EXTERNAL AND INTERNAL STRUCTURE OF ANKYLOSAUR (DINOSAURIA, ORNITHISCHIA) OSTEOOERMS AND THEIR SYSTEMATIC RELEVANCE

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ABSTRACT—Ankylosaurian systematics can be assessed using morphological, textural, and histological characters of osteoderms. Archosaur osteoderms have cortices surrounding cancellous cores. Ankylosaurs are united by an external cortex distinguishable from the core and by the presence of mineralized structural fibers. Nodosaur osteoderms lack a well-developed basal cortex and have dense external cortical fibers. Ankylosaur osteoderms are thinner than those of other ankylosaurs. Polacanthine osteoderms have a cancellous core, but share this feature with other derived and primitive taxa. Cortical thickness overlaps among groups, so a thick cortex is not diagnostic for polacanthines. Specialized elements diverge histologically from the primitive condition to suit their specific functions. Some shapes and external textures are diagnostic for specific taxa, such as Ankylosaurus and Glyptodontopterus. Parsimony analyses suggest osteodermal support for a monophyletic Polacanthinae (excluding Mycocephalus) and Shamosaurinae.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The ankylosaurs are a group of dinosaurs known, in part, for their extensive system of osteoderms, composed of individual elements that vary in size and shape and cover part of the skull and most of the body (Coombs, 1971, 1978). Although known for over 175 years, these animals are still poorly understood. The morphology of their osteoderms varies in shape, microanatomy, and external sculpturing. Thus, the osteoderms of ankylosaurs present a host of problems in taxonomic identification and conducting phylogenetic analyses.

Over 40 years ago, Coombs (1971:313) wrote that dermal armor is perhaps the most frequently encountered ankylosaur fossil material, “and consequently a great deal of ink has been spilt describing individual plates,” which for the most part were considered not diagnostic. Despite this dismissal, he did note some differences between nodosaurids and ankylosaurs as well as accurately detailing the basic layout of osteoderms across the body. He noted that osteoderms were arranged in transverse rows down the length of the body. According to Coombs (1971), isolated osteoderms from ankylosaurids generally exhibit excavated basal (= internal) surfaces, whereas those of nodosaurids are relatively thick and display flat basal surfaces. Also, tall, solid, conical spines (at least twice as tall as their greatest diameters) were observed only in nodosaurids (although some spines from Hylaeosaurus armatus Mantell, 1833, and Sauronotosaurus edwardsoni Ostrom, 1970, were deemed almost indistinguishable from stegosaur caudal spikes). Coombs (1971) also noted marked differences in the cervical half rings of ankylosaurids and those of nodosaurids. In ankylosaurids, the osteoderms of the cervical half rings are generally separated from one another, whereas those of nodosaurids abut, often fusing with one another (Coombs, 1971). Finally, over the pelvic region, fusion of the osteoderms can sometimes form a shield, which presented no taxonomic importance to Coombs (1971). Others have disagreed with this assessment of the pelvic shield, arguing that it is in fact a synapo-

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great potential for clarifying issues regarding ankylosaur taxonomy, ontogeny, and behavior. However, this can only occur by establishing a baseline for comparison. Once established, issues regarding normal morphological variation can be understood and deviant morphologies recognized.

To date, there has been little published on the histology of ankylosaur osteoderms, although several recent studies increase what we know about the internal structure of these elements. Vickaryous et al. (2001) studied *Euoplocephalus*, focusing on the histological interactions between the dermalcranum and overlying cranial osteoderms. De Ricqlès et al. (2001) analyzed postcranial ossicles from *Antarctopelta*. These authors were the first to recognize a regular organization of structural fibers in the ossicles. In addition, de Ricqlès et al. (2001) histologically discussed osteoderm skeletogenesis, suggesting that a differentiated histology indicated neoplasia rather than metaplasia (the latter would have resulted in a uniform distribution of structural fibers matching the parent dermis, which they did not observe). Barrett et al. (2002) briefly described the histology of osteoderms belonging to *Polacanthus foxii* and *Scelidosaurus harrisonii* Owen, 1861. Scheyer and Sander (2004) were the first to systematically investigate variation in the histology of ankylosaur osteoderms. They showed that the tissue type and arrangement of internal structural fiber bundles differed among three groups of ankylosaurs (ankylosaurids, nodosaurids, and polacanthids). Main et al. (2005) also examined ankylosaur osteoderms and included an analysis of basal thyreophorans, tracing the evolution of ankylosaur osteoderms as modified basal thyreophoran osteoderms. Most recently, Hayashi et al. (2010) investigated specialized osteoderms (tail club osteoderms and nodosaur spines). They reported that these specialized osteoderms have the same histology as those of unmodified dorsal osteoderms, and that three morphgroups can be distinguished.

There is evidence to suggest that osteodermal (and integumentary) characters are crucial to our understanding of vertebrate evolutionary relationships. A study on the phylogeny of the Amniota by Hill (2005) demonstrates the effects of increasing taxonomic and character sampling and highlights the worth of the integument as a source of meaningful morphological character data. This study is important in that the incorporation of data from the integument resolves relationships that traditionally studied anatomical characters do not, revealing phylogenetic signals that were previously obscured by incomplete taxonomic or character sampling. Carpenter (1990), Ford (2000), and Perissaki (2001) noted that osteoderm form and sculpturing have been used taxonomically in other groups such as actosaurus, crocodylians, glyptodonts, and lizards.

Sources of Osteodermal Variation

Possible sources of variation in osteoderm histology and morphology include taxonomy, individual variation, sexual dimorphism, ontogeny, and pathology. Individual variation likely accounts for some of the diversity observable in ankylosaur osteoderms; however, there are not many ankylosaur specimens preserving in situ osteoderms. Therefore, it is difficult to test the effects of individual variation on osteoderm morphology and histology. It is safe to assume that, given emerging patterns across taxa in osteoderm morphology (Carpenter, 1990; Ford, 2000; Burns, 2008) and histology (Scheyer and Sander, 2004; Burns, 2008; Hayashi et al., 2010), real taxonomic differences are being observed.

The hypothesis of sexual dimorphism in ankylosaur osteoderms is difficult to test, given the small sample sizes available. This would also presuppose that at least some of the osteoderms have a sex-linked intraspecific function, which may be true for specialized osteoderms but seems unlikely for the most of the body osteoderms. There is evidence to suggest that this may be a source of variability in tail club osteoderms (Arbour, 2009). Carpenter (1990) has suggested a sexual selection role for anteriorly projecting distal cervical spines in *Edmontonia rugosidens*. This interpretation of dimorphism, however, is based on three specimens, and the apparent dimorphism is just as likely caused by individual, ontogenetic, or geographic differences.

Some recent studies have investigated ontogenetic changes in osteoderms in various extant organisms such as armadillos and crocodylians (Vickaryous and Hall, 2006, 2008). Both of these groups display a delayed onset of osteoderm development, and this development occurs asynchronously across different regions of the body. The same may have occurred in ankylosaurs as well, as suggested by juvenile ankylosaur material from Asia. Juvenile *Pinacosaurus grangeri* Gilmore, 1933, specimens develop ossified cervical half rings early in ontogeny, whereas the remaining osteoderms do not fully develop until later (Burns et al., 2011).

**Objectives**

This study describes the internal and external morphology of osteoderms from various ankylosaur taxa, emphasizing specimens associated with other diagnostic skeletal material. Previous studies (Scheyer and Sander, 2004; Hayashi et al., 2010) have relied on material lacking definitive taxonomic identification, although these papers did not investigate variation below the family level. In some cases, access to specimens for destructive analysis is limited. Characters identified via this process are then incorporated into existing character-taxon matrices to test the effects of incorporating this new data on existing phylogenetic hypotheses for the Ankylosauria as demonstrated by Hill (2005).

**Terminology**

Although discourse on terminology may seem redundant, a lack of consistent descriptions is one of the greatest impediments to our understanding of osteoderm variation and comparison for ankylosaurs. Although several attempts (e.g., Ford, 2000; Blows, 2001; Scheyer and Sander, 2004) have been made to do this for ankylosaur osteoderms, they have not been adopted by other workers. These studies are reviewed and revised to create a system for the consistent holistic description of osteoderm position, morphology, surface texture, and histology. Even if not adopting the terminology presented herein (Fig. 1), future studies should clearly describe and illustrate the meaning of their given terminologies to avoid the ineffectuality inherent in many descriptions.

The term ‘osteoderm’ unambiguously refers to a bony structure of the dermal skeleton that develops in the dermis. Other ambiguous synonyms, including ‘armor,’ ‘dermal ossification,’ ‘plate,’ ‘osteostyler,’ and ‘scute’ (Vickaryous and Sire, 2009), should be avoided due to inconsistent use. The term ‘median’ when used in the context of a median keel or apex refers to position relative to the osteoderm itself and not to the overall anatomical position on the animal. Surface textures for different osteoderm morphologies have been detailed for only a few ankylosaur taxa (Burns, 2008). Although this feature is often included in the description of osteoderms, there is no standard. Here, terminology for describing bony surface textures follows Hieronymus et al. (2009).

‘Dorsal’ and ‘ventral’ refer to anatomical directions relative to the body (i.e., a ventral osteoderm is located on the belly of the animal). This is in contrast to similar directions specific to osteoderms, defined by Scheyer and Sander (2004) and Cerda and Desojo (2011), in which ‘basal’ (= ‘internal’; ‘deep’ of Hill [2006]; ‘proximal’ of Main et al. [2005]) refers to the direction towards the deeper layers of the dermis and ‘external’ (= ‘apical’; ‘superficial’ of Hill [2006]; ‘distal’ of Main et al. [2005]) to the direction towards the more external epidermis. These terms are confused in osteoderm descriptions because workers often fail to
imagine the elements as distributed throughout the animal’s der-
mis (e.g., ‘external’ is not always the same as ‘dorsal’).

Histologically, osteoderms are described as having a ‘cortex’
or two ‘cortices’ (external and/or basal) and a core (the terms
‘medulla’ and ‘medullary’ are not used to avoid implying that
the region is associated with or similar to the medullary re-
gions of long bones). The most frequently encountered mor-
phology in ankylosaurs (also present in the basal thyreophorans
Scelidosaurus and Scutellosaurus lawleri Colbert, 1981) includes
circular or oval osteoderms (‘unmodified’), each with some de-
velopment of a roughly longitudinal keel or apex. Osteoderms
that deviate perceptibly from such a morphology (ankylosaurid
tail clubs and nodosaur cervical spines) are referred to as ‘spe-
cialized.’ This is an important distinction because, as will be
demonstrated, specialized osteoderms can diverge from the his-
tology/morphology otherwise characteristic for unmodified os-
teoderms of a group. The definition for ‘ossicles’ adopted here
is modified from Blows (2001): small (<70 mm), amorphous min-
eralized dermal elements often found interstitial to major osteo-
dermal elements.

Finally, published descriptions of ankylosaur osteoderm histol-
ogy have tended to distinguish between ‘Sharpey’s fibers’ for col-
lagen fibers that cross the boundary of mineralization in an os-
teoderm, and ‘structural fibers’ for collagen fibers that are fully
incorporated into the mineralized matrix (Scheyer and Sander,
2004; Hayashi et al., 2010). This convention is followed here,
and the term interwoven structural fiber bundles (ISFB; sensu
Scheyer and Sander, 2004; Scheyer and Sánchez-Villagra, 2007)
is used to refer to metaphlastic bone dominated by structural fibers.

MATERIALS AND METHODS

Osteoderms were examined from North American and Asian
ankyosaurid, nodosaurid, and polacanthine taxa, as well as speci-
mens of the basal thyreophoran Scelidosaurus. External variation
in osteoderm shapes and textures among these specimens was
studied through measurements, observations, and photographs.
In addition, previously described osteoderm specimens (Scheyer
and Sander, 2004; Hayashi et al., 2010) have been reviewed from

Other Abbreviations—CI, consistency index; ISFB, interwoven
structural fiber bundles; MPTs, equally most parsimonious
trees; PPL, plane-polarized light; RI, retention index; TL, tree
length; XPL, cross-polarized light.
the literature and published figures (not first-hand specimens) where noted. Due to the overwhelming number of osteoderm specimens available for study, gross morphology of these elements is not listed for each specimen. Instead, overall descriptions for individual taxa are given.

When available, representative osteoderms were selected for paleohistological analysis. These samples were stabilized via resin impregnation using Buehler EpoThin low-viscosity resin and hardener. Thin sections were prepared petrographically to a thickness of 60–80 μm and polished using CeO₂ powder. Sections were examined on a Nikon Eclipse E600POL trinocular polarizing microscope with an attached Nikon DXM 1200F digital camera. Scans of the slides were taken with a Nikon Super Coolscan 5000 ED using polarized film. Histological measurements were taken from imaged slides, or from published figures where noted, using ImageJ 1.40g.

The relative thickness of different histological layers was evaluated via a two-sample t-test assuming unequal variances in PAST 2.12 (Hammer et al., 2001), comparing each of the three ankylosaur groups against one another. Interstitial ossicles were excluded from these analyses. Osteoderms of indeterminate taxonomic assignment were originally excluded from the tests. The addition of these, however, in a subsequent test did not affect the results, so they are included here.

The effects of adding osteodermal characters to existing ankylosaur phylogenies were tested. Test 1 examined 21 ingroup and two outgroup taxa (Huayangosaurus taiibaii Dong, Tang, and Zhou, 1982, and Scelidosaurus) and a total of 63 characters, 50 cranial characters from Hill et al. (2003) and 13 postcranial characters from Vickaryous et al. (2004) (see Supplementary Data). The cranial characters were chosen from Hill et al. (2003) because they included and revised some of the characters of Vickaryous et al. (2001) and incorporated data from other studies. Scorings for Scelidosaurus are from Parsons and Parsons (2009). Nodosaurus kirtlandensis Sullivan, 1999, was coded by M.E.B. and Pinacosaurus spp. were coded from Burns et al. (2011). Newly identified osteodermal characters were adapted to this data matrix to create the final character-taxon matrix of 91 characters.

Test 2 included Scelidosaurus as the outgroup with 16 ingroup taxa. Data were modified from Kirkland (1998) (see Supplementary Data). Character 32 in this test combines characters 32 and 33 from Kirkland (1998) to reduce overweighting acromion morphology. Character 25 included an a priori assumption in Kirkland (1998) about the secondary loss of a jugal/quadratognath osteoderm and is recoded as ‘absent’ rather than ‘lost.’ Characters 38–44 from Kirkland (1998) were removed due to overlap with characters from this study, leaving a matrix of 38 characters without osteodermal data and 66 characters with osteodermal data.

Data were analyzed in TNT 1.1 (Goloboff et al., 2008) with the tree bisection reconnection (TBR) swapping algorithm with 1000 repetitions for each search. All characters were treated as unordered and of equal weight. A heuristic parsimony search using random addition sequences was performed. Bootstrap and jackknife searches used the same criteria, the latter with a resampling probability of 0.36. For Bremer support analysis, suboptimal trees were retained up to 50 steps and values were mapped onto the majority rule consensus trees from the heuristic searches. Tree and matrix editing were performed in Mesquite 2.75 (Maddison and Maddison, 2011).

DESCRIPTIVE RESULTS

In the following descriptions, percentages that appear as cortical and core thicknesses represent the thickness of each histological layer relative to the overall thickness of the osteoderm in a given thin section. In a compact osteoderm (those without a trabecular core), the core and cortices can be difficult to delineate. In some cases, the core is distinguishable as a region of remodeled Haversian bone. In others, however, osteoderms can be composed almost entirely of woven-fibered bone and lack any stratification into cores and cortices. Even in a case where there is a core region, its precise delimitation from an adjacent cortex can be difficult due to the retention of primary woven-fibered bone in the core. Instances in which the cortex and core were difficult to delineate have been noted in individual descriptions.

Basal Thyreophora

Scelidosaurus—Osteoderm morphology and arrangement are well known for Scelidosaurus based on several fully articulated specimens with osteoderms preserved in situ. Most of the osteoderms are relatively thin-walled (exhibit excavated bases) and are externally relatively smooth, exhibiting sparse pitting. Osteoderms in the cervical region are not fully fused into cervical half rings, but rather are in contact via interdigitating sutures. There is no fusion of individual osteoderms anywhere else on the body. Compared with derived ankylosaurs, osteoderm morphology is fairly homogenous across the body: they are conical in shape and grade towards more elongate both posteriorly and laterally along the body. Distal osteoderms are dorsoventrally compressed and triangular. The caudal region is completely encircled by osteoderms.

UOP 03/TS2, described by Scheyer and Sander (2004), is an oval-based spine. The base is concave, making the osteoderm walls equally thick throughout. Although originally described as rugose (Scheyer and Sander, 2004), the external surface is characterized by sparse pitting and is actually smooth relative to osteoderms of some derived ankylosaurs. The compact cortices are thin (both 6%) and composed of lamellar bone invested with fibers arranged at regular angles to the osteoderm surfaces (Scheyer and Sander, 2004:fig. 12). The core is thick (88%) and entirely trabecular, containing no Sharpey’s fibers or osteons.

Nodosauridae

Edmontonia—Edmontonia is represented by many well-preserved specimens. The morphology of individual osteoderms differs in the cervical half rings. Medial osteoderms of the first and second cervical half rings in Edmontonia rugosidens are square to polygonal and have keels that diverge posteriorly (Fig. 2). Those of Edmontonia longiceps have more rounded edges and their overall shape in external/dorsal view is more posterolaterally skewed than those in Edmontonia rugosidens. Distal osteoderms of the second half ring are specialized as anterolaterally directed spines. Similar spines are found in the distal position

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FIGURE 3. Thoracic osteoderm and interstitial ossicle of Edmontonia rugosidens. Osteoderm is shown in external (A) and basal (B) views, with complete thin section in PPL (C) and XPL (D). Detailed sections of osteoderm showing the external cortex (E, PPL; F, XPL), core (G, PPL; H, XPL), and basal cortex (I, PPL; J, XPL). Osteoderm is dominated by ISFB, with some resorption cavities in the core. Ossicle (K) view and orientation uncertain) with complete thin section in PPL (L) and XPL (M). Detailed sections of ossicle showing peripheral zonation (N, PPL; O, XPL) and core (P, PPL; Q, XPL) both dominated by ISFB. External is up in all sections. The thin lines in A, B, and K indicate planes of thin sectioning. Lettered boxes in C, D, L, and M show locations of detailed sections. Scale bars equal 1 cm for whole osteoderms and sections, 1 mm for detailed sections.
on the pectoral half ring that exhibit various degrees of bifurcation in different specimens, but they project more laterally (as opposed to anterolaterally) in *Edmontonia longiceps* (Carpenter, 1990). Posterior to the pectoral half ring is a pair of distal thoracic spines, one projecting anteriorly and one posteriorly. Fusion of these distal thoracic spines is individually variable. Over the dorsum of the thoracic region, osteoderms are circular with median keels. Over the pelvis, osteoderms are transversely oval with median keels. No osteoderms are known that are preserved in association with the caudal region.

TMP 1998.98.1 (Fig. 2) includes a well-preserved skull and is unequivocally identifiable as *Edmontonia rugosidens* (Vickaryous, 2006). Along with the first cervical half ring, which is preserved in situ posterior to the skull, much of the postcranial is preserved. All osteoderms possess the same surface texture—strong, uniform, pitted rugosity with sparse, reticular neurovascular grooves, and normal to obliquely oriented neurovascular foramina.

Several ossicles and one osteoderm (a flat oval) were selected for thin sectioning from this specimen. The osteoderm (Fig. 3A–J) is composed almost entirely of ISFB. In a centrally located section (Fig. 3G, H), a core (53%) is visible as a region of diffuse primary and secondary osteons and resorption cavities. Both the thick external (24%; Fig. 3E, F) and basal (23%; Fig. 3J) cortices are dominated by ISFB. However, there is no clear demarcation (e.g., a continuous resorption line) between the core and cortices. Therefore, delimitation of the core is more subjective in this specimen and is identified as a region of denser osteons and resorption cavities than in the cortices.

The ossicles (Fig. 3K–Q) associated with TMP 1998.98.1 show less differentiation than the larger osteoderm. They are compact structures composed entirely of ISFB, with few primary osteons scattered diffusely throughout the elements. Near the external/basal margins, zonation is distinct and overprints the ISFB pattern (Fig. 3N, O). In all of the ossicles, structural fiber bundles are orthogonally arranged throughout, unlike the radial pattern described for the ossicles of *Antarctopelta* (de Ricqlès et al., 2001).

Two nodosaur distal spines, identified as *Edmontonia* sp. (DMNH 2452 and TMP 1979.147.94), are described by Hayashi et al. (2010:figs. 4, 5). DMNH 2452 is characterized by a smooth external surface texture with a sparse reticulate pattern of neurovascular grooves. The base is flat. The external cortex (14%) is composed of ISFB-dominated bone and lacks zonation. The basal cortex (8%) is trabecular and invested with neurovascular canals that connect neurovascular foramina on the base of the osteoderm with the grooves on the external surface. In the external cortex, two distinct systems of dense orthogonally arranged structural fibers are observable under XPL. Some secondary osteons are visible where the external cortex contacts the core (Hayashi et al., 2010:fig. 4).

TMP 1979.147.94 was sectioned in four locations along its length by Hayashi et al. (2010:fig. 5). The external surface is ornamented with sparse, uniformly distributed pits. Only one neurovascular groove/foramen is visible near the apex. Histologically, it lacks a basal cortex and has a trabecular core. The cortex is relatively thinner near the base than at the apex (Hayashi et al., 2010:fig. 5).

*Panoplosaurus*—Although no osteodermal specimens of *Panoplosaurus* have been sectioned to date, diagnostic morphological characters may be derived from the holotype (CMN 2759).

External osteoderm texture is pitted with a dense reticulate pattern of neurovascular grooves. Medial osteoderms of the cervical half rings are suboval and the posteriorly diverging keels curve laterally. Lateral and distal cervical osteoderms are transversely elongate and have relatively high, sharp keels. The arrangement of the osteoderms on the remainder of the body is not known (Carpenter, 1990).

**FIGURE 4.** Thin section through osteoderm of *Glyptodontopelta mimus* (SMP VP-1580 D) in PPL (A) and XPL (B). Detailed sections of osteoderm showing the external cortex (C, PPL; D, XPL), core (E, PPL; F, XPL), and basal cortex (G, PPL; H, XPL). External is up in all sections. Scale bars for thin sections equal 1 cm, and for detailed sections, 0.5 mm.

*Glyptodontopelta*—Three osteoderms from SMP VP-1580 were obtained from a referred specimen of *Glyptodontopelta*. SMP VP-1580 C is a partial keeled osteoderm (Morphotype A or B, sensu Burns, 2008), whereas SMP VP-1580 D (Fig. 4) and E are flat (Morphotype D). The texture of each of the three is characterized by a smooth surface and a dense pattern of reticular neurovascular grooves. Neurovascular foramina are oriented obliquely to the surface. These osteoderms all share the basic histology, which is similar to the larger osteoderm described for TMP 1998.98.1 (*Edmontonia*) in that cores are visible in some osteoderms as concentrations of osteons and...
resorption cavities within the central areas of the sections; however, a solid demarcation between cortex and core is not clear, and in some specimens, ISFB dominates throughout (Fig. 4G, H). The primary bone in all osteoderms is composed of ISFB (Fig. 4E–J). Burns (2008) sectioned a fragmentary medial cervical osteoderm from SMP VP-1580 (Morphotype F). This specimen has a compact external cortex (dominated by ISFB) and trabecular core, but lacks a basal cortex.

**Sauropelta**—A skeleton of Sauropelta (AMNH 3036) is among the most complete nodosaur specimen known and preserves a complete series of articulated osteoderms (Carpenter, 1984). AMNH 3035 completes the cervical series and has a partial skull. Each of the three half rings has two paired osteoderms: medial and lateral. Medial osteoderms are oval with rounded posterior apices. Lateral osteoderms are specialized as transversely elongate triangular spines that project posterolaterally, each with a sharp keel. A larger lateral thoracic spine posterior to the half rings matches this morphology. Thoracic and caudal osteoderms resemble medial elements of the half rings but are more circular. Apices on these osteoderms become taller in lateral and distal elements. Pelvic osteoderms are also circular.

Two osteoderms from a specimen of Sauropelta (DMNH 18206) were sectioned by Hayashi et al. (2010:fig. 6). One is keeled, whereas the other, smaller (roughly one-quarter the size) osteoderm is circular with an offset apex. Both have uniform, pitted, rugose surfaces and sparse, reticulate patterns of neurovascular grooves. The base is concave in each. Also, neither specimen has a basal cortex; the thick (86 ± 3%) trabecular core is instead exposed at the base. The external cortex is, by contrast, well developed, of average thickness (14 ± 3%), and is largely composed of azonal ISFB. Secondary osteons are found at the boundary between cortex and core; there are also several, however, near the base. Structural fibers are dense in the external cortex and arranged either perpendicular or parallel to the surface (Hayashi et al., 2010:fig. 6).

**Nodosauridae Indet**—TMP 1967.10.29 is an isolated, keeled nodosaurid osteoderm from the Upper Cretaceous Dinosaur Park Formation, Alberta, Canada, that was sectioned by Scheyer and Sander (2004:fig. 6). It is circular with an offset apex. The external cortex (8%) is composed of ISFB. Structural fibers in this region are dense and arranged in two sets of orthogonal meshworks set at 45° to one another. The trabecular core is thick (92%). Scattered secondary osteons are also found more basally in the external cortex (Scheyer and Sander, 2004:fig. 6).

**Ankylosauridae**

**Ankylosaurus**—There are few specimens of Ankylosaurus (Carpenter, 2004); therefore, none were available for thin sectioning. Osteoderms of this taxon are smooth and each has a distinctive pattern of prominent but sparse neurovascular grooves. The size and depth of each groove approach the texture seen on many ceratopsian frill and craniofacial bones. Most of the osteoderms are flat, and only a few have low keels near the lateral margins. Others include median keeled and flat circular osteoderms (Carpenter, 2004:figs. 19, 20).

**Nodocephalosaurus**—SMP VP-2067 (Fig. 5) is a referred specimen that was found near the same locality and at the
same stratigraphic horizon as other specimens referred to *Nodocephalosaurus* (Sullivan and Fowler, 2006). Being a fragment, the overall shape is unknown. The external surface texture has uniformly distributed, projecting rugosities, and sparse distribution of reticular neurovascular grooves. Neurovascular foramina penetrate the surface normally to obliquely. The external (13%; Fig. 5E, F) and basal (8%; Fig. 5I, J) cortices are thin and composed of ISFB. The thick cortex (79%; Fig. 5G, H) is composed of a mixture of trabecular (identified by larger resorption cavities) and Haversian (identified by accumulations of secondary osteons) bones but also includes some interstitial primary ISFB.

**Euoplocephalus**—Osteoderms assigned to *Euoplocephalus tutus* (Lambe, 1910) are the most variable of any ankylosaur taxon. This is likely attributable to various sources, but primarily includes taxonomic differences (Carpenter, 1982; Penkalski, 2001, in press; Arbour et al., 2009; Penkalski and Blows, 2012; Arbour and Currie, 2013). Most of the information on the arrangement of osteoderms across the body in *Euoplocephalus* is actually from the holotypes of *Dyoplosaurus acutosquameus* (Kirkland, 1998; Scheyer and Sander, 2004:fig. 8C, D). The external surface texture is smooth and lacks neurovascular grooves and foramina. The base is flat. The external (7%) and basal (11%) cortices are relatively thin and consist of ISFB. Few secondary osteons are scattered throughout the cortex, but are concentrated near the border with the core. The core (82%) is trabecular. Structural fibers are dense throughout the cortices and exhibit an orthogonal arrangement.

**Gastonia**—Two cervical half rings of *Gastonia* have triangular plates distally, although no complete or articulated half rings have been described. Posteriorly, *Gastonia* possesses the same osteoderm morphologies as seen in *Gargoyleosaurus*. Osteoderms in the pelvic region are similarly fused into a continuous shield (Kirkland, 1998; Arbour et al., 2011). Unique to the taxon are elongate, keeled spines that twist ~90° towards their apex (Kirkland, 1998).

Three specimens from DMNH 53206 were collected from a monospecific bone bed assemblage and, as such, can be confidently assigned to *Gastonia* (they are labeled A, B, and C for convenience). DMNH 53206 A is a lateral or distal spine, whereas DMNH 53206 B (Fig. 7A, B) and DMNH 53206 C are both circular osteoderms with central apices. Each of the three specimens is characterized by a smooth external surface texture and a lack of neurovascular grooves and foramina. DMNH 53206 A possesses a thin (3 ± 3%) compact cortex. The thick (92%) core is composed of trabecular bone. The few osteons preserved in the cortex are secondary. The other two osteoderms also have trabecular cores (60 ± 15%); however, the cortices are relatively thicker (14 ± 10%) in both DMNH 53206 B and C to the point where the cores are pinched out laterally. The cortices in each are composed of orthogonally arranged structural fibers. A single neurovascular foramen is visible near the margins of each ossicle.

**Pinacosaurus**—Scheyer and Sander (2004) sectioned an osteoderm fragment from *Pinacosaurus grangeri* (ZPAL MgD-II/27). Its overall morphology cannot be determined, but the surface is smooth, lacking neurovascular foramina and grooves. The external (6%) and basal (17%) cortices are compact. The core (77%) is largely composed of trabecular bone, although Haversian bone does occur at the junction of the core and the cortices. Structural fibers are extensive throughout the osteoderm (Scheyer and Sander, 2004:fig. 8C, D).

**Other Ankylosaurs**

**Gargoyleosaurus**—Two cervical half rings of *Gargoyleosaurus* are composed of six partially fused, paired, keeled osteoderms (an unfused median osteoderm had been reported by Kilbourne and Carpenter [2005], but is reinterpreted here as one of a pair of medial osteoderms because an odd number of osteoderms is unknown in any thyreophoran cervical half ring). Flat and keeled oval osteoderms characterize the thoracic region. Laterally, osteoderms of this region become elongate and triangular with excavated bases. Pelvic osteoderms have flat to apical circular morphologies. Larger osteoderms are interspersed by smaller osteoderms of identical morphology and are fused to form a continuous shield covering the pelvis (Arbour et al., 2011).

One keeled osteoderm was described by Hayashi et al. (2010) and is associated with the holotype of *Gargoyleosaurus parkinsonii* (DMNH 27726). The external surface texture is smooth and lacks neurovascular grooves and foramina. The base is flat. The external (7%) and basal (11%) cortices are relatively thin and consist of ISFB. Few secondary osteons are scattered throughout the cortex, but are concentrated near the border with the core. The core (82%) is trabecular. Structural fibers are dense throughout the cortices and exhibit an orthogonal arrangement.
STATISTICAL RESULTS

There are no significant differences among any group with respect to relative core thickness (ankylosaurid/polacanthines: t = 0.64, df = 16, α = 0.05; ankylosaurid/nodosaurid: t = 1.25, df = 9, α = 0.05; polacanthine/nodosaurid: t = 0.89, df = 10, α = 0.05). A relative comparison of basal cortical thickness shows a significant difference separating nodosaurids from ankylosaurs (t = 5.80, df = 6, α = 0.05) and polacanthines (t = 4.59, df = 7, α = 0.05). Conversely, there is no difference for this comparison between ankylosaurs and polacanthines (t = 0.25, df = 12, α = 0.05). With respect to total osteoderm thickness, ankylosaurs showed a significant difference relative to nodosaurids (t = 2.24, df = 17, α = 0.05) and polacanthines (t = 2.49, df = 13, α = 0.05). There was no such difference between nodosaurids and polacanthines (t = 1.08, df = 21, α = 0.05). A plot of relative (%) osteoderm cortical thickness versus total osteoderm thickness (Fig. 8) reveals a similar logarithmic trend when comparing the thickness of the osteoderm with the ratio of cortex to overall thickness to what is observed in osteoderms of *Caiman crocodilus* (Burns et al., 2013). All three groups of ankylosaurs plot separately but show an allometric decrease in the contribution of the cortex to overall thickness as the osteoderm thickness increases. Likely due to their thinner osteoderms, ankylosaurs show no significant allometric trend in the contribution of the cortex to overall osteoderm thickness (Table 1).

FIGURE 7. Osteoderms of putative polacanthines. Transverse thin section through DMNH 53206 B (*Gastonia* sp.) in PPL (A) and XPL (B). Arrows indicate the border between the core and external cortex. Thoracic osteoderm of MWC 211 (*Mymoorapelta maysi*) in external (C) and basal (D) views (anterior is up). The thin line in C and D indicates plane of thin section in PPL (E) and XPL (F). The core in both is trabecular. External is up for thin sections. Scale bars equal 1 cm.
TABLE 1. Summary of histological measurements used in analyses arranged by group (ankylosaurid, nodosaurid, and polacanthine).

| Specimen        | Taxon                        | Histological measurements |
|-----------------|------------------------------|---------------------------|
| TMP 1985.36.218/1 | Ankylosauridae indet.       | TT 7.959 TS 0.333 Tcore 7.021 TD 0.605 TCortex 0.938 %S 4 %Core 8 %D 8 %Cortex 12 |
| TMP 1985.36.218/2 | Ankylosauridae indet.       | TT 9.579 TS 0.844 Tcore 7.89 TD 0.845 TCortex 1.689 %S 9 %Core 8 %D 9 %Cortex 18 |
| TMP 1996.75.1 A.1 | Euoplocephalus tatus        | TT 8.426 TS 0.729 Tcore 6.714 TD 0.983 TCortex 1.712 %S 9 %Core 8 %D 10 %Cortex 20 |
| TMP 1996.75.1 A.2 | Euoplocephalus tatus        | TT 10.512 TS 1.797 Tcore 8.1 TD 0.615 TCortex 2.412 %S 17 %Core 77 %D 6 %Cortex 23 |
| UALVP 31 A.1     | Euoplocephalus tatus        | TT 8.257 TS 1.947 Tcore 4.966 TD 1.614 TCortex 3.561 %S 24 %Core 57 %D 20 %Cortex 43 |
| ZPAL MgD-1/188   | Ankylosauridae indet.       | TT 12.932 TS 1.244 Tcore 10.184 TD 1.504 TCortex 2.748 %S 10 %Core 79 %D 12 %Cortex 21 |
| ZPAL MgD-II/27 A | Pinacosaurus grangeri       | TT 14.529 TS 0.802 Tcore 11.222 TD 2.505 TCortex 3.307 %S 6 %Core 77 %D 17 %Cortex 23 |
| DMNH 2452        | Edmontonia sp.              | TT 52.395 TS 7.286 Tcore 43.812 TD 1.297 TCortex 8.583 %S 14 %Core 84 %D 2 %Cortex 16 |
| DMNH 18206-1     | Sauropelta edwardsorum     | TT 39.587 TS 4.916 Tcore 34.671 TD 0.916 TCortex 4.916 %S 12 %Core 88 %D 0 %Cortex 12 |
| DMNH 18206-2     | Sauropelta edwardsorum     | TT 9.629 TS 1.588 Tcore 8.041 TD 0.841 TCortex 1.588 %S 16 %Core 84 %D 0 %Cortex 16 |
| SMP VP-1580 C.1  | Glyptodontoptela minus      | TT 10.991 TS 1.852 Tcore 9.139 TD 0.852 TCortex 1.852 %S 17 %Core 83 %D 0 %Cortex 17 |
| SMP VP-1580 D.1  | Glyptodontoptela minus      | TT 5.736 TS 0.788 Tcore 4.84 TD 0.108 TCortex 0.896 %S 14 %Core 84 %D 2 %Cortex 16 |
| SMP VP-1580 E.1  | Glyptodontoptela minus      | TT 10.826 TS 1.335 Tcore 9.491 TD 1.335 TCortex 1.335 %S 12 %Core 88 %D 0 %Cortex 12 |
| TM F 1967.10.29 | Nodosauridae indet.        | TT 32.834 TS 2.483 Tcore 30.351 TD 2.483 TCortex 2.483 %S 8 %Core 92 %D 0 %Cortex 8 |
| TMP 1987.113.4 A.1 | Ankylosauridae indet.     | TT 11.931 TS 4.317 Tcore 7.614 TD 4.317 TCortex 3.64 %S 64 %Core 0 %D 36 %Cortex 36 |
| TMP 1998.98.1 A.2 | Ankylosauridae indet.     | TT 6.633 TS 3.398 Tcore 2.38 TD 0.855 TCortex 4.253 %S 51 %Core 36 %D 13 %Cortex 64 |
| NHMUK R9293 1   | Polacanthus foxii          | TT 13.533 TS 1.956 Tcore 9.696 TD 1.881 TCortex 3.837 %S 14 %Core 72 %D 14 %Cortex 28 |
| DMNH 27726      | Gargasorella parkipini     | TT 18.661 TS 1.306 Tcore 15.306 TD 2.049 TCortex 3.355 %S 7 %Core 82 %D 11 %Cortex 18 |
| DMNH 49754-1    | Gastonia sp.               | TT 20.154 TS 2.193 Tcore 16.66 TD 1.301 TCortex 3.494 %S 11 %Core 83 %D 6 %Cortex 17 |
| DMNH 53206 A.1  | Gastonia sp.               | TT 17.236 TS 0.912 Tcore 15.911 TD 0.177 TCortex 1.325 %S 5 %Core 92 %D 1 %Cortex 8 |
| DMNH 53206 B.1  | Gastonia sp.               | TT 8.253 TS 1.181 Tcore 5.799 TD 1.273 TCortex 2.454 %S 14 %Core 70 %D 15 %Cortex 30 |
| DMNH 53206 C.1  | Gastonia sp.               | TT 5.687 TS 1.493 Tcore 2.798 TD 1.396 TCortex 2.889 %S 26 %Core 49 %D 25 %Cortex 51 |
| IPB R481        | Gastonia sp.               | TT 14.924 TS 3.322 Tcore 10.201 TD 1.401 TCortex 4.723 %S 22 %Core 68 %D 9 %Cortex 32 |
| MWC 210 A.1     | Mymooarpetla maysi         | TT 6.764 TS 2.101 Tcore 3.384 TD 1.279 TCortex 3.38 %S 31 %Core 50 %D 19 %Cortex 50 |

All measurements are in mm. Relative thicknesses are presented as a percentage of total osteoderm thickness. Abbreviations: %Core, relative core thickness; %Cortex, relative thickness of the overall cortex; %D, relative deep cortical thickness; %S, relative superficial cortical thickness; Tcore, total core thickness; TD, total deep cortical thickness; TS, total superficial cortical thickness; TT, total osteoderm thickness.

The second search (Fig. 9B) for this set used 91 combined cranial, postcranial, and osteoderm characters (78 parsimony informative) and returned six MPTs (TL = 199, CI = 0.538, RI = 0.687). The addition of osteodermal characters has little effect on resolution but increases overall branch support for all major clades, including a sister-group relationship of Shamosaurus scutatus Tumanova, 1983, and Tsagantegia longicranials Tumanova, 1993. Pinacosaurus is moderately supported as monophyletic in the first search. In the second, Edmontonia and Pinacosaurus are well supported as monophyletic genera, and the Nodosauridae is moderately supported as monophyletic. The addition of osteodermal characters creates a clade including Sauropelta and Silvisaurus condrai Eaton, 1960. The basal position of Gargoylesaurus is not supported by osteodermal characters, and its relationship to either Nodosauridae or Ankylosauridae is ambiguous.

Test Set 2

The first search using Test Set 2 (Fig. 9C) examined 38 characters (33 parsimony informative) and returned four MPTs (TL = 117, CI = 0.628, RI = 0.702). In this test, the addition of osteodermal characters increases resolution at the expense of overall branch support. Low taxonomic and character sampling likely plays a role and the osteodermal characters reveal affinities more readily than in Test Set 1. Without osteodermal characters,
FIGURE 9. Effects of the addition of osteodermal characters into existing hypotheses of ankylosaurian phylogeny. A, Test 1 included 63 cranial and postcranial characters (57 parsimony informative) from Hill et al. (2003) and Vickaryous et al. (2004) and returned 20 MPTs (TL = 149, CI = 0.480, RI = 0.672). B, the addition of osteodermal characters created a matrix of 91 (78 parsimony informative) and returned six MPTs (TL = 199, CI = 0.538, RI = 0.687). C, Test 2 included 38 characters (33 parsimony informative) from Kirkland (1998) and returned four MPTs (TL = 62, CI = 0.729, RI = 0.846). D, the addition of osteodermal data created a matrix of 66 characters (50 parsimony informative) returned 12 MPTs (TL = 117, CI = 0.628, RI = 0.702). Fifty percent majority rule consensus trees presented. Support values above branch are majority rule percentages and Bremer support values. Those below are bootstrap and jackknife support. Blanks indicate Bremer support below 1 and bootstrap/jackknife support below 50. Higher taxa listed to left of trees correspond to nodes indicated by black circles.
the positions of Minmi, Mymoorapelta, and Shamosaurus are unresolved. Including these characters recovers Minmi as a basal ankylosaur. Shamosaurus is the most basal ankylosaurid, with Mymoorapelta nested deeper, as sister to the clade Polacanthinae + Ankylosaurinae.

DISCUSSION

Osteodermal Characters

Most unmodified ankylosaur postcranial osteoderms possess external cortices that are distinguishable from the cores, and have structural fibers in at least part of the osteoderms. Mature nodosaur osteoderms can be distinguished from those of other ankylosaurs on the basis of poorly developed or absent basal cortices. Most of the larger osteoderms examined have trabecular cores, but a few exhibit more compact cores, consisting of a mixture of primary ISFB bone, scattered osteons, and resorption cavities. Likewise, an external cortex dominated by ISFB is common. This layer is complete with a dense pattern of orthogonal structural fibers, as demonstrated by Scheyer and Sander (2004) and Hayashi et al. (2010). Ankylosaurid osteoderms, on average, are thinner than those of other ankylosaurs. Some possess compact Haversian bone in their cores, whereas in others this layer has been remodeled into trabecular bone.

Oscicles—The histology of interstitial oscicles is variable, even within a single individual, although they do have some patterns. They are predominantly composed of primary ISFB arranged in orthogonal patterns. Although a radial pattern of structural fibers has been reported for Antarctopelta (de Ricqlès et al., 2001), such was not observed in the taxa sampled here. It is possible that oscicles represent different stages of osteoderm development. In addition, these elements show no consistent histological differences between ankylosaurs and nodosaurus. Both specimens examined (TMP 1998.98.1 and UALVP 31) show predominantly compact ISFB and strong marginal zonation. Oscicles may represent incipient osteoderms that stopped mineralizing before reaching maturity, or they may be developmentally distinct from larger body osteoderms. Either way, because they do not exhibit the taxon-specific characters seen in the larger osteoderms, they provide no taxonomic information.

Specialized versus Unmodified Osteoderms—Hayashi et al. (2010) examined specialized osteoderms. They concluded that spines and clubs maintain the same characteristic features for their respective clades despite the differences in sizes and morphologies. This study came to the opposite conclusion—specialized osteoderms have a correspondingly modified histology. This is supported by evidence from extant Caiman osteoderms, in which even relatively minor changes in shape can produce significant changes in histology even in a single individual (Burns et al., 2013). Polacanthine and nodosaur spines exhibit lower relative cortical thicknesses than unmodified osteoderms. In ankylosaurs, although the unmodified body osteoderms may be relatively thin and have cores composed of Haversian bone, those of the tail club knob are thick and have trabecular cores (Arbour, 2009; Hayashi et al., 2010:fig. 10). Therefore, osteoderms that are specialized to perform specific functions for their respective clades may be distinguished in terms of their histology, although their histology may be taxonomically uninformative.

Structural Fibers—The presence, density, and arrangement of mineralized structural fibers have been previously identified by Scheyer and Sander (2004) as characteristic of three distinct ankylosaur groups. Their conclusions are supported here. In nodosaurs, there are alternating three-dimensional layers of structural fibers in the external cortex: one with fibers arranged parallel and perpendicular to the surface, and one with fibers arranged 45°. Ankylosaurs also possess structural fibers in the cortex that insert perpendicularly into the osteoderms, but become more diffuse in the core because they are generally remodeled to form secondary bone. Whereas fibers in the core are randomly distributed in polacanthines, they attain a more regular arrangement near the margins, although they are not as highly organized as in nodosaurs.

Cortical Relationships—The distinction of ankylosaurs and polacanthines based on the relative development (thickness) of the cortex (Scheyer and Sander, 2004) is not supported here. Statistical tests show that there is significant overlap in the overall thicknesses of the cortices. In nodosaurs, the basal cortex contributes little to the overall osteoderm thickness or is absent entirely. This is consistent with the findings of Scheyer and Sander (2004) and Hayashi et al. (2010). When present, this cortical layer is made up of ISFB. Because this represents a significant difference between nodosaurs and all other ankylosaurs, it is treated here as a synapomorphy for the group.

Core Histology—There is more overlap in core histology than previously suggested. Scheyer and Sander (2004) distinguished ankylosaur osteoderms based on a Haversian core. Hayashi et al. (2010), on the other hand, identified trabecular cores in ankylosaurs, in one case examining the same thin section (TMP 1985.36.218/1) as Scheyer and Sander (2004). The discrepancy is here attributed to the highly vascular nature of the compact bone in ankylosaur osteoderms and their random arrangement of Haversian canals, supporting the interpretation of Scheyer and Sander (2004). A mixture of histologies is found in ankylosaur osteoderms—whereas some are Haversian, others are composed of trabecular bone. This may be based on the fact that core histology is more dependent on osteoderm shape, function, and/or osteogeny than on taxonomic position. Nodosaural, although their cores are largely trabecular, can have compact cortical bone present as in some of the osteoderms known from Edmontonia and Glyptodontopelta. Only the polacanthines exhibited a consistent trabecular core histology. Therefore, the retention of compact bone in the osteoderm core is a characteristic of derived nodosaurs and ankylosaurs. Due to the overlap among these higher taxa, however, it is not a basis on which to distinguish ankylosaur groups.

Osteoderm Thickness—Osteoderms of ankylosaurs have often been described as “thin-walled” or having “excavated” bases (Coombs, 1971). These terms have been alternately considered diagnostic (Coombs, 1971) or as subjective assessments, with too much overlap with other taxa to be of real value (Burns, 2008). The sample of ankylosaur osteoderms examined here is significantly thinner than the nodosaur osteoderms. Whereas the polacanthine osteoderms were also found to be significantly thicker than the ankylosaur osteoderms, our analyses do not include distal polacanthine spines. Therefore, little confidence can be placed in this difference between ankylosaurs and polacanthines at present.

External Surface Texture—Burns (2008) differentiated North American ankylosaurs and nodosaurs at the species level based on the textures of the external osteoderm surfaces. The increased sample size in this study shows that there is more overlap among these textures than previously suggested, and only a few derived taxa may be distinguished based on this character alone. Polacanthine osteoderms are consistently smooth and lack (for the most part) neurovascular grooves and foramina. Nodosaural may have smooth or uniformly pitted osteoderms and can develop reticular patterns of neurovascular grooves and foramina. As an autapomorphy, Glyptodontopelta has a dense pattern of neurovascular grooves, as opposed to the sparse patterns seen in other nodosaurs. Ankylosaurs may also retain smooth osteoderms but can develop strongly projecting surface rugosities. This distinguishing feature of Nodoscelphalus may represent a taxonomic difference, or variation in epidermal covering. In
addition, the characteristic pattern of prominent yet sparse neurovascular grooves in *Ankylosaurus* (Burns, 2008) is supported as an autapomorphy for the genus.

**Osteoderm Development**

Osteoderm growth in ankylosaurs is far from understood. In the absence of a growth series for any member of the *Ankylosauria* (let alone a complete series with associated osteoderms), comparative material must be relied on to hypothesize the mode(s) of osteoderm skeletogenesis. In crocodilians, osteoderms develop via the direct transformation of preexisting dense irregular connective tissue in the dermis (= tissue metaplasia; Vickaryous and Hall, 2008). Evidence of extensive mineralized inclusions from the dermis suggests that that is also the case in the osteoderms of ankylosaurs. Their high level of organization in the fully mineralized osteoderm is indicative of the preexisting organization of collagen bundles within the dermis, likely the stratum compactum, prior to metaplastic mineralization (Moss, 1972; Scheyer et al., 2007; Vickaryous and Hall, 2008; Sire et al., 2009; Cerda and Powell, 2010).

Ankylosaur osteoderms also have delayed onset of skeletogenesis relative to the remainder of the body skeleton, as is the case in *Stegosaurus* (Hayashi et al., 2009). Modern archosaurs also exhibit this delay (Vickaryous and Hall, 2008), their osteoderms appearing only well after hatching. Juvenile ankylosaurs (i.e., *Pinacosaurus*; Burns et al., 2011) do not have osteoderms posterior to the cervical half rings. It is presumed, therefore, that their osteoderms similarly have delayed skeletogenesis as in other saurispid groups.

**Ankylosaur Integument**

Osteoderms, prior to bone remodeling if it occurs, represent mineralization of soft tissue, and in essence are an in vivo mineralization of the dermis of an animal (Moss, 1969; Moss, 1972). Therefore, these structures present unique opportunities to study the soft-tissue histology of extinct organisms. Tetrapod osteoderms primordially share a common site of origin at the interface between the stratum superficiale and stratum compactum in the dermis (Vickaryous and Sire, 2009). In some cases, the osteoderm may extend into the stratum compactum itself. Given the densities of structural fibers in ankylosaur osteoderms, there is a relatively greater contribution from the stratum compactum. This is in marked contrast to the situation in osteoderm-bearing crown members of the Archosauria. Crocodilian osteoderms are localized in the stratum superficiale, and only the most basal margins may contact the stratum compactum (Martill et al., 2000; Salisbury and Frey, 2000; Vickaryous and Hall, 2008; Vickaryous and Sire, 2009). It is possible that the stratum compactum is relatively thick in ankylosaurs (and possibly other dinosaurs). Based on the largest dinosaur osteoderms, which belong to titanosaurid sauropods, the thickness of dermis is likely more than twice that of modern elephants (Haynes, 1991; Dodson et al., 1998).

Although there is some variation in surface textures, all of the specimens in this study can be best interpreted as having cornified sheathes as described by Hieronymus et al. (2009). This suggests that whereas there would have been some soft dermal/epidermal component covering the osteoderm, it was relatively minor compared with the keratinized structure overlaying it. In extant correlates (e.g., bovid horns), the bony attachments of these structures are characterized by densely concentrated metaplastic dermal collagen fibers. These fibers also interact obliquely with the bone surface and may approach an orthogonally arranged network.

**Homology and Evolution**

Most osteoderm-bearing archosaurs share a common primitive osteoderm histology: (1) a periodically growing external cortex of compact bone with numerous collagen fibers, and (2) a central core of trabecular bone demonstrating evidence of localized resorption and secondary remodeling (Enlow and Brown, 1957; Moss, 1969; Martill et al., 2000; de Ricqlès et al., 2001; Barrett et al., 2002; Scheyer and Sander, 2004; Main et al., 2005; Hall and Lucas, 2006; Vickaryous and Sire, 2009; but, for exceptions, see Cerda and Powell, 2010; Cerda and Desojo, 2011; Scheyer and Desojo, 2011).

The histological condition in *Scelidosaurus* can be considered as the basal condition for the *Ankylosauria* because *Scelidosaurus* is likely the sister to all ankylosaurs (Carpenter, 2001). These osteoderms also exhibit histologies that ally them with the basal archosaurian condition with a circumferential cortex enclosing a trabecular core (Vickaryous and Sire, 2009). In most other osteoderm-bearing archosaurian lineages (aetosaurs, crocodylomorphs, parasuchians, etc.), a conservative yet distinct pattern of external pitting is common. In the most basal thyreophorans, this is not the case. Instead, the surfaces of the osteoderms are relatively smooth. This smooth texturing is retained in polacanthines, whereas the pattern diverges in derived ankylosaurids and nodosaurids.

Histological similarities among ankylosaur osteoderms from each of the three groups examined indicate similar development and evolution, as hypothesized by Hayashi et al. (2010). However, morphologically distinct (specialized) osteoderms were elaborated by modification of the external morphology and internal histology (contra Hayashi et al., 2010). Primitive, basal thyreophorans lack extensive structural fibers in their osteoderm cortices (de Buffrénil et al., 1986; Scheyer and Sander 2004; Main et al., 2005; Hayashi et al., 2009, 2010). Hayashi et al. (2010) concluded that the presence of such systems in ankylosaurs indicates that either their osteoderms evolved differently or their skin differed from that of other thyreophorans. This study lends support to the former hypothesis because it demonstrates that the integument does not need to be different in order to produce these divergent histologies. It is likely that greater contributions from the dense connective tissues of the stratum compactum were involved in osteoderm skeletogenesis. Therefore, ankylosaurs utilized different developmental pathways to achieve the diversity observed in their osteoderms.

**Phylogenetic Tests**

Overall, the inclusion of osteodermal characters into phylogenetic analyses of the *Ankylosauria* can increase branch support and/or resolution, depending upon taxonomic sampling. In Test Set 2, inclusion of osteodermal characters retains a monophyletic Polacanthinae within *Ankylosauridae*; however, it reduces branch support for the clade. This may be caused by an affinity of *Mymoorapelta* to the Polacanthinae, as suggested by Kirkland (1998) based on osteodermal characters. An affinity of *Shamosaurus* to *Tsagantegia* is also recovered in Test Set 2. This is supported in Test Set 1 by the recovery of *Shamosaurus + Tsagantegia*, a clade for which osteodermal characters increased branch support. This demonstrates support for Shamosaurinae and Polacanthinae based on cranial/postcranial and osteodermal characters. The inclusion of *Mymoorapelta* in the Polacanthinae is also plausible, but will require further data. These tests do not suggest a nodosaurid affinity for the Polacanthinae in contrast with the results of Thompson et al. (2012), which included more taxa and recovered polacanthines as a grade of basal nodosaurids. That analysis examined more taxa and characters than those used here, but included only 16% osteodermal characters, compared with 31% and 42% (Test Sets 1 and 2, respectively) here.
Cranial characters have been utilized in systematic studies of the Ankylosauria and have proven to be informative (Hill et al., 2003; Vickaryous et al., 2004). The postcrania and osteoderms, however, have received relatively little attention. This study demonstrates that major anatomical systems besides the cranium are useful in systematic studies of ankylosaurs. A combination of cranial characters, the osteodermal characters identified herein, and a new suite of postcranial characters should be included in such a study.

CONCLUSIONS

Osteoderm morphology is systematically useful at the familial, generic, and specific levels. The lateral cervical and thoracic spines of nodosaurids are supported as valid taxonomic indicators for that clade. Absolute osteoderm thickness is a useful character for distinguishing between nodosaurids and ankylosaurids, the latter of which have thinner osteoderms. Polacanthine ankylosaurs share a mixture of primitive and derived characters, including lateral spines (shared with nodosaurids) and basally excavated, dorsoventrally compressed triangular distal osteoderms (shared with ankylosaurs).

The histology of an ankylosaur osteoderm is somewhat dependent on the specific function(s) of the element itself; however, there are several characters that are useful for higher-level taxonomy. Only unmodified body osteoderms are histologically useful as familial indicators. Interstitial ossicles are histologically homogenous across ankylosaur taxa. Specialized osteoderms that perform specific functions (e.g., major tail club knob osteoderms) do not always retain the basic histology of unmodified osteoderms. The overall thickness of the cortex (absolute or relative) is a character that overlaps considerably among ankylosaurs. The retention of compact bone in the core of the osteoderm is characteristic of derived nodosaurids and ankylosaurs; however, it is not a basis on which to distinguish ankylosaur groups due to overlap among disparate taxa. An osteoderm that retains a compact core can be positively identified only as belonging to a derived taxon. The basal cortex of a nodosaurid osteoderm is generally absent or poorly developed. Structural fiber arrangement is also a useful character. Nodosaurids have two-three-dimensional sets of these fibers in the external cortex. Ankylosaursids have perpendicularly inserting fibers in the cortices of their osteoderms, but they become more diffuse in the core. Fibers can have a more regular arrangement near the margins in a polacanthine osteoderm.

The external surface textures of ankylosaur osteoderms exhibit more variability than previously thought. Nonetheless, certain textures are observable only in certain taxa, and can be considered autapomorphic for them. The primitive thyracoparian superficial condition (also retained in primitive ankylosaurs) is that of relatively smooth osteoderms, with only isolated patches or sparsely distributed rugosities, foramina, or grooves. A relatively smooth surface coupled with dense reticular neurovascular grooves is diagnostic for the nodosaurid Glyptodontoptopelta. Smooth osteoderms with sparse but prominent neurovascular grooves are characteristic of Ankylosaurus. Based on bone surface textures in extant osteoderms, ankylosaurs likely had a relatively thick, keratinized sheath covering each osteoderm, similar to the condition in the modern horn of a bovid.

Our data support the interpretation of Scheyer and Sander (2004) that evidence of extensive mineralized inclusions from the stratum compactum indicates that direct metaplasia is responsible for osteoderm development in ankylosaurs; it had a greater role than in other taxa such as crocodilians. Given their structure, ankylosaur osteoderms are optimized towards a primary protective function. The osteoderms of crocodilians may not have a primary protective function, and their lack of mineralized structural fibers corroborates this. Despite this, examination of other extant and extinct taxa reveals that a single, panoptic function for the osteoderms of a species or group is rarely a feasible hypothesis. Therefore, this study cannot reject the possibility of other, secondary osteoderm functions for ankylosaurs. These may include thermoregulation, or intra- and interspecific display.

Exception for bones of the dermatocranium, the dermal skeleton (and the integument in general) is a major anatomical system that has been historically underrepresented in the morphological systematics of vertebrates. This study supports the conclusion of Hill (2005), that this system does provide meaningful character data. Far from homogenous elements, ankylosaur osteoderms were physiologically active tissues that were morphologically and histologically optimized for specific functional roles.

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