. These cortices are composed of woven or structural fiber bone tissue and lack LAGs. In the external

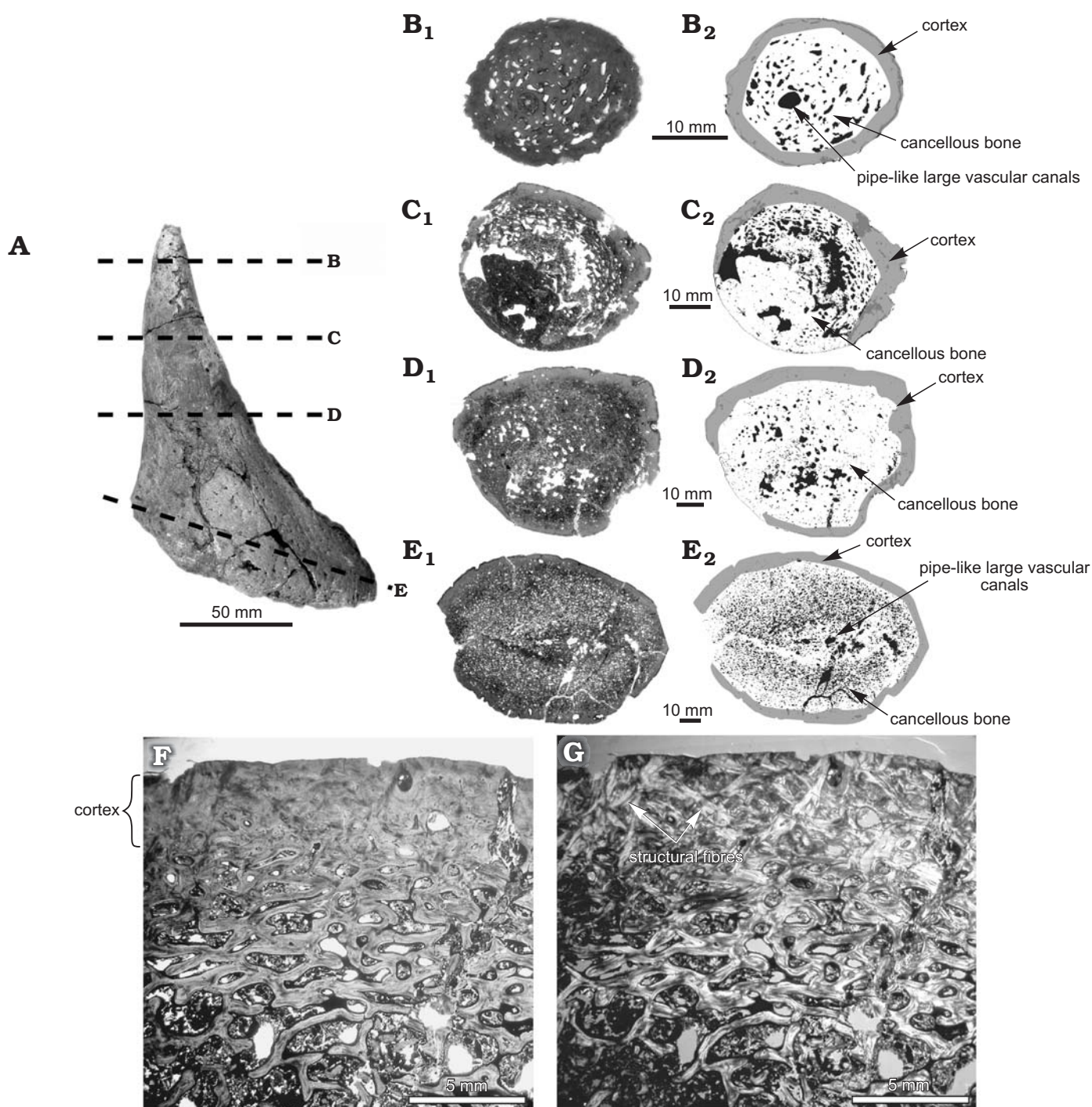


Fig. 5. A spike from the nodosaurid *Edmontonia* (TMP 1979.147.94) from the Upper Cretaceous Dinosaur Park Formation of Alberta. **A**. External surface photograph of specimen. **B–E**. Thin-sections of a spike, dashed lines in **A** indicate cutting planes. The cortex in the sections surrounds the inner cancellous bone; dark gray: cortical bone consisting of woven or structural fiber bone with many structural fiber bundles; white: cancellous bone. Pipe-like large vascular canals can be seen in the apical and basal part (**B**, **E**). Photographs (**B₁–E₁**) and interpretive drawings (**B₂–E₂**). **F**, **G**. Cortical bone tissue of the osteoderm. Detail of the cortex and inner trabecular bone in normal (**F**) and polarized (**G**) light; bone surface is to the top. Bone histology of the spike is identical to that of a small osteoderm (DMNH 2452). Structural fiber bundles oriented both perpendicular and parallel to the osteoderm surface occur within the cortex.

cortex, structural fibers can be observed that project perpendicular or parallel to the osteoderm surface (Fig. 6E–H). More deeply, most of the cortex is dominated by structural fibers and accumulations of secondary osteons. In trabeculae of the cancellous bone, structural fibers are seen, but the den-

sity is lower than that of compact bone. A few secondary osteons appear in the lower part of the cortex. Some trabeculae in the cancellous bone show secondary reconstructions with centripetally deposited lamellar bone tissue, while the whole bone tissue is in various stages of remodelling.

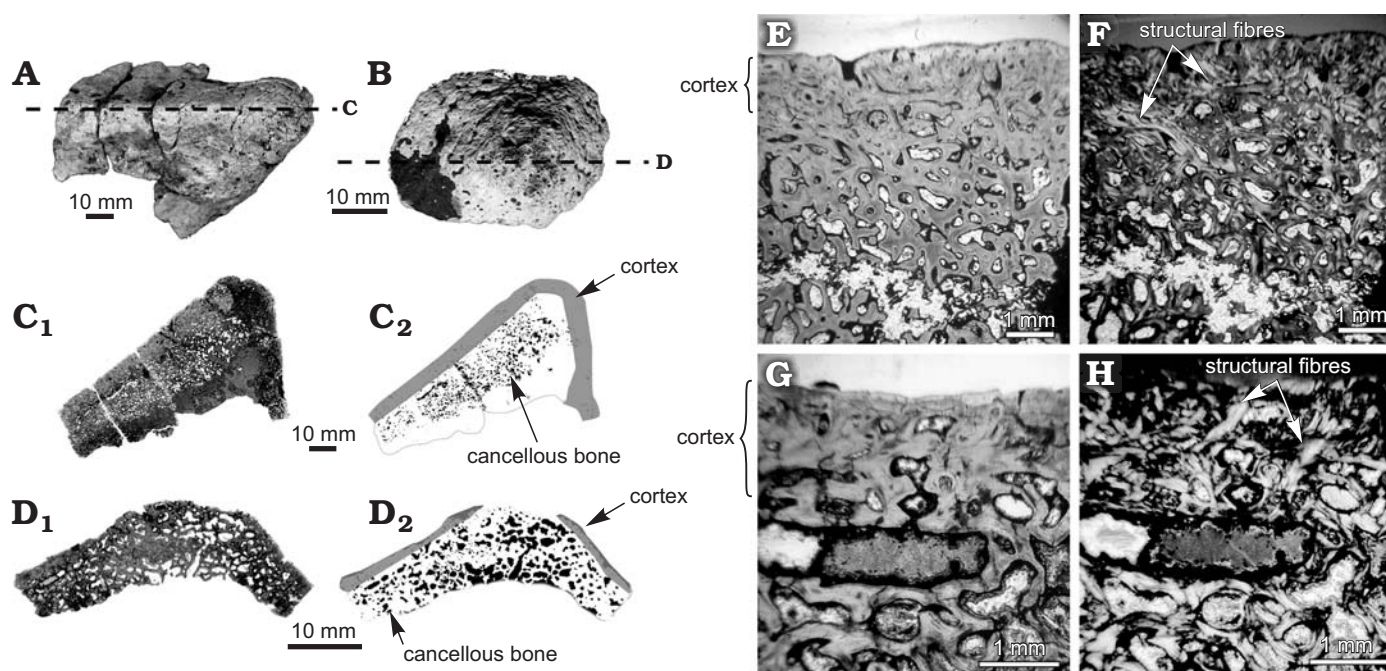


Fig. 6. Osteoderms from the nodosaurid *Sauropelta* (DMNH 18206) from the Lower Cretaceous Cloverly Formation of Wyoming. **A, B.** External surface photograph of a large DMNH 18206-1 (**A**) and small DMNH 18206-2 (**B**) osteoderms. **C, D.** Thin-sections of osteoderms, cut along indicated by dashed lines **C** (in **A**) and **D** (in **B**). The thin-section was cut parallel to the ridge of the osteoderms. Dark gray, cortical bone consisting of woven or structural fiber bone; white, cancellous bone. Photographs (**C₁**, **D₁**) and interpretive drawings (**C₂**, **D₂**). **E–H.** Cortical bone tissue of osteoderms. **E, F.** Detail of the cortex and inner trabecular bone of large osteoderm (DMNH 18206-1) in normal light (**E**) and in polarized (**F**) light. **G, H.** Detail of the cortex and inner trabecular bone of small osteoderm (DMNH 18206-2) in normal (**G**) and polarized (**H**) light. External surface is to the top. Both osteoderms share identical histological features, despite the difference in size. Many structural fiber bundles occur within the cortex.

Ankylosauridae

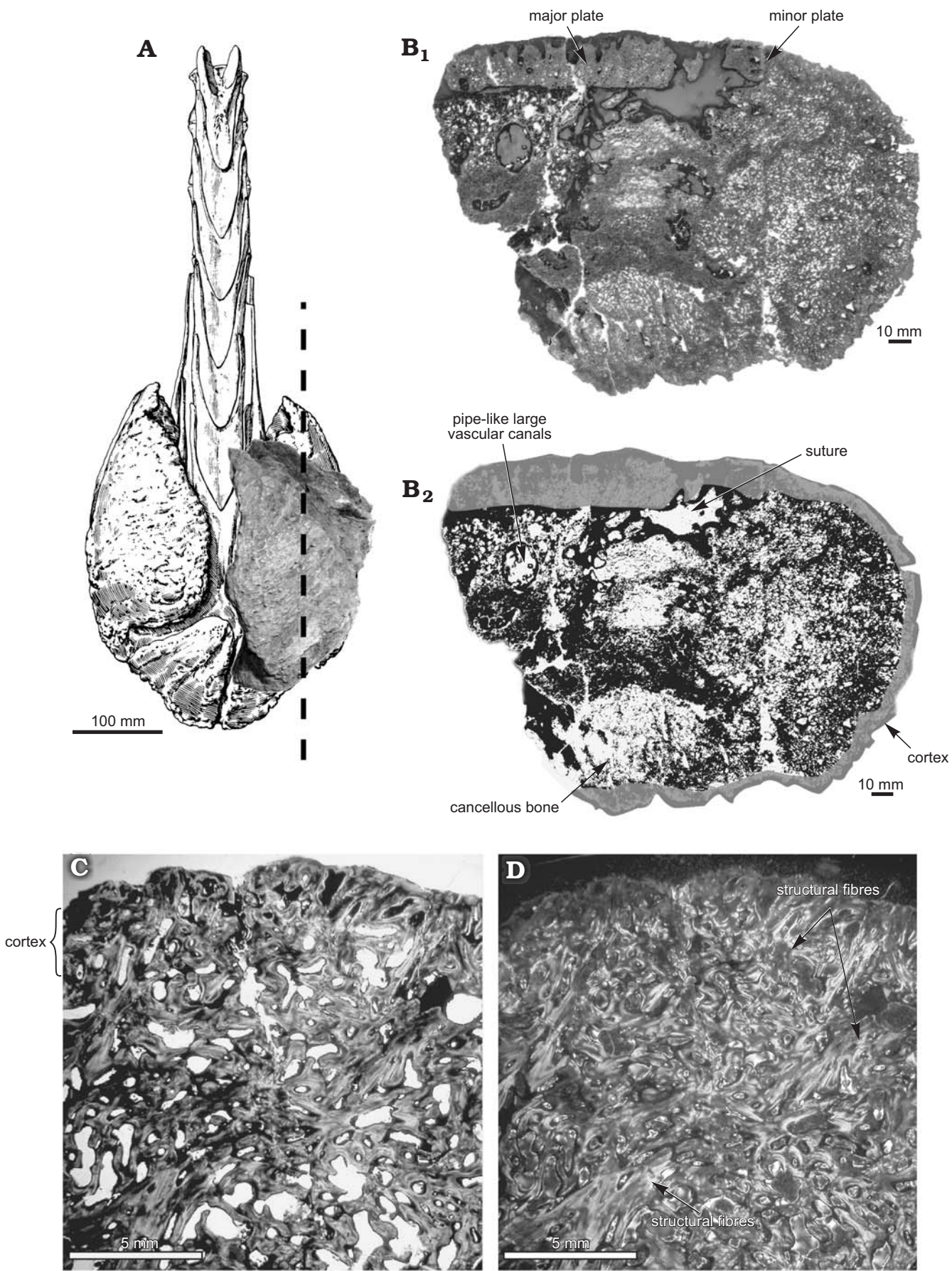
Ankylosaurid osteoderms show a relatively thin cortex, but their cores are built up by many secondary osteons, often forming Haversian bone and structural fibers.

Ankylosauridae indet.—TMP 2000.57.03 is a fragmentary tail club from an indeterminate ankylosaurid (23 cm in maximum length; Fig. 7). This specimen may belong to *Euoplocephalus*, which is the only ankylosaurid found in the Upper Cretaceous Judith River Group of Dinosaur Park Formation of Canada (Coombs 1971; Vickaryous et al. 2004). Generally, the club is composed of a pair of major plates laterally, a midline of minor plates ventrally, and a terminal pair of minor plates (Coombs 1995; Carpenter 2004). In this specimen, a major plate and minor plate with irregular grooves and pits are preserved. A suture between these osteoderms can be observed on the external surface. Although the tail club is a massive bone in its external morphology, the inside is very cancellous composed of thick trabeculae (average 0.82 mm). It is similar in histology to a small osteoderm (TMP 85.36.218/1; trabeculae diameters average 0.62 mm), despite the distinctly different morphologies and sizes (Figs. 7, 8). Apart from a thickened cortex under the major osteoderm, the club is composed of a thin outer layer of compact bone and inner cancellous bone. However, the ratio of compact bone area to total area is greater than that of a small osteoderm (TMP 85.36.218/1; Table 2). The suture between the major plate

and minor plate is visible as a large crack in the thin-section (Fig. 7B). The thickened cortex under the major plate is different from other cortex in having a distinct boundary to the inner layer of cancellous bone, indicative of incomplete fusion of the club. A large vascular canal (1 cm in width) that is mantled by a wall of lamellar bone is present. CT images of this osteoderm show that the large cavity makes a complex vascular network, connecting with grooves and pits on the external surface (Fig. 9).

The cortical bone consists of primary woven or structural fiber bone tissue, heavily overprinted by structural fibers, which insert almost perpendicularly from the bone surface into the osteoderm (Fig. 7C, D). There are no LAGs. Crossing and branching of the structural fibers is common. Secondary reconstructions are extensive in some regions of the cortex. The secondary osteons of Haversian bone seem to “fray out” (Scheyer and Sander 2004) at the margin because of the high content of structural fibers. In the cancellous bone, structural fibers are randomly distributed, crossing and interlocking with the secondary osteons.

TMP 85.36.218/1 is a thin-section from a fragmentary pup-tent shaped osteoderm (9 cm in maximum length; Fig. 8). This specimen, previously described by Scheyer and Sander (2004), was used as a reference. The bone histology is identical to that of the tail club. This osteoderm exhibits a remarkably thin cortex and a thick cancellous bone. The cortex consists of woven or structural fiber bone with extensive



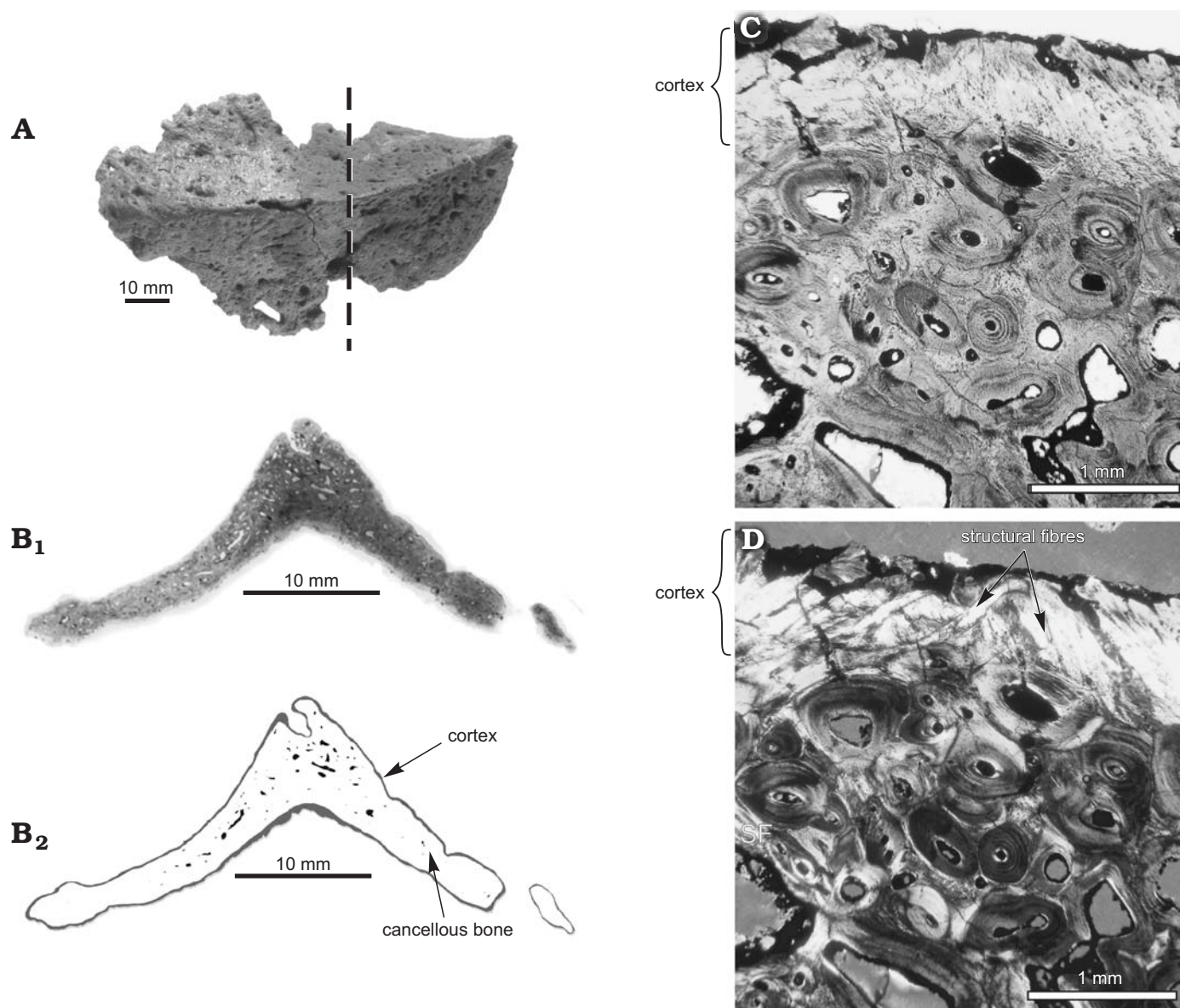


Fig. 8. An osteoderm from an indeterminate ankylosaurid (probably *Euoplocephalus*), TMP 85.36.218/1, from the Upper Cretaceous Dinosaur Park Formation of Alberta. This specimen was previously described by Scheyer and Sander (2004). **A**. Photograph of the external surface of the specimen. **B**. Thin-section of an osteoderm, cut along indicated by dashed lines in A. The thin-section was cut parallel to the ridge of the osteoderms. The bone histology is similar to that of the tail club (TMP 2000.57.03). This osteoderm exhibits a remarkably thin cortex (gray) and a thick cancellous bone (white). Photograph (B₁) and interpretive drawing (B₂). **C**, **D**. Cortical bone tissue of the osteoderm. Detail of the cortex and inner trabecular bone in normal (**C**) and polarized (**D**) light; external surface is to the top. The cortex consists of a woven or structural fiber bone with extensive remodeling. Structural fibers are oriented perpendicular in the cortex, but are randomly oriented in the cancellous bone (**D**).

remodeling. Structural fibers develop perpendicularly in the cortex, but are randomly distributed in the cancellous bone (Fig. 8D).

Saichania chulsanensis.—The skeleton of MPD 100/305 is one of the most complete specimens of an ankylosaur in the world. The specimen preserves a complete tail club and six

← Fig. 7. A tail club from an indeterminate ankylosaurid (probably *Euoplocephalus*), TMP 2000.57.03, from the Upper Cretaceous Dinosaur Park Formation of Alberta. **A**. External surface photograph of specimen. The sketch in panel A is from Carpenter (2004). **B**. Thin-section of a tail club, cut perpendicularly through the dorsal surface of the osteoderm. Dashed line in A indicates the cutting plane. The tail club is generally composed of a thin layer of compact bone except at a region at the top and a thick cancellous bone with large vascular canals. Note that a suture between the major plate and minor plate of the club is still visible; dark gray, cortical bone consisting of woven or structural fiber bone with most structural fibers inserting perpendicularly from the dermis into the bone; white, cancellous bone built up of bone trabeculae that show moderately remodeling. Photograph (B₁) and interpretive drawing (B₂). **C**, **D**. Cortical bone tissue of the club. Detail of the cortex and inner trabecular bone in normal (**C**) and polarized (**D**) light; external surface is to the top. The tail club is identical to a small osteoderm (TMP 85.36.218/1) in histology, despite a difference in size and morphology.

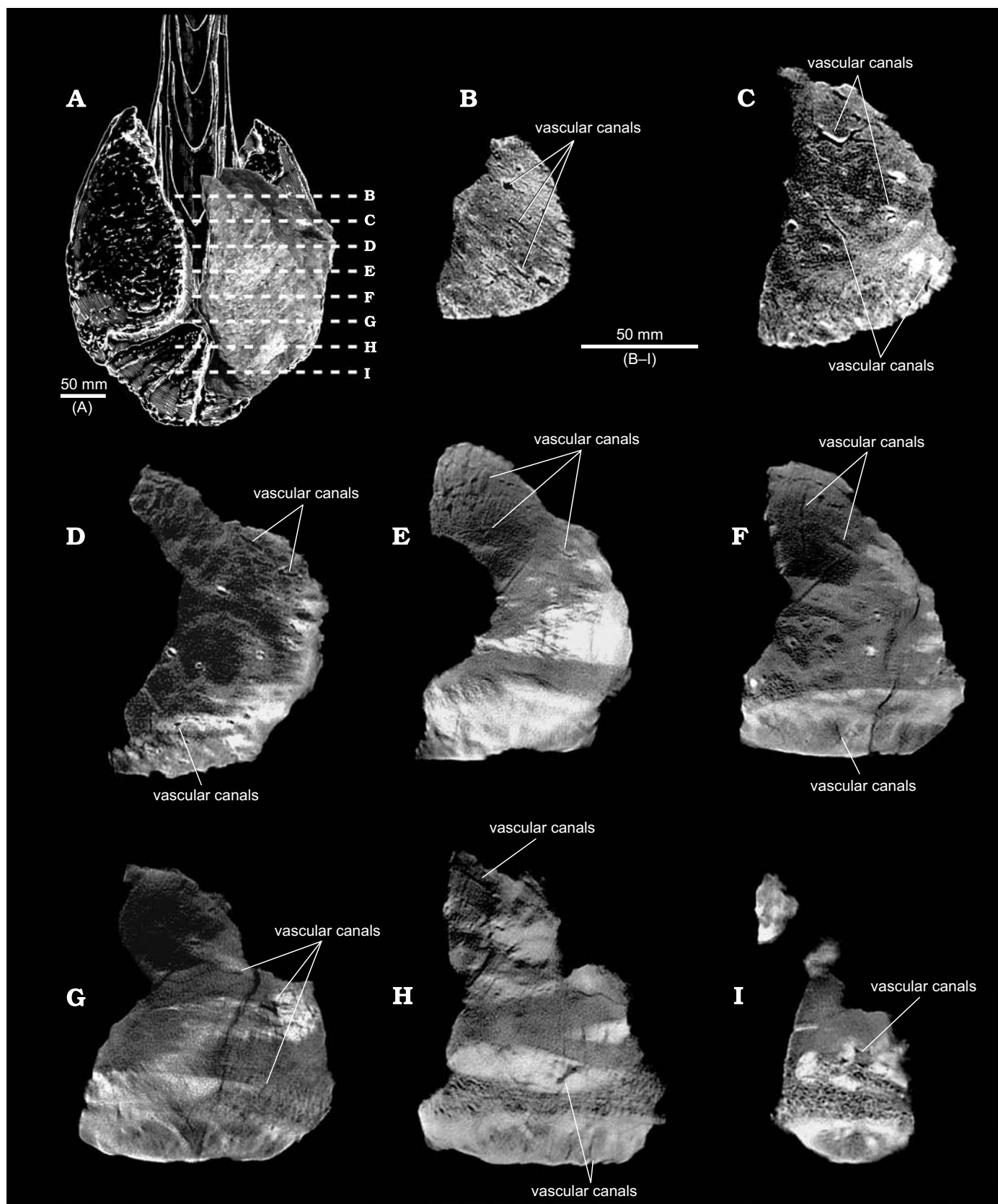


Fig. 9. A tail club from an indeterminate ankylosaurid (probably *Euoplocephalus*), TMP 2000.57.03, from the Upper Cretaceous Dinosaur Park Formation of Alberta. **A**. External surface photograph of specimen. The sketch in panel A is from Carpenter (2004). **B–I**. CT images of a terminal osteoderm of the tail club of an indeterminate ankylosaurid (TMP 2000.57.03) from the Upper Cretaceous Dinosaur Park Formation of Alberta; see also Fig. 7. The tail club has a complex vascular network. Dashed lines in A indicate cutting planes.

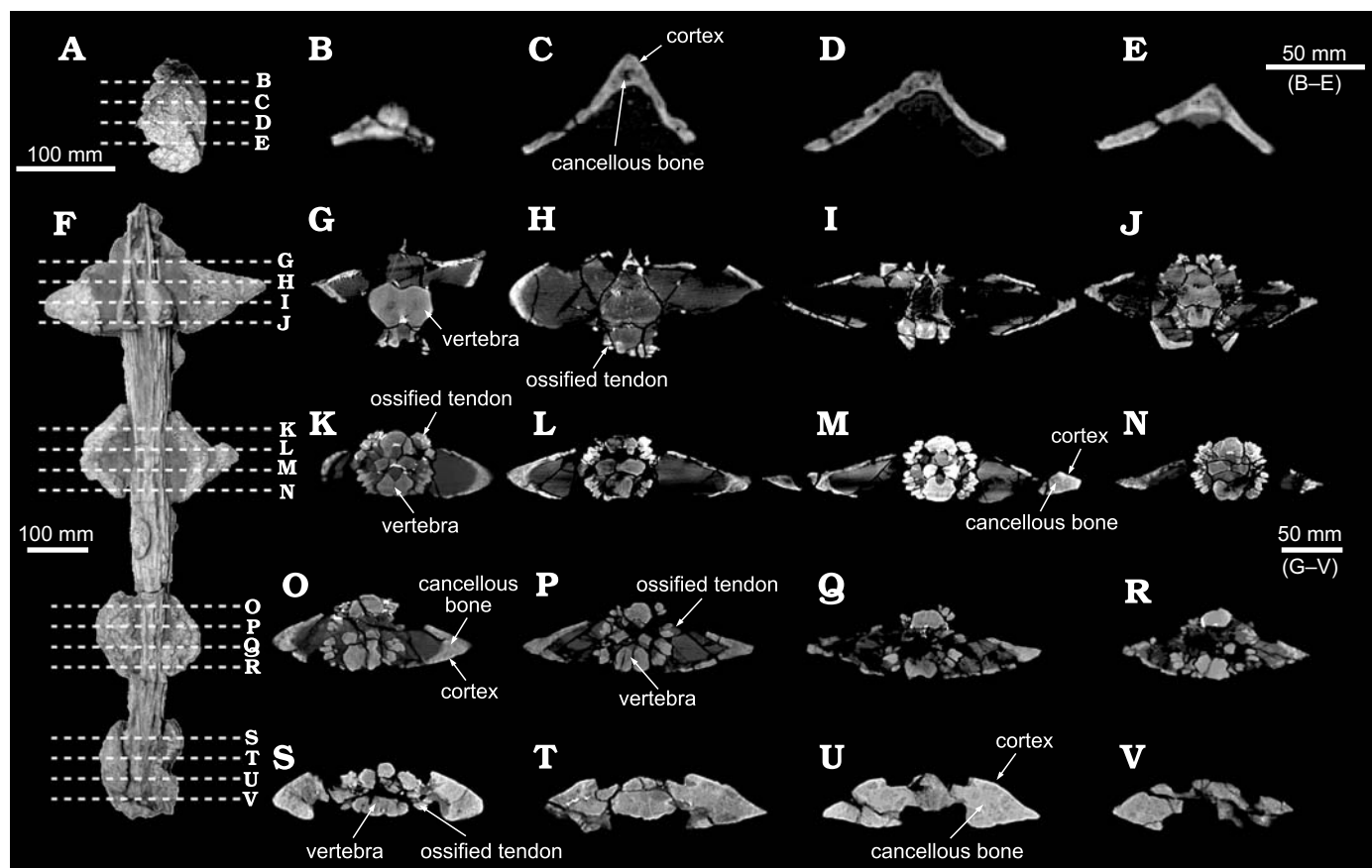


Fig. 10. Osteoderms from the ankylosaurid *Saichania chulsanensis* Maryańska, 1977 (MPD 100/1305) from the Upper Cretaceous Barun Goyot Formation of Mongolia. A. Photograph of the external surface of an osteoderm (MPD 100/1305-1). B–E. CT images of A. F. Photograph of the external surface of plates and club (MPD 100/1305-2). G–V. CT images of F. Dashed lines in A and F indicate cutting planes. All osteoderms are comprised of a very thin outer layer of cortex and an inner area of thick cancellous bone, but the club differs from other osteoderms in the fusion with the body skeleton. In the club, the boundaries among the osteoderms, vertebrae, and ossified tendons are still present in the anterior side (see S of the CT image).

plates on the tail, as well as numerous small osteoderms on the trunk and limbs. In this study, the internal structures of the tail club, six caudal plates, and a small osteoderm were observed from this individual using CT scanning (Fig. 10). Unfortunately, the cortical bone tissues could not be observed in this study because thin-sections could not be taken.

The tail club (18.4 cm in maximum length; Fig. 10S–V) consists of a terminal minor plate and a pair of the lateral major plates. This club is distinctly small in size, only one-third the size of adult clubs of North American ankylosaurids (see Carpenter 2004). The six caudal plates of MPD 100/305 (17.5 to 14.38 cm in maximum length; Fig. 10G–R) are thin, triangular osteoderms comprising a tall keel with sharp point, except for the last pair. The bases are hollow and strongly concave. Both plate surfaces are extensively pitted and grooved. A small pup-tent shaped osteoderm (10.7 cm in maximum length; Fig. 10A–E) located on the back of the body skeleton was examined. The osteoderm is thin, and the base is strongly concave.

All osteoderms examined are comprised of a relatively thin outer cortical layer and an inner area of thick cancellous bone. The club differs from other osteoderms in fusion with

the caudal vertebrae and ossified tendons (Fig. 10S–V). CT images of the club revealed that the boundaries among the osteoderms, vertebrae and ossified tendons are still present on the anterior side (proximal to the body skeleton; Fig. 10S), suggesting the incomplete fusion of these elements.

Discussion

Evolution

The histological features of the spikes, plates, and clubs are similar to those of small osteoderms in having relatively thin compact bone and thick cancellous bone with abundant fibers, although differences among these osteoderms in compact bone area are recognized. Scheyer and Sander (2004) demonstrated that each of the three groups of ankylosaurs (Polacanthidae, Nodosauridae, and Ankylosauridae) have distinct characteristic arrangements of structural collagen fibers in small osteoderms. The present study shows that spikes, plates, and clubs of ankylosaurs maintain the same characteristic features for each group despite differences in

shapes and sizes. These histological similarities, i.e., relatively thin compact bone layers and thick cancellous bone layers with abundant fibers, suggest that the various types of osteodermal armor in ankylosaurs (including small osteoderms) evolved along similar developmental pathways. Therefore, various morphologically different osteoderms were elaborated mainly by the modification of the external morphologies from small osteoderms. These results also suggest that it is possible to identify osteoderms to family just by osteoderm histology. Osteoderms in the basal thyreophorans (i.e., *Scutellosaurus* and *Scelidosaurus*) and in *Stegosaurus* lack extensive structural fibers (de Buffrénil et al. 1986; Scheyer and Sander 2004; Main et al. 2005; Hayashi et al. 2009). On the other hand, all ankylosaur osteoderms possess extensive fibers. These suggest that ankylosaurs used different strategies to evolve their osteoderms from other thyreophorans, or that ankylosaurs had a skin that differed from that of basal thyreophorans and *Stegosaurus*.

Growth

The cortical bone of ankylosaur osteoderms shows primary woven or structural fiber bone tissue having extensive reticular vascularity. In the present samples, LAGs were absent, and secondary reconstruction was not extensive. Conversely, previous studies have reported that cortical bone tissues in ankylosaur osteoderms are composed of primary lamellar bone tissue with LAGs (Scheyer and Sander 2004; Main et al. 2005). The difference from previous results may be due to ontogeny, because the histological features of osteoderms in this study indicate a rapid growth of the bone as seen in other juvenile dinosaurs (e.g., Sander 2000). Therefore, bone histology of ankylosaur osteoderms might change from woven or structural fiber bone tissue to lamellar bone throughout ontogeny such in *Stegosaurus* osteoderms (Hayashi et al. 2009). This also may indicate that growth maturity of osteoderms is delayed compared to the body skeleton such as in living reptiles (Vickaryous et al. 2001; Vickaryous and Hall 2008) and in *Stegosaurus* (Hayashi et al. 2009), because most of the specimens in this study (except *Sauropelta*) are adults or subadults based on the size and/or the fusion of neurocentral sutures.

Functions

Small osteoderms.—The deeper parts of osteoderms are reinforced by numerous structural fibers. In particular, nodosaurid and ankylosaurid osteoderms differ from those of polacanthids by incorporating abundant structural fibers. This result supports the hypothesis of Scheyer and Sander (2004) that ankylosaur osteoderms served as efficient lightweight armor.

Tail clubs.—The large tail club (TMP 2000.57.03), which might belong to an adult based on the size, still shows a suture on the external surface and rapid bone deposition in the cortical bone tissue. In addition, the tail club from *Saichania*

chulsanensis (MPD 100/305) lacks the fusion between osteoderms and caudal vertebrae in the anterior side despite the large body size (5 m in body length). These results suggest that the tail club keeps growing through a late ontogenetic stage and may explain size differences seen in the tail clubs of adult ankylosaurs (see Coombs 1995). Also, previously, it was reported that juvenile *Pinacosaurus* specimens lack the tail club (Currie 1991). This might indicate that tail clubs appeared later in ontogeny. It is possible that the tail club was used in intraspecific display and reflected social status and/or sexual attraction. A weapon function for defense may have been acquired in a late ontogenetic stage, as in *Stegosaurus* spikes (Hayashi and Carpenter 2006). The hypothesis is also supported by functional studies of ankylosaur tail clubs using the finite element analysis (FEA), suggesting that small and medium size clubs were not used as effective weapons (Arbour 2009; Arbour and Snively 2009).

Spikes and plates.—The nodosaurid spike (TMP 1979.147.94) has a conical morphology and retains a compact bone area strengthened by highly ordered structural fibers from small osteoderms (Table 2). Conversely, the polacanthid spike (DMNH 49754) has a reduced compact bone area from that seen in the small osteoderm and shows fewer collagen fibers than spikes and clubs of other ankylosaurs. Also, ankylosaurid plates (MPD 100/305) with hollow bases are very thin in morphology and show thin compact bone. These results may imply that nodosaurid spikes had a weapon function, as well as a display function. On the other hand, the polacanthid spike and ankylosaurid plates are lower in strength than spikes and clubs of other ankylosaurs, suggesting that they may have been used more probably for display and/or thermoregulation rather than a weapon. The possibility of thermoregulation is based upon similarities with crocodiles in having “pipe”-like large vascular networks between the vascularization of the osteoderms, for which thermoregulation has already been suggested (Seidel 1979). The functional variations in ankylosaur osteoderms may imply that these structures played more than just a defensive role.

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References

- Arbour V. 2009. Estimating impact forces of tail club strikes by ankylosaurid dinosaurs. *PLoS ONE* 4: e6738. <http://dx.doi.org/10.1371/journal.pone.0006738>
- Arbour, V. and Snively, E. 2009. Finite element analyses of ankylosaurid dinosaur tail club impacts. *The Anatomical Record* 292: 1412–1426. <http://dx.doi.org/10.1002/ar.20987>
- Bakker, R.T. 1986. *Dinosaur Heresies*. 481 pp. William Morrow, New York.
- Barrett, P.M., Clarke, J.B., Brinkman, D.B., Chapman, S.D., and Ensom, P.C. 2002. Morphology, histology and identification of the “granicones” from the Purbeck Limestone Formation (Lower Cretaceous: Berriasian) of Dorset, southern England. *Cretaceous Research* 23: 279–295. <http://dx.doi.org/10.1006/cres.2002.1002>
- Blows, W.T. 1987. The armoured dinosaur *Polacanthus foxii* from the Lower Cretaceous of the Isle of Wight. *Palaeontology* 30: 557–580.
- Blows, W.T. 2001. Dermal armor of the polacanthine ankylosaurs. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 363–385. Indiana University Press, Bloomington.
- Buffrénil, V. de, Farlow, J.O., and de Ricqlès, A. 1986. Growth and function of *Stegosaurus* plates: evidence from bone histology. *Paleobiology* 12: 459–473.
- Carpenter, K. 1982. Skeletal and dermal armor reconstructions of *Euoplocephalus tutus* (Ornithischia: Ankylosauridae) from the Late Cretaceous Oldman Formation of Alberta. *Canadian Journal of Earth Sciences* 19: 689–697.
- Carpenter, K. 1997. Ankylosaurs. In: J.O. Farlow and M.K. Brett-Surman (eds.), *The Complete Dinosaur*, 307–316. Indiana University Press, Bloomington.
- Carpenter, K. 1998. Armor of *Stegosaurus stenops*, and the taphonomic history of a new specimen from Garden Park, Colorado. *Modern Geology* 23: 127–144.
- Carpenter, K. 2001. Phylogenetic analysis of the Ankylosauria. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 455–483. Indiana University Press, Bloomington.
- Carpenter, K. 2004. Redescription of *Ankylosaurus magniventris* Brown 1908 (Ankylosauridae) from the Upper Cretaceous of the Western Interior of North America. *Canadian Journal of Earth Sciences* 41: 961–981. <http://dx.doi.org/10.1139/e04-043>
- Carpenter, K. and Breithaupt, B. 1986. Latest Cretaceous occurrence of nodosaurid ankylosaurs (Dinosauria: Ornithischia) in western North America and the gradual extinction of the dinosaurs. *Journal of Vertebrate Paleontology* 6: 251–257.
- Carpenter, K., Miles, C., and Cloward, K. 1998. Skull of a Jurassic ankylosaur (Dinosauria). *Nature* 393: 782–783. <http://dx.doi.org/10.1038/31684>
- Carpenter, K., Sanders, F., McWhinny, L.A., and Wood, L. 2005. Evidence for predatory-prey relationships. Examples for *Allosaurus* and *Stegosaurus*. In: K. Carpenter (ed.), *The Carnivorous Dinosaurs*, 325–350. Indiana University Press, Bloomington.
- Castanet, J., Francillon-Vieillot, H., Meunier, F. J., and de Ricqlès, A. 1993. Bone and individual aging. In: B.K. Hall (ed.), *Bone, Vol. 7. Bone Growth—B*, 245–283. CRC Press, Boca Raton.
- Coombs, W. 1971. *The Ankylosauria*. 487 pp. Columbia University, New York.
- Coombs, W. 1978a. The families of the ornithischian dinosaur order Ankylosauria. *Journal of Paleontology* 21: 143–170.
- Coombs, W. 1978b. Forelimb muscles of the Ankylosauria (Reptilia: Ornithischia). *Journal of Paleontology* 52: 642–658.
- Coombs, W. 1979. Osteology and myology of the hindlimb in the Ankylosauria (Reptilia, Ornithischia). *Journal of Paleontology* 53: 666–684.
- Coombs, W.P. 1986. A juvenile ankylosaur referable to the genus *Euoplocephalus* (Reptilia: Ornithischia). *Journal of Vertebrate Paleontology* 6: 162–173.
- Coombs, W.P. 1995. Ankylosaurian tail clubs of middle Campanian to early Maastrichtian age from western North America, with description of a tiny club from Alberta and discussion of tail orientation and tail club function. *Canadian Journal of Earth Sciences* 32: 902–912.
- Coombs, W. and Maryańska, T. 1990. Ankylosauria. In: D. Weishampel, P. Dodson, and H. Osmolska (eds.), *The Dinosauria*, 456–483. University of California Press, Berkeley.
- Coombs, W.P. Jr. 1979. Osteology and myology of the Hindlimb in the Ankylosauria (Reptilia, Ornithischia). *Journal of Paleontology* 52: 642–658.
- Currie, J.P. 1991. The Sino/Canadian dinosaur expeditions 1986–1990: *Geotimes* April: 19–21.
- Curry, K.A. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *Journal of Vertebrate Paleontology* 19: 654–665.
- Ford, T.L. 2000. A review of ankylosaur osteoderms from New Mexico and a preliminary review of ankylosaur armor. *New Mexico Museum of Natural History and Science Bulletin* 17: 157–176.
- Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F. J., Sire, J. Y., Zylberberg, L., and de Ricqlès, A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: J. G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Vol. 1*, 471–530. Van Nostrand Reinhold, New York.
- Hayashi, S. and Carpenter, K. 2006. Osteoderm histology of *Stegosaurus stenops* (Ornithischia: Thyreophora): implications for plate and spike growth. *Journal of Vertebrate Paleontology* 26 (Supplement to No. 3): 73A.
- Hayashi, S., Carpenter, K., and Suzuki, D. 2009. Different growth patterns between the skeleton and osteoderm of *Stegosaurus* (Ornithischia: Thyreophora). *Journal of Vertebrate Paleontology* 29: 123–131.
- Hill, V., Witmer, L., and Norell, M. 2003. A new specimen of *Pinacosaurus grangeri* (Dinosauria: Ornithischia) from the Late Cretaceous of Mongolia: ontogeny and phylogeny of ankylosaurs. *American Museum Novitates* 3395: 1–29.
- Kilbourne, B. and Carpenter, K. 2005. Redescription of *Gargoylesaurus parkpinorum*, a polacanthid ankylosaur from the Upper Jurassic of Albany County, Wyoming. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 237: 111–160.
- Kirkland, J.I. 1998. A polacanthine ankylosaur (Ornithischia: Dinosauria) from the Early Cretaceous (Barremian) of Eastern Utah. In: S.G. Lucas, J.I. Kirkland, and J.W. Estep (eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin* 14: 271–281.
- Klein, N. and Sander, P.M. 2007. Bone histology and growth of the prosauropod *Plateosaurus engelhardti* Meyer, 1837 from the Norian bonebeds of Trossingen (Germany) and Frick (Switzerland). *Special Papers in Paleontology* 77: 169–206.
- Main, R.P., de Ricqlès, A., Horner, J.R., and Padian, K. 2005. The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. *Paleobiology* 31: 291–314. [http://dx.doi.org/10.1666/0094-8373\(2005\)031%5B0291:TEAFOT%5D2.0.CO;2](http://dx.doi.org/10.1666/0094-8373(2005)031%5B0291:TEAFOT%5D2.0.CO;2)
- Maryańska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologia Polonica* 37: 85–151.
- Pisani, D., Yates, A.M., Langer, M.C., and Benton, M.J. 2002. A genus-level

- supertree of the Dinosauria. *Proceedings of the Royal Society of London, Series B* 269: 915–921. <http://dx.doi.org/10.1098/rspb.2001.1942>
- Sander, P.M. 2000. Long bone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* 26: 466–488. [http://dx.doi.org/10.1666/0094-8373\(2000\)026%3C0466:LHOTTS%3E2.0.CO;2](http://dx.doi.org/10.1666/0094-8373(2000)026%3C0466:LHOTTS%3E2.0.CO;2)
- Sander, P.M., Mateus, O., Laven, T., and Knötschke, N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature* 441: 739–741. <http://dx.doi.org/10.1038/nature04633>
- Scheyer, T., and Sander, P.M. 2004. Histology of ankylosaur osteoderms: implications for systematics and function. *Journal of Vertebrate Paleontology* 24: 874–893. [http://dx.doi.org/10.1671/0272-4634\(2004\)024%5B0874:HOAOF%5D2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2004)024%5B0874:HOAOF%5D2.0.CO;2)
- Seidel, M. 1979. The osteoderms of the American alligator and their functional significance. *Herpetologica* 35: 375–380.
- Suzuki, D., Murakami, G., and Minoura, N. 2002. Histology of the bone-tendon interfaces of limb muscles in lizards. *Annals of Anatomy* 184: 363–377. [http://dx.doi.org/10.1016/S0940-9602\(02\)80057-7](http://dx.doi.org/10.1016/S0940-9602(02)80057-7)
- Suzuki, D., Murakami, G., and Minoura, N. 2003. Crocodilian bone-tendon and bone-ligament interfaces. *Annals of Anatomy* 185: 425–433. [http://dx.doi.org/10.1016/S0940-9602\(03\)80100-0](http://dx.doi.org/10.1016/S0940-9602(03)80100-0)
- Thulborn, T. 1993. Mimicry in ankylosaurid dinosaurs. *Record of the South Australian Museum* 27: 151–158.
- Vickaryous, M. and Hall, B. 2008. Development of the dermal skeleton in Alligator mississippiensis (Archosauria, Crocodylia) with comments on the homology of the osteoderms. *Journal of Morphology* 269: 398–422. <http://dx.doi.org/10.1002/jmor.10575>
- Vickaryous, M. and Sire, J.-Y. 2009. The integument skeleton of tetrapods: origin, evolution, and development. *Journal of Anatomy* 214: 407–644. <http://dx.doi.org/10.1111/j.1469-7580.2009.01051.x>
- Vickaryous, M., Maryńska, T., and Weishampel, D. 2004. Ankylosauria. In: D. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* (2nd edition), 427–434. University of California Press, Berkeley.
- Vickaryous, M., Russell, A., and Curry, P. 2001. Cranial ornamentation of ankylosaurs (Ornithischia: Thyreophora): reappraisal of development hypothesis. In: K. Carpenter (ed.), *The Armored Dinosaurs*, 318–340. Indiana University Press, Bloomington.