Although we humans cut nature up in different ways, and we have different courses in different departments, such compartmentalization is really artificial.

Richard Feynman

University of Alberta

External and internal structure of ankylosaur (Dinosauria; Ornithischia) osteoderms

by

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This thesis is dedicated to to all the members of my family, who have, over the years, financed my career with much more than just finances.

Abstract

Here I assess the use of osteoderms in systematics with comparative material from fossil and extant tetrapod taxa. Putative differences among three groups (ankylosaurid, nodosaurid, and polacanthid) were evaluated. Archosaur osteoderms have cortices surrounding a cancellous core. Ankylosaurs are united by a superficial cortex distinguishable from the core, lack of Sharpey's fibers, and mineralized structural fibers. Nododsaurids lack a deep cortex and have dense superficial cortical fibres. Ankylosaurid osteoderms are thinner than those of other ankylosaurs. Polacanthids (and some nodosaurids and ankylosaurids) have a cancellous core. Cortical thickness overlaps among groups, so a thick cortex is not diagnostic for polacanthids. Modified elements diverge histologically from the primitive condition for specific functions. Haversian bone in the core is not indicative of any group. Some shapes and superficial textures are diagnostic for specific taxa. Parsimony analyses show support for the Ankylosauridae and Nodosauridae, but not a monophyletic polacanthid clade.

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Institutional Abbreviations

AMNH – American Museum of Natural History, New York, New York, USA

BMNH – British Museum of Natural History, London, England

CCM – Carter County Museum, Ekalaka, Montana, USA

CMN – Canadian Museum of Nature, Ottawa, Ontario, Canada

IGM – Institute of Geology, Ulaanbaatar, Mongolia

IMM – Inner Mongolia Museum, Hohhot, Inner Mongolia, PRC

IPB – Goldfuss-Museum, Institute of Paleontology, University of Bonn, Bonn, Germany

MPC – Geological Institute, Section of Palaeontology and Stratigraphy, Academy of Sciences of the Mongolian People's Republic, Ulaanbataar, Mongolia (KID: Korea-Mongolia International Dinosaur Project Collection; PJC: Nomadic Expeditions Collection)

MWC – Museum of Western Colorado

PIN – Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia

ROM – Royal Ontario Museum, Toronto, Ontario, Canada

SMP – State Museum of Pennsylvania, Harrisburg, Pennsylvania, USA.

TMP – Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada

UALVP – University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada

USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

ZPAL – Zoological Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other Abbreviations

CI – Consistency index

Fm – Formation

LAG – Line of arrested growth

Mbr – Member

MPT – Most parsimonious tree

PPL – Plane polarized light

RI – Retention index

TL – Tree length

XPL – Cross polarized light

Chapter 1 Introduction

1.1 Introduction

Two distinct skeletal systems are recognized amongst vertebrates. The endoskeleton is situated deep in the body (i.e. deep to striated musculature), forming from the embryonic mesenchyme. First formed as a cartilaginous precursor, this system is associated with periosteal/perichondral and endochondral ossification when bone is formed later in ontogeny. Conversely, the dermal skeleton (=exoskeleton, dermoskeleton *sensu* Francillon-Vieillot et al., 1990) is derived from the embryonic dermatome mesenchyme and neural crest. This skeletal system is actually more primitive than the vertebrate endoskeleton and was dominant in many early gnathostomes (Sire et al., 2009). Among more deeply nested lineages, tetrapods in particular, this dermal skeleton has undergone widespread reduction and/or modification (Moss, 1972; Krejsa, 1979; Zylberberg et al., 1992). The resulting osteoderm systems in tertrapods are highly variable in terms of morphology and histology (Goodrich, 1907; Francillon-Vieillot et al., 1990; Zylberberg et al. 1992; Sire & Huysseune, 2003; Vickaryous and Sire, 2009).

The ankylosaurs are a group of dinosaurs known, in part, for their extensive system of osteoderms, composed of individual osteoderms that vary in size and shape and cover the skull and most of the body. Although known for over 175 years, these animals are still poorly understood. The morphology of their osteoderms varies in patterns, body distribution and external sculpturing. Thus, the osteoderms of ankylosaurids and nodosaurids present a host of problems in deciphering cranial features, taxonomic identification, and conducting phylogenetic analyses.

1.2 Systematic History of the Ankylosauria and Osteoderm Characters

Ankylosauria (Fig. 1.1) is generally divided into Ankylosauridae and Nodosauridae (Coombs, 1971; 1978). Some argue for the existence of a third family, the Polacanthidae (Carpenter, 2001)–or, at times, the subfamily Polacanthinae, nested in the family Ankylosauridae) (Kirkland, 1998)–both of which encompass some of what are generally considered basal ankylosaurids. The phylogenetic and taxonomic status of many ankylosaur taxa remains in limbo. In any case, the most arresting unambiguous synapomorphy of the Ankylosauria is the pervasion of a pattern of osteoderms across the entirety of the body, especially on the dorsal surface (Vickaryous et al., 2004).

Over 35 years ago, Walter Coombs (1971) wrote that “[d]ermal armor is perhaps the [most] frequently encountered fossil material of the Ankylosauria, and consequently a great deal of ink has been spilt describing individual plates.” He did, however, note some differences between nodosaurids and ankylosaurids, as well as accurately detail the basic layout of osteoderms across the body. He noted that the osteoderms were arranged in transverse “rows” down the length of the body (“rows” will herein refer to the parasaggital arrangement of osteoderms and “bands” will refer to their transverse arrangement). According to Coombs (1971), isolated osteoderms from ankylosaurids generally exhibit excavated deep surfaces, whereas those of nodosaurids are relatively thick and displayed flat deep surfaces. Also, tall, solid, conical spines (at least twice as tall as the greatest diameter) were observed only in nodosaurids (although some spines from *Hylaeosaurus* and *Sauropelta* were deemed almost indistinguishable from stegosaur caudal spikes).

Combs (1971) also noted marked differences in the cervical half rings of ankylosaurids and those of nodosaurids. It is here necessary to note that ankylosaur osteoderms can be differentiated into distinct body regions: cervical, thoracic, pelvic, and caudal (Blows, 2001; Burns, 2008). In ankylosaurids, the osteoderms of the cervical half rings are generally oval and well-separated from one another, whereas those of nodosaurids are generally rectangular and abut, often fusing with, one another (Coombs, 1971). Finally, over the pelvic region, fusion of the osteoderms can sometimes form a buckler, which presented no taxonomic importance to Coombs (1971). Others have disagreed with this assessment of the pelvic buckler, arguing that it is in fact a distinguishing characteristic of the Polacanthidae (Blows, 2001; Carpenter, 2001).

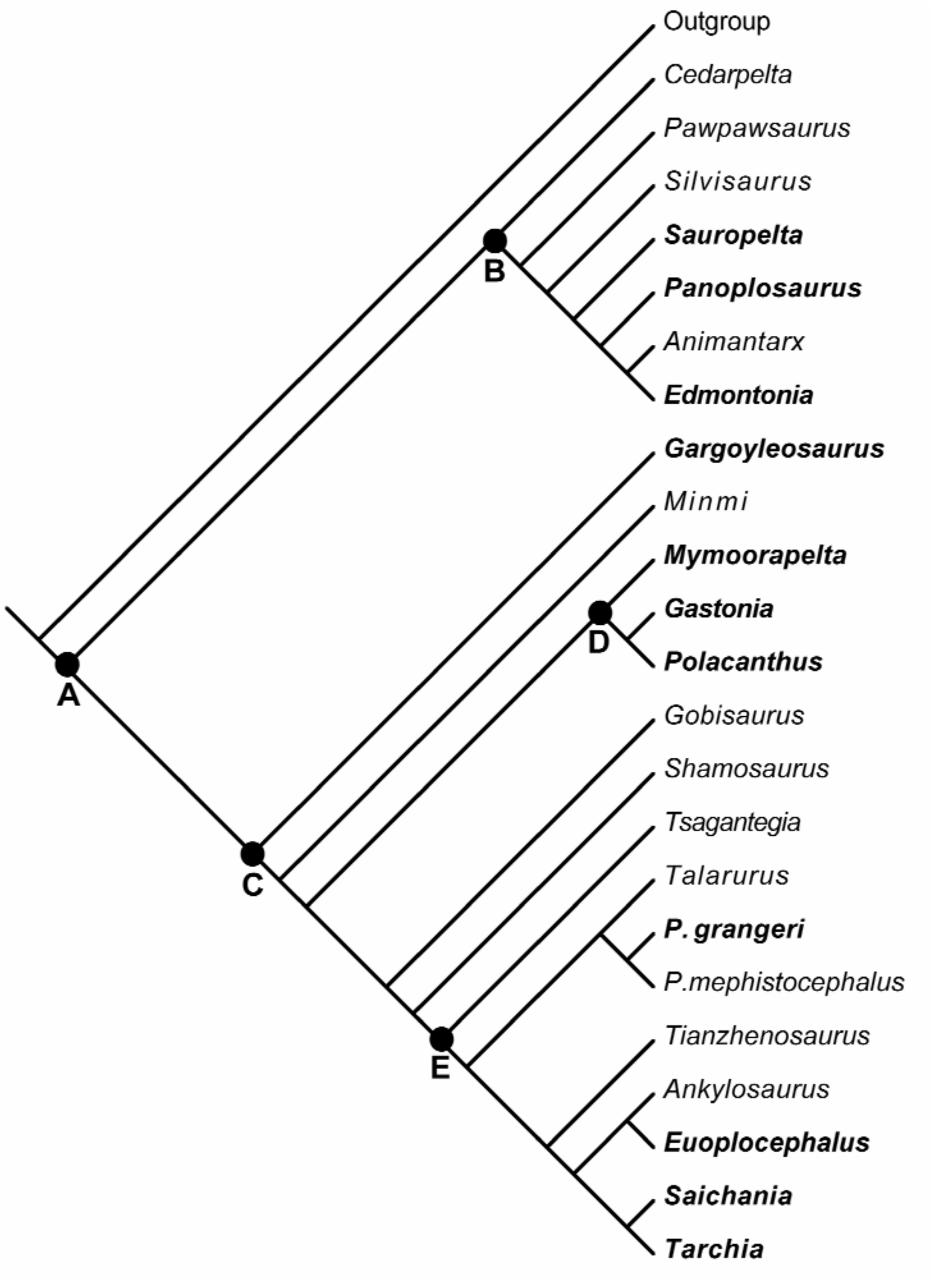


FIGURE 1.1. Supertree of the Ankylosauria showing one possible arrangement of ankylosaur relationships. Majority rule consensus of 63 MPTs (TL=85, CI=0.694, RI=0.887) found via heuristic and branch and bound searches of 59 characters derived from the trees of Kirkland (1998), Carpenter (2001), Hill et al. (2003), and Vickaryous et al. (2004). Taxa examined histologically in this study are in bold. Nodes are as follows: **A**, Ankylosauria; **B**, Nodosauridae; **C**, Ankylosauridae; **D**, Polacanthinae; **E**, Ankylosaurinae.

Despite great confusion in our current understanding of ankylosaur osteoderm morphology, it has historically (and recently) played a prominent role in the diagnoses of ankylosaur taxa (Coombs, 1971;

Maryańska, 1977). *Dracopelta* Galton, 1980, was identified entirely on the basis of *in situ* pelvic osteoderms (note that stratigraphic and provenance information for ankylosaur taxa discussed in this thesis is provided in Table 1.1). The North American taxa, *Edmontonia longiceps* Sternberg, 1928, *Edmontonia rugosidens* (Gilmore, 1930), and *Panoplosaurus mirus* Lambe, 1919, are in large part differentiated on the basis of osteoderm morphology and textures (Carpenter, 1990). Osteoderms contributed the primary characters in the diagnosis of *Aletopelta coombsi* Ford and Kirkland, 2001 and contributed to the clarification of the familial assignment of the taxon (Coombs and Demere, 1996; Ford and Kirkland, 2001). In a review of *Ankylosaurus*, Carpenter (2004) partially rediagnosed this name-bearing genus of the Ankylosauria using characters of the cervical half rings, osteoderm surface texture, and osteoderm keel placement. Salgado and Gasparini (2006) defined *Antarctopelta*, in part, as exhibiting at least six distinct osteoderm morphotypes. In addition to these, other examples of ankylosaurs that contain osteoderm characters in their diagnoses include *Polacanthus foxii*, *Talarurus plicatospineus* Maleev, 1952 (Maryańska, 1977), *Mymoorapelta maysi* Kirkland and Carpenter, 1994, *Gastonia burgei* Kirkland, 1998, *Gargoyleosaurus parkpinorum* Carpenter et al., 1998, *Glyptodontopelta mimus* Ford, 2000 (Burns, 2008), and *Liaoningosaurus paradoxus* Xu et al., 2001.

TABLE 1.1. Provenance and stratigraphic information for ankylosaur taxa discussed, arranged stratigraphically by earliest occurence. Data on *Glyptodontopelta* from Burns (2008), *Antarctopelta* from Salgado and Gasparini (2006), *Aletopelta* from Ford and Kirkland (2001), all others from Vickaryous et al. (2004).

Taxon	Occurrence	Stratigraphic Range
Ankylosaurus	Frenchman Fm. (SK), Hell Creek Fm. (MT), Lance Fm. (MT), Lance Fm. (WY), Scollard Fm. (BC)	late Maastrichtian (Late Cretaceous)
Glyptodontopelta	Ojo Alamo Fm. (NM)	early Maastrichtian (Late Cretaceous)
Edmontonia	Aguija Fm. (TX), Dinosaur Park Fm. (AB), Ferris Fm. (WY), Hell Creek Fm. (MT, SD), Horseshoe Canyon Fm. (AB), Judith River Fm. (MT), Lance Fm. (SD), Matanuska Fm. (AK), St. Mary River Fm. (AB), Two Medicine Fm. (MT)	Campanian–Maastrichtian (Late Cretaceous)
Tarchia	Nemegt Fm. (Mongolia)	?late Campanian–early Maastrichtian (Late Cretaceous)
Euoplocephalus	Dinosaur Park Fm. (AB), Horseshoe Canyon Fm. (AB) Two Medicine Fm. (MT),	late Campanian–early Maastrichtian (Late Cretaceous)
Aletopelta	Point Loma Fm. (CA)	late Campanian (Late Cretaceous)
Antarctopelta	Santa Maria Fm. (Antarctica)	late Campanian (Late Cretaceous)
Panoplosaurus	Dinosaur Park Fm. (AB)	late Campanian (Late Cretaceous)
Nodocephalosaurus	Kirtland Fm. (NM)	late Campanian (Late Cretaceous)
Saichania	Baruungoyot Fm. (Mongolia)	?middle Campanian (Late Cretaceous)
Pinacosaurus	Bayan mandahu Fm. (People's Republic of China), Djadokhta Fm. (Mongolia)	?late Santonian–?middle Campanian (Late Cretaceous)
Liaoningosaurus	Yixian Fm. (People's Republic of China)	Barremian (Early Cretaceous)
Polacanthus	Wessex Fm. (England), Vectis Fm. (England)	Barremian (Early Cretaceous)
Gastonia	Cedar Mountain Fm. (UT)	Berriasian–Hauterivian (Early Cretaceous)
Talarurus	Bayanshiree Fm. (Mongolia)	Cenomanian–Campanian (Late Cretaceous)
Mymoorapelta	Morrison Fm. (CO)	Kimmeridgian–Tithonian (Late Jurassic)
Gargoyleosaurus	Morrison Fm. (Wyoming)	Kimmeridgian–Tithonian (Late Jurassic)

Osteoderms have played a major role in our understanding of the higher-level taxonomy in the Ankylosauria. The tradition of categorization of all osteoderm-bearing Ornithischians into a distinct group had persisted in one form or another (with little justification or supporting evidence) until Coombs (1971) revised the Ankylosauria, prior to which the complexity of the group's classification was too daunting to be at all informative or useful. Coombs (1971) noted consistent family-level differences in ankylosaur osteoderms, including some of the characters in his diagnoses for the Ankylosauria, Ankylosauridae, and Nodosauridae. Despite this apparent utility, he stated that "for the most part, armor plates are not diagnostic" (313). In a review of Asian ankylosaurs (Maryańska, 1977), these osteoderm characters were retained in the diagnosis for the Ankylosauridae. In his review of North American nodosaurid systematics, Carpenter (1990) relied heavily on characters of osteoderm morphology and arrangement to differentiate between *Edmontonia* and *Panoplosaurus* at the generic level, and *E. longiceps* and *E. rugosidens* at the specific level.

It appears that, regardless of the early assessment of the possible utilities of ankylosaur osteoderms (Coombs, 1971), these elements have played a prominent role in the progression of how we interpret the biology and systematics of ankylosaurs. The history outlined suggests that different osteodermal characters can be useful to distinguish among ankylosaur taxa at different taxonomic levels. More recent studies have investigated the utility of external textures and other osteodermal features in more rigorous ways (Ford, 2000; Penkalski, 2001; Scheyer and Sander, 2004; Burns, 2008). Because osteoderms are the most common osteological elements from these dinosaurs, they have great potential for clarifying issues regarding ankylosaur taxonomy, ontogeny and, perhaps, even 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 properly describe osteoderms, and their variation, one must study all the specimens known that have preserved osteoderms, determine their body distribution, and see how variation is affected by body placement, ontogeny, etc. Recent research has attempted to look at osteoderms for taxonomically useful characters in external morphology (Ford, 2000; Burns, 2008). It appears that surface texture may prove to be one way in which to discriminate ankylosaur taxa (Burns, 2008). However, determining taxa based on external surface structures that vary due to growth changes (ontogeny) or those as a result of some pathology, is far from understood.

To date, there has been little published on the histology of ankylosaur osteoderms, although several recent studies are beginning to increase what we know about the internal structure of these elements. Vickaryous et al. (2001) studied *Euoplocephalus*, focusing on the histological interactions between the dermatocranium and overlying cranial osteoderms. De Ricqlés et al. (2001) analyzed postcranial ossicles from *Antarctopelta*. These authors were the first to recognize a regular organization of structural fibres in the ossicles. In addition, de Ricqlés et al. (2001) histologically discussed osteoderm skeletogenesis, suggesting that a differentiated histology indicated neoplasia rather than simple metaplasia (the latter would have resulted in a uniform distribution of structural fibres matching the parent dermis, which they did not observe). Barrett et al. (2002) briefly described the histology of osteoderms belonging to *Scelidosaurus* and *Polacanthus foxi*.

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 collagen fibers differed among three groups of ankylosaurs (ankylosaurids, polacanthids, and nodosaurids). 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. (in press) investigated specialized osteoderms (tail club osteoderms and nodosaur spines). They report that these specialized osteoderms have the same histology as those of standard dorsal osteoderms, and that three distinct groupings (ankylosaurid, nodosaurid, and polacanthids) can be distinguished.

There is evidence to suggest that osteoderm (and integument) characters are crucial to our understanding of vertebrate evolutionary relationships. A study on the phylogeny of the Amniota by Hill (2005) demonstrates the important effects of increasing both 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 and osteoderms resolve relationships that traditional anatomical characters do not, revealing phylogenetic signals that were previously obscured by incomplete taxonomic or character sampling. Despite systematic ambiguity among traditional phylogenetic analyses on the Ankylosauria (Kirkland, 1998; Carpenter, 2001; Vickaryous et al., 2004), the Thyreophora was the only ingroup clade with any resolution in parsimony analysis of 78 amniote taxa by Hill (2005).

1.3 Sources of Variation and Comparative Material

Possible sources of variation in osteoderm histology and morphology include taxonomy (the focus of this project), individual variation, sexual dimorphism, ontogeny, and pathology. Individual variation likely accounts for some of the variation observable in ankylosaur osteoderms; however, there are not many ankylosaur specimens preserving *in situ* osteoderms (or even a sizeable number of disarticulated osteoderms).Therefore, it becomes difficult to test the effects of individual variation on osteoderm morphology and histology. It seems 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., in press), we are observing real taxonomic differences. The effect of individual variation on these characters plays a minor role in our interpretations.

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 modified 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 spines in *Edmontonia rugosidens*. This interpretation of dimorphism, however, was based on three specimens, and the apparent dimorphism is just as likely caused by individual, ontogenetic, or geographical differences.

Some recent studies have investigated ontogenetic changes in various extant organisms like crocodilians and armadillos (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 ankylosaurids as well, as suggested by juvenile ankylosaur material from

Asia. Juvenile *Pinacosaurus* specimens develop ossified cervical half rings early in ontogeny, while the remaining osteoderms does not fully develop until later (Currie, pers. comm., 2008).

1.4 Project Goals

(1) Describe the internal and external morphology of osteoderms from various species level ankylosaur taxa, emphasizing specimens associated with adequate diagnostic skeletal material. Whereas several studies have investigated histological (Scheyer and Sander, 2004; Hayashi et al., in press) and surface variation (Ford, 2000; Blows, 2001; Penkalski, 2001) in ankylosaur osteoderms, only one preliminary study (Burns, 2008) has combined the two comprehensively. In addition, most studies (Scheyer and Sander, 2004; Hayashi et al., in press) 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, although an effort is made in this work to refrain from using material of indeterminate identity wherever possible.

In addition, the various surface textures for different osteoderm morphologies have been detailed for only a few ankylosaur taxa (Burns, 2008). Although surface texture is often included in the description of osteoderms, there is no standardization in terminology. Hieronymus et al. (2009) performed an extensive review of correlates between integumentary covering and histology/osteology including a convenient key for categorical variables used to describe bone surfaces. This method will be applied here in order to homogenize the categorization of ankylosaur osteoderm surface textures.

(2) Determine which characters are useful taxonomic indicators for ankylosaurs, noting at which taxonomic level(s) they are valid. As demonstrated by Hill (2005), the addition of integumentary characters into a character-taxon matrix has potential for clarifying a currently confused phylogeny for the Ankylosauria. A comprehensive survey of ankylosaur osteoderms is required to determine (quantitatively, if possible) which characters are consistent enough to be useful in the systematics of the group. Furthermore, an overview of surface texture variation in ankylosaur osteoderms (Burns, 2008) has suggested that this may provide useful diagnostic characters below the subfamily level.

(3) Incorporate these characters into a revised phylogenetic analysis of Ankylosauria to see if they increase or decrease the resolution of ankylosaur phylogeny as it is currently understood. One persistent problem in ankylosaur systematics is the status of the polacanthid-grade ankylosaurs. These animals likely occupy a position basal to both the Ankylosauridae and Nodosauridae and, thus, represent an important transition between basal thyreophorans and derived ankylosaurs. Various workers have come to different conclusions about this group, and they have been variously placed as members of a grade of primitive ankylosaurids (Vickaryous et al., 2004), members of the ankylosaurid subfamily Polacanthinae (Kirkland, 1998), or in their own family, the Polacanthidae (Carpenter, 2001). Two comprehensive overviews of ankylosaur osteoderm histology (Scheyer and Sander, 2004; Hayashi et al., in press) have offered evidence to suggest that polacanthids are a clade distinct from nodosaurids and ankylosaurids. Although they recovered diagnostic histological characters for the three groups, these studies did not attempt to analyze them in a phylogenetic context.

(4) Using comparative material, describe the likely integumentary covering of ankylosaur osteoderms and comment on their likely resultant function(s). It is usually assumed that ankylosaur osteoderms were covered either by normal epidermis or a thickened keratinous sheath (=stratum corneum of the epidermis). Hieronymus et al. (2009) demonstrated that the surface texture of various integumentary coverings (epidermal and dermal) can be correlated with specific underlying bone surface morphologies. After a study incorporating various extant and fossil taxa, Hieronymus et al. (2009) described these correlates as well as developed a useful method by which to categorize various surface textures. The application of this information to ankylosaur osteoderms, which vary in their range of external surface textures (Burns, 2008), would allow them to be systematically categorized as well as offer definitive evidence of their likely covering.

Various possibilities have been postulated as to the likely function(s) of the extensive dermal skeleton of ankylosaurs: defense (Blows, 2001), display (Thulborn, 1993); sexual selection (Arbour, 2009; Arbour and Snively, 2009); thermoregulation (Blows 2001; Carpenter, 1997), and/or offense (Coombs, 1979). In Ankylosauria, only the osteoderms of the tail club have received rigorous investigation into their function (Arbour, 2009; Arbour and Snively, 2009). Although defense is often assumed as the primary role of ankylosaur osteoderms, evidence suggests that this is not always the case in related groups (e.g., the stegosaurs according to Main et al., 2005), despite possessing taxonomically homologous osteoderms.

1.5 Comments on Terminology

Herein, the term “ontogeny” refers to the origin and development of an entire organism/individual into its mature form. “Skeletogenesis” refers to the ontogeny of a single skeletal element (one osteoderm). This is important as one individual can (and likely does) possess many osteoderms, all at different stages of skeletogenesis during any give stage of the ontogeny of an individual. “Osteoderm” refers to a bony structure of the dermal skeleton that develops in the dermis.

Terms for the different regions of osteoderms on the body (e.g., “cervical,” “pelvic”) do not imply homology with those regions in ankylosaurs (*sensu* Burns, 2008). Rather, they denote a consistent morphological difference among osteoderms in these body regions in an individual or taxon. The term “median” when used in the context of a median keel refers to position relative to the osteoderm itself and not to the overall anatomical position on the animal (Fig. 1.2).

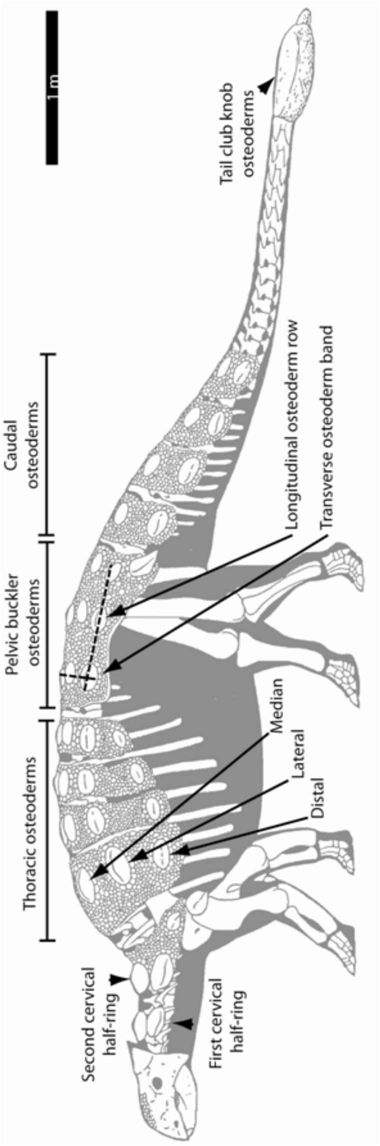


FIGURE 1.2. Summary of positional terminology used to describe osteoderms. The reconstruction used is *Ankylosaurus* modified from Ford (2003).

Terminology for describing the surface textures of osteoderms is from Hieronymus et al. (2009). Rugosity can be described as projecting, hummocky, pitting, or tangential, and, in a relative sense, weak to strong. Neurovascular grooves may be absent, sparse, or dense and can be described as reticular, anastomosing, or ordered. In addition, the orientation relative to the surface of neurovascular foramina, if present, may be oblique or normal.

"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, in which "deep" refers to the direction towards the deeper layers of the dermis and "superficial" to the direction towards the more external epidermis or keratinous sheath. Histologically, osteoderms are described as having a "cortex" or two "cortices" (superficial and/or deep) and core (the terms "medulla" and "medullary" are not used to avoid implying that the region is necessarily composed of trabecular bone). Herein, percentages following descriptions of relative thickness for these different regions denote the percent thickness of the layer relative to the total, maximum thickness of the osteoderm. Osteoderms with specialized functions (ankylosaurid tail clubs and stegosaur tail spikes) are referred to as "modified" in contrast to "unmodified" osteoderms, which in ankylosaurs form the pervasion of osteoderms across most of the dorsum. This is an important distinction because, as will be demonstrated, modified osteoderms can diverge from the histology/morphology otherwise characteristic for unmodified osteoderms of a group.

Chapter 2 Variation in Extant and Fossil Crocodylian Osteoderms

2.1 Introduction

All crocodilians possess numerous osteoderms along the dorsal and dorsolateral portions of the body, from the cervical region (immediately posterior to the skull), past the pelvic region and to the posterior terminus of the tail (=caudal region). In some species (e.g., *Alligator mississippiensis*, many species of *Crocodylus*) osteoderms do not develop on the ventral surface of the body; however, they do in others (e.g., *Alligator sinensis* and other alligatorids). Osteoderms are arranged in transverse rows. Parasagittal elements often articulate but do not fuse, whereas more laterally positioned osteoderms become incrementally more separated along a row. Successive osteoderms in any given row may imbricate on an immediately posterior osteoderm (Vickaryous and Hall, 2008).

2.1.2 Overview of skeletally mature osteoderms and skeletogenesis

As is the case with all bone, the histology of osteoderms changes with ontogeny. Because ontogeny is a major determinant of morphological diversity in animals, an understanding of this process is key to an evaluation of variation at any level of biological organization. Until recently, this process as it applies to the dermal skeleton has been poorly understood. Recent studies (e.g., Vickaryous and Hall, 2008) have, however, provided a histological baseline condition for the dermal skeleton in crocodilians at different stages in skeletogenesis.

Scalation begins in the embryo prior to osteoderm formation, establishing the accommodation of the integument to the forthcoming osteoderms. Before the onset of osteoderm calcification, the integument is readily divisible into the dermis and epidermis. Calcification of any given osteoderm proceeds radially outward from a center of mineralization while incorporating collagen fibres from the dermis. The mineralization front spreads into the dense, irregular connective tissue. Ossified spicules form next and radiate from this center of mineralization, following the same pattern as the basic calcification process. Interstices between the spicules are filled with loosely coherent tissue. The spicules anastomose and become more robust (Vickaryous and Hall, 2008). Afterwards, internal remodelling takes place following the same radial pattern. Primary and secondary Haversian canals are formed at this time. A scalloped line of osteoclastic resorption is evident around the remodelling front.

2.2 Materials and Methods

Two osteoderms from *Alligator mississippiensis* were serially sectioned longitudinally and prepared using histological methods. Six of the eight sections represent subadult osteoderms from the right side of precaudal position 21. The remaining two are from adult individuals and also come from the right side of precaudal position 21. The individuals were morphologically staged to the Normal Table of Development (Ferguson 1985, 1987) to determine their respective ontogenetic stages. Preparation involved decalcification in Tris-buffered 10% EDTA (ph 7.0) for a period from five days to four weeks. Specimens were then dehydrated in 100% ethanol, cleared in CitriSolv, embedded in low melting paraffin (Paraplast X-tra) at 54°C, and cut at 6 to 7 μm. The sections were stained with Mallory's trichrome (see Vickaryous and Hall, 2008, for staining protocols) and mounted with Di-n-butyl Phthalate in Xylene.

Dried dorsal osteoderms from two separate specimens of the spectacled caiman (*Caiman crocodilus*; ROM R6587 and ROM R7719) made up a portion of the extant material examined. Those from ROM R 6587 represent osteoderms from the caudal region of an individual (snout vent length = 65.5 cm) from the Indian River Reptile Zoo. No data was available for those belonging to ROM R7719. Four osteoderms were acquired from each specimen. In ROM R6587, A is a square caudal osteoderm (Fig. 2.1) whereas B (Fig. 2.2) and C (Fig. 2.3) are laterally placed, due to their spine-like morphology. ROM R6587 D is of unknown origin, although it is likely lateral due to its one crenulated margin (Fig. 2.4). ROM R7719 A and B are medially-situated square osteoderms (Fig. 2.5). ROM R7719 C (Fig. 2.6) and D (Fig. 2.7) are also square, but are flat as opposed to keeled. They likely represent osteoderms from the lateral surface of the tail.

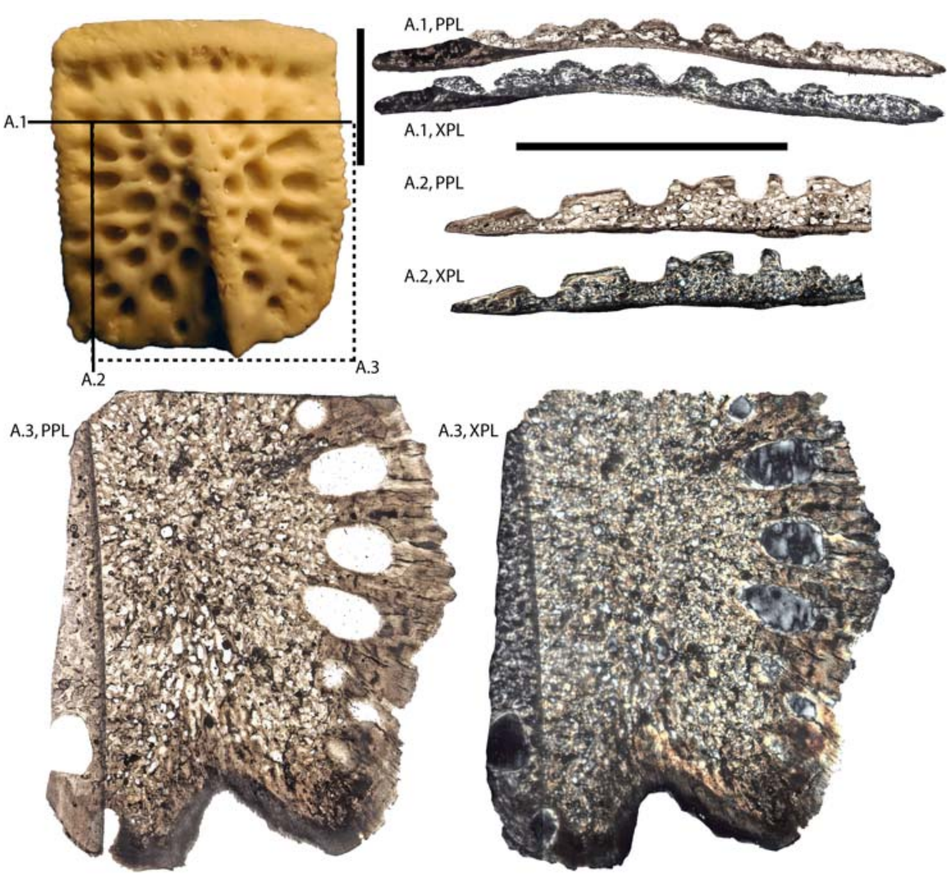


FIGURE 2.1. Dorsal osteoderm of *Caiman crocodylus*. (ROM 6587 A) in superficial view (anterior is up) and corresponding thin sections. The core is composed of compact bone consisting of randomly-oriented Haversian canals. Near the margins, this is replaced by fibrolamellar and Sharpey's fiber bone. Scale bars for whole osteoderm and thin sections equal 1 cm.

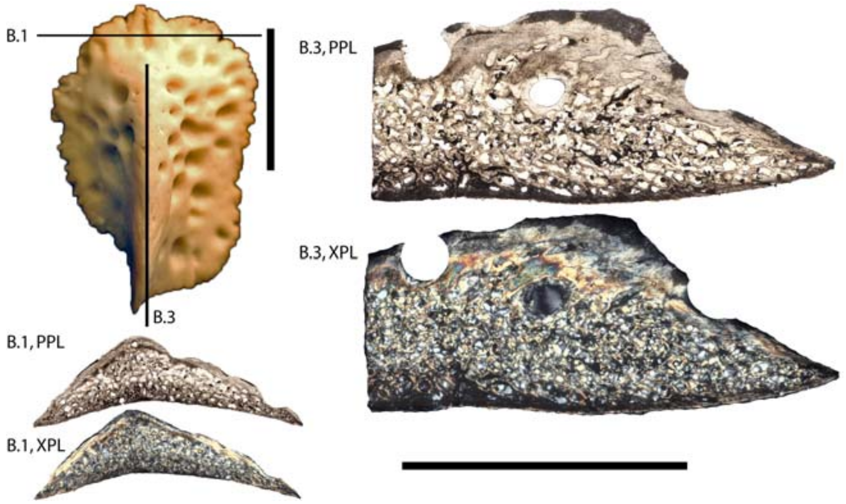


FIGURE 2.2. Dorsal, prominently keeled osteoderm of *Caiman crocodylus* (ROM 6587 B) in superficial view (anterior is up) and corresponding thin sections. Scale bars equal 1

All but one of the osteoderms were prepared via resin impregnation (using Buehler EpoThin Low Viscosity Resin and Hardener) and petrographic thin sectioning. The remaining osteoderm was decalcified as for the *A. mississippiensis* osteoderms and sectioned in the transverse plane. Four sections were stained with hematoxylin and eosin (Presnell and Schreibman, 1997) and two with Masson's trichrome (Witten and Hall, 2003).

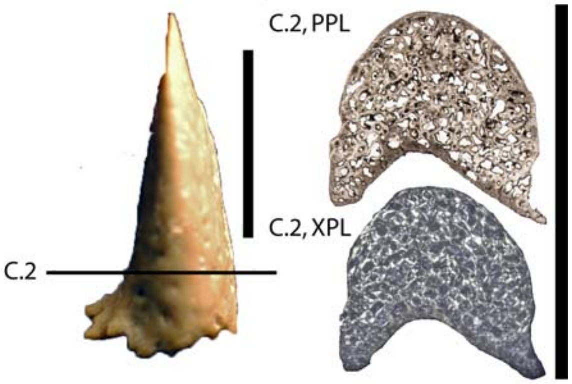


FIGURE 2.3. Dorsal spine of *Caiman crocodylus*. (ROM 6587 C) in superficial view (lateral is up) and corresponding thin sections. The core is Haversian and the cortex is highly reduced relative to the square osteoderms from this specimen. Scale bars equal 1 cm.

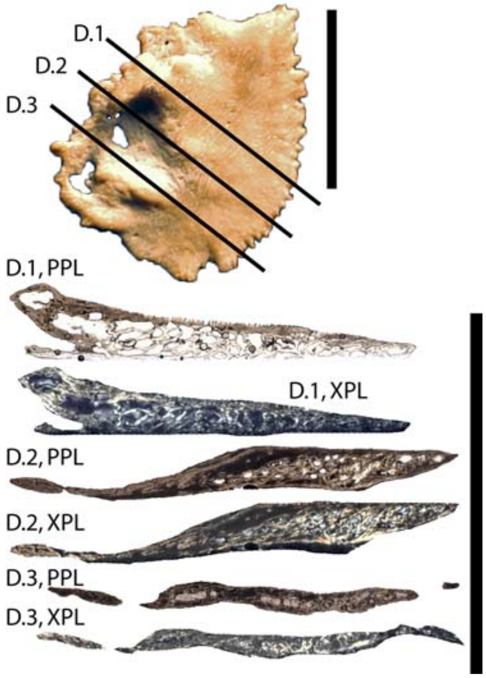


FIGURE 2.4. Dorsal osteoderm of *Caiman crocodylus*. (ROM 6587 D) in superficial view (orientation uncertain) and corresponding thin sections. A largely Haversian core grades into trabecular bone in D.1. The large pit/perforation (in D.2 and D.3) has no apparent effect on the underlying histology. Scale bars equal 1 cm.

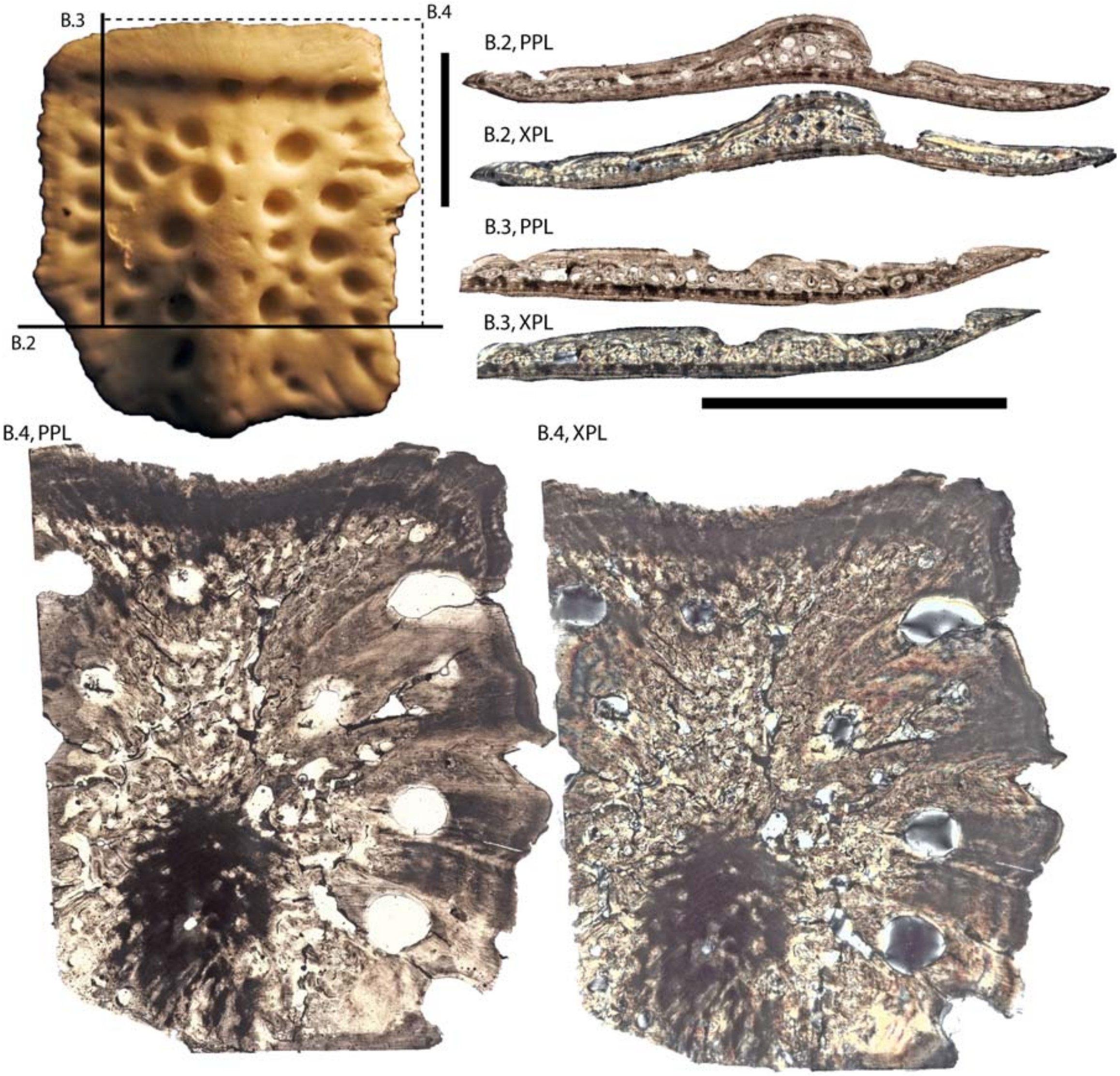


FIGURE 2.5. Dorsal square osteoderm of *Caiman crocodylus*. (ROM 7719 B) in superficial view (anterior is up) and corresponding thin sections. The compact core grades into a fibrolamellar cortex, with LAGs and Sharpey's fibres visible near the margins (B.4). Scale bars equal 1 cm.

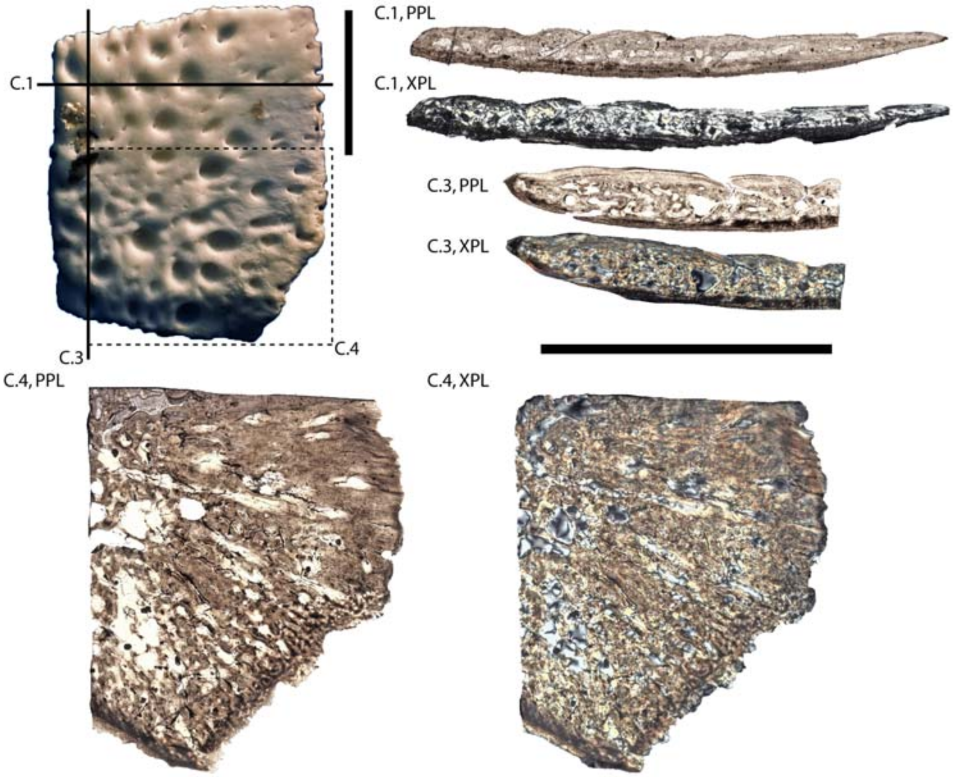


FIGURE 2.6. Dorsal square osteoderm of *Caiman crocodylus*. (ROM 7719 C) in superficial view (orientation uncertain). Numbered lines on whole osteoderm correspond to plane of thin sections (to the right and below). The core is a mixture of compact and (centrally) trabecular bone. Cortical bone is fibrolamellar with prominent Sharpey's fibres. Scale bars for whole osteoderm and thin sections equal 1 cm.

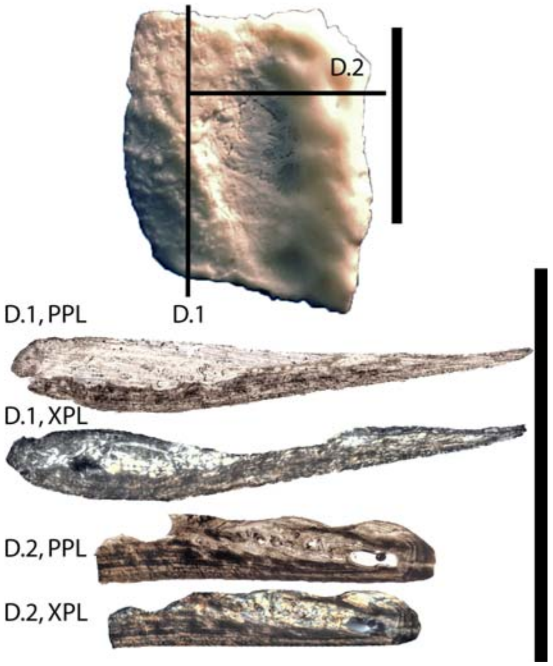


FIGURE 2.7. Osteoderm of *Caiman crocodylus*. (ROM 7719 D) in superficial view (anterior is up) and corresponding thin sections. The core is Haversian and surrounded by a thick fibrolamellar cortex. LAGs are numerous and prominent, wrapping around the lateral margins of the osteoderm from the deep cortex (D.2). Scale bars equal 1 cm.

Fossil crocodilian specimens include three osteoderms from Crocodylidae indet., TMP 1979.14.445. Two are likely from the thoracic region: A (Fig. 2.8) is more medial in origin and B (Fig. 2.9) is more lateral due to a rounded edge and offset keel. Osteoderm C is likely from the lateral tail region as it is flat but still ornamented (Fig. 2.10). *Leidyosuchus* sp./Crocodylidae indet. (TMP 1984.39.13) consists of a single isolated elongate, flat dorsal osteoderm. Two osteoderms from *Leidyosuchus* sp. (TMP 1987.48.54) were sectioned. Osteoderm A was likely caudal (Fig. 2.11), whereas B represents a dorsolateral spine (Fig. 2.12). Crocodylidae indet. (TMP 1991.36.105) provided three dorsal osteoderms from various positions (Figs. 2.13, 2.14, 2.15). Finally, two dorsal osteoderms from *Leidyosuchus* sp./*Albertochampsa* sp. (TMP 1997.88.1) were chosen from a lateral (Fig. 2.16) and medial (2.17) position.

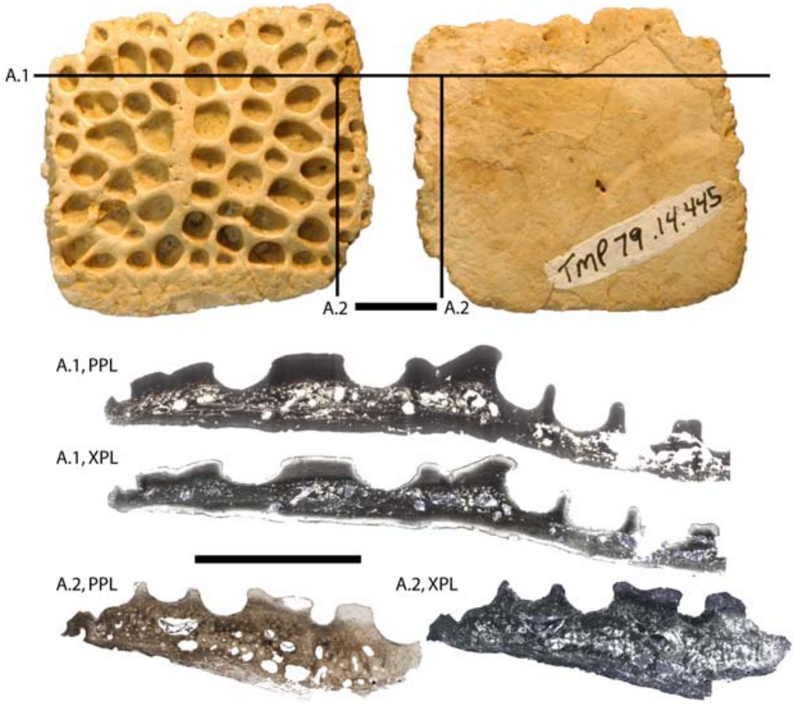


FIGURE 2.8. Dorsal square osteoderm of Crocodylidae indet. (TMP 79.14.445.A) in superficial and deep views (anterior is up) and corresponding thin sections. The core is compact despite a few larger vacuities. The cortex is fibrolamellar. Scale bars equal 1 cm.

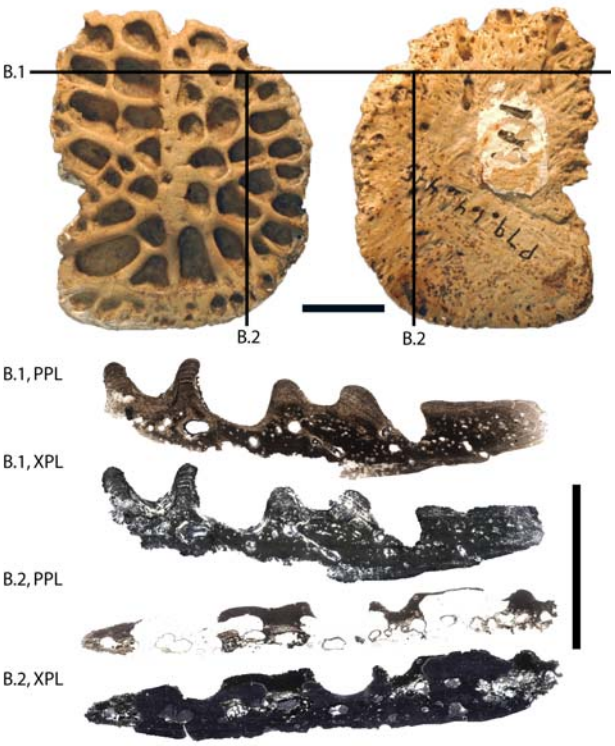
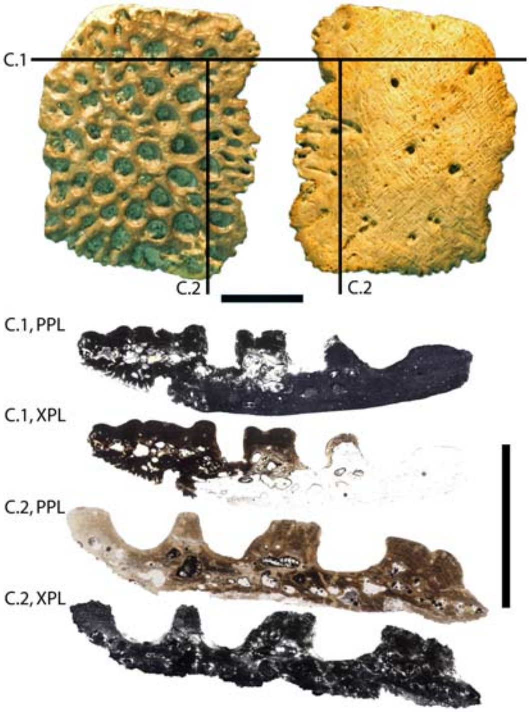


FIGURE 2.9. Dorsal square osteoderm of Crocodylidae indet. (TMP 79.14.445.B) in superficial and deep views (anterior is up) and corresponding thin sections. The core is a mixture of Haversian and trabecular bone and is surrounded by fibrolamellar bone in the cortex. Some of the LAGs are visible in the superficial cortex between pits (B.1, XPL). Scale bars equal 1 cm.

FIGURE 2.10. Dorsal square osteoderm of Crocodylidae indet. (TMP 79.14.445.C) in superficial and deep views (orientation uncertain) and corresponding thin sections. There is a mixture of bone histology in the core and a thick fibrolamellar cortex. Sharpey's fiber bone is visible in the lower left of the deep cortex in C.1. Scale bars equal 1 cm.



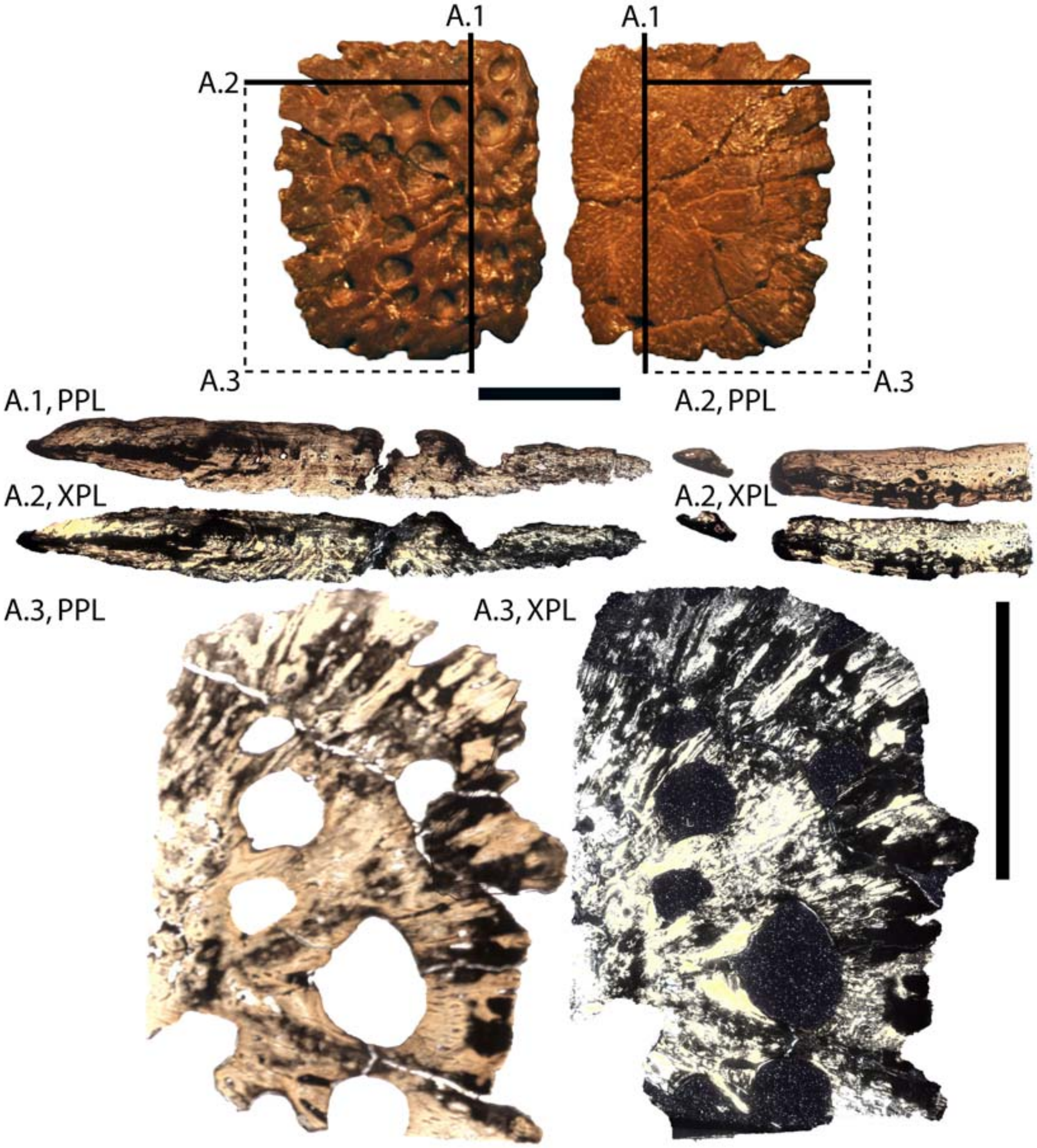


FIGURE 2.11. Dorsal square osteoderm of *Leidyosuchus* sp. (TMP 87.48.54.A) in superficial and deep views (orientation uncertain) and corresponding thin sections. The compact core is relatively thin and surrounded by a much thicker cortex. Mineralized collagen and Sharpey's fibers are prominent in the deep cortex in A.2 and near the margins of A.3. Scale bars equal 1 cm.

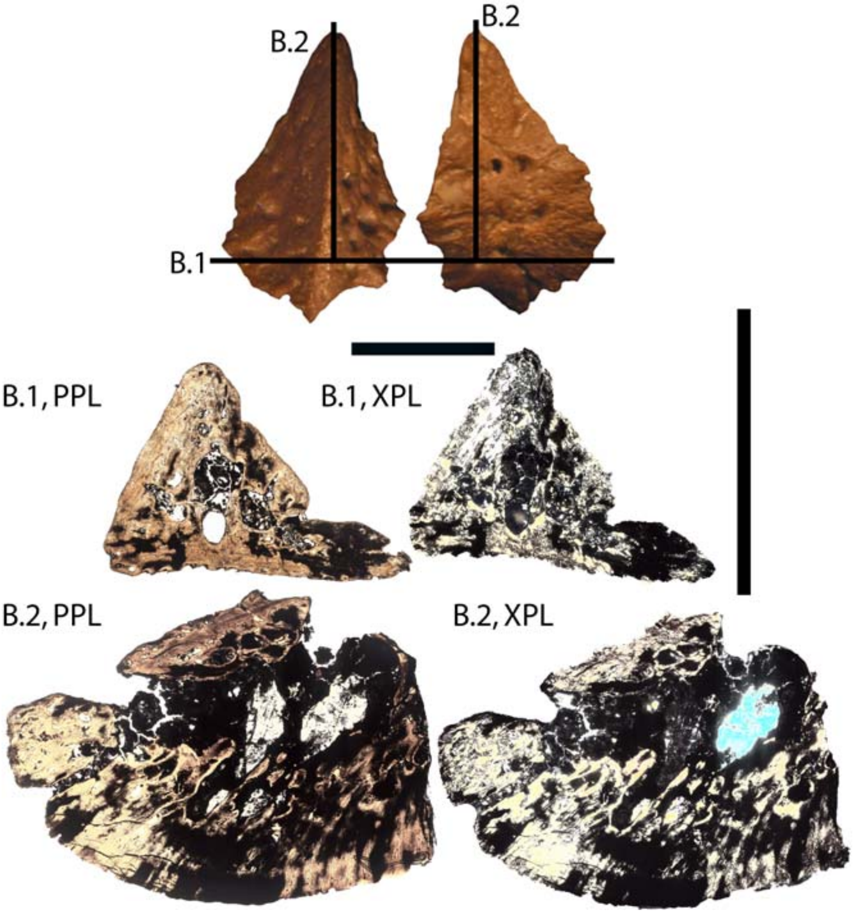


FIGURE 2.12. Lateral spine of *Leidyosuchus* sp. (TMP 87.48.54.B) in superficial and deep views (posterior is up) and corresponding thin sections. A fibrolamellar cortex completely surrounds the trabecular core. LAGs and Sharpey's fibers are pronounced in the deep cortex (B.2). Scale bars equal 1 cm.

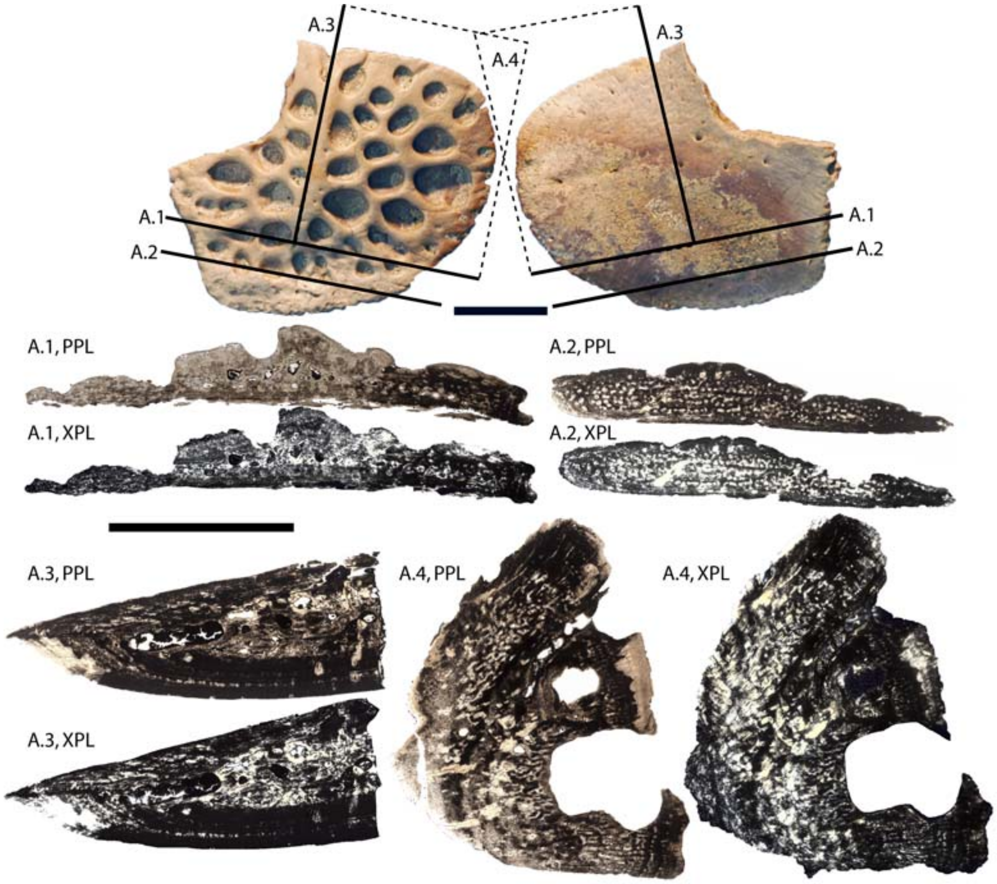


FIGURE 2.13. Dorsal square osteoderm of Crocodylidae indet. (TMP 91.36.105.A) in superficial and deep views (anterior is up) and corresponding thin sections. The core is compact and composed of densely packed osteons (A.2). In the cortex, fibrolamellar bone is marked by multiple LAGs (A.3, A.4). Scale bars equal 1 cm.

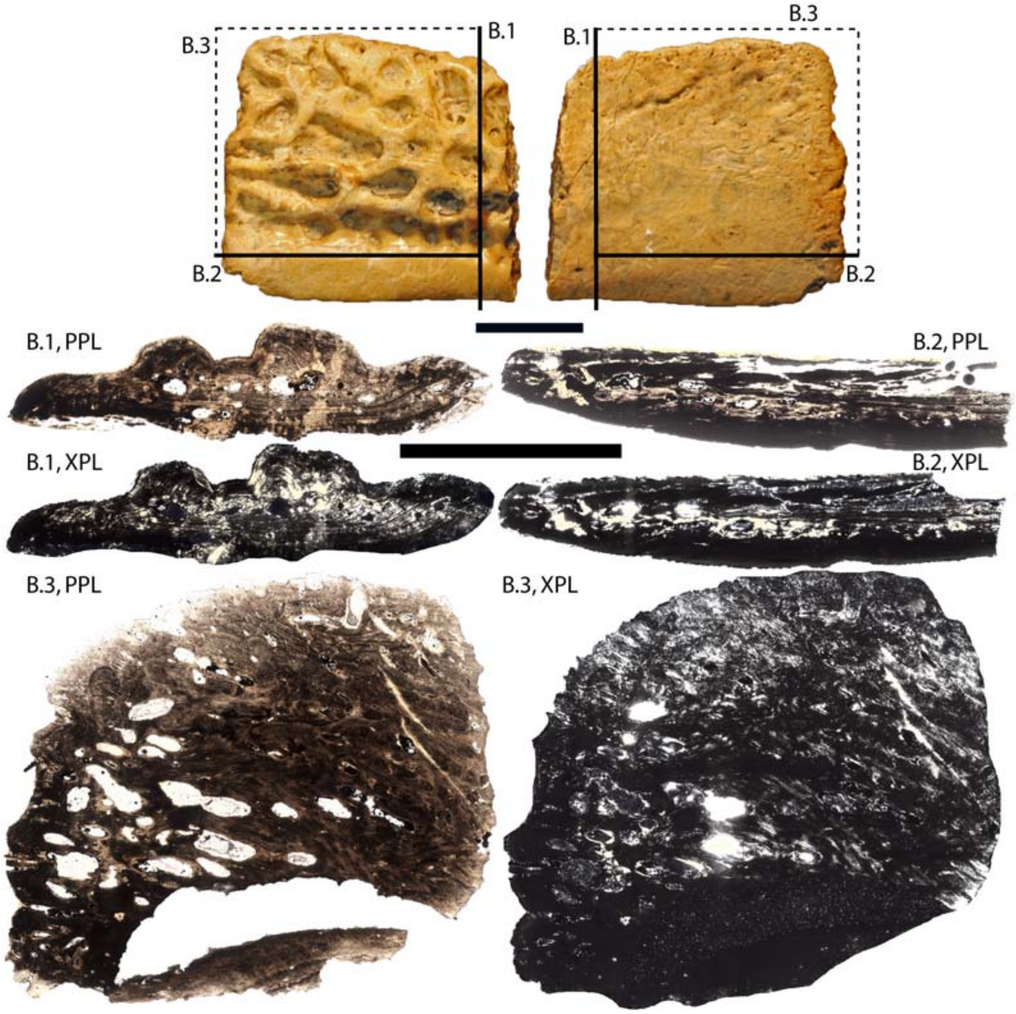


FIGURE 2.14. Dorsal square osteoderm of Crocodylidae indet. (TMP 91.36.105.B) in superficial and deep views (anterior is up) and corresponding thin sections. A mixture of Haversian and trabecular bone characterizes the core. LAGs, Sharpeys fiber bone, and fibrolamellar bone constitute the cortices. One relatively large, conspicuous Sharpey’s fiber is visible in the center of the deep cortex in B.1, PPL. Scale bars equal 1 cm.

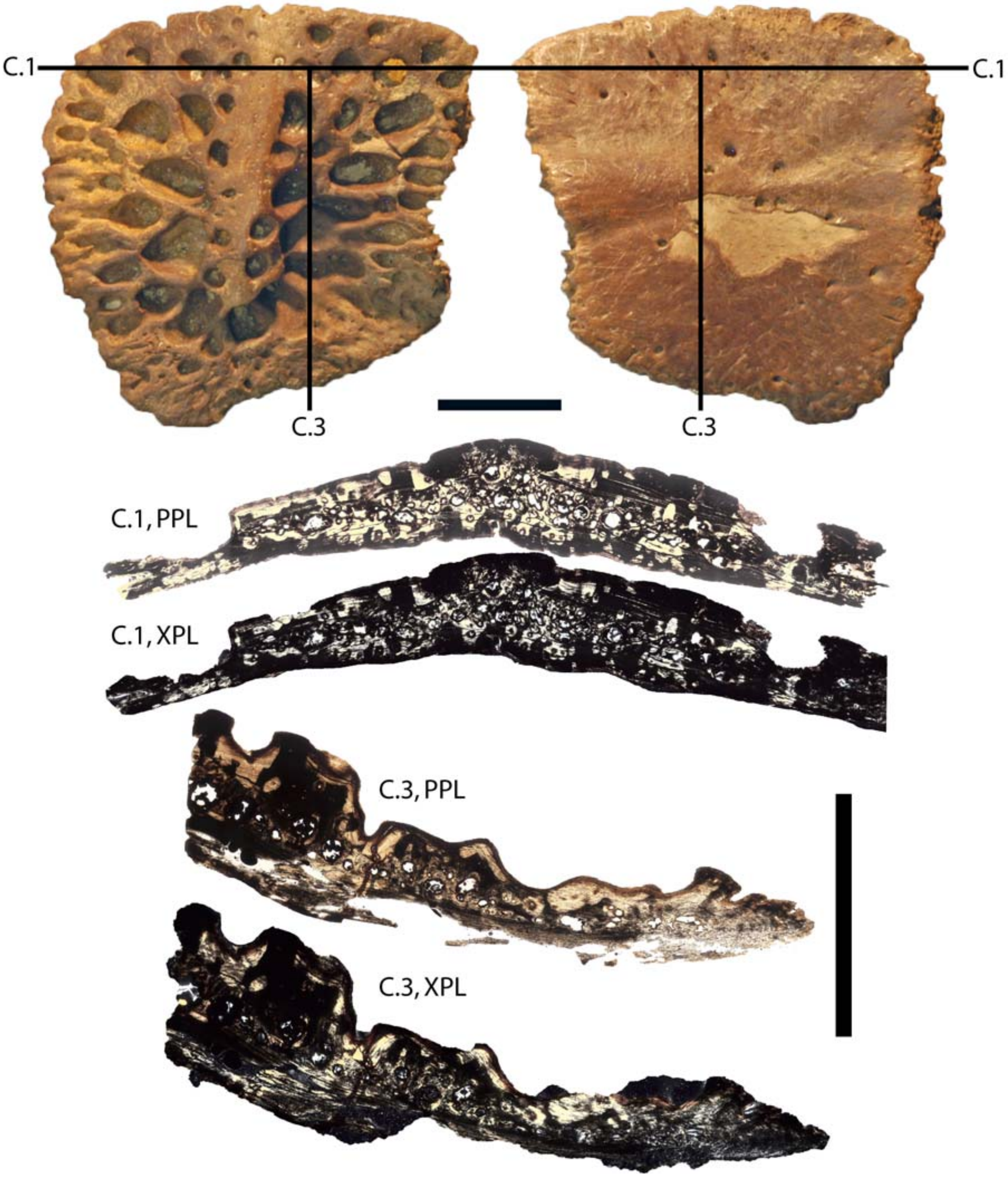


FIGURE 2.15. Dorsal osteoderm of Crocodylidae indet. (TMP 91.36.105.C) in superficial and deep views (anterior is up) and corresponding thin sections. The core is a mixture of Haversian bone that, in places, opens into a few scattered trabecular cavities. Mineralized fibers in the cortex are arranged parallel to the surface (deep cortex of C.3, XPL). Scale bars equal 1 cm.

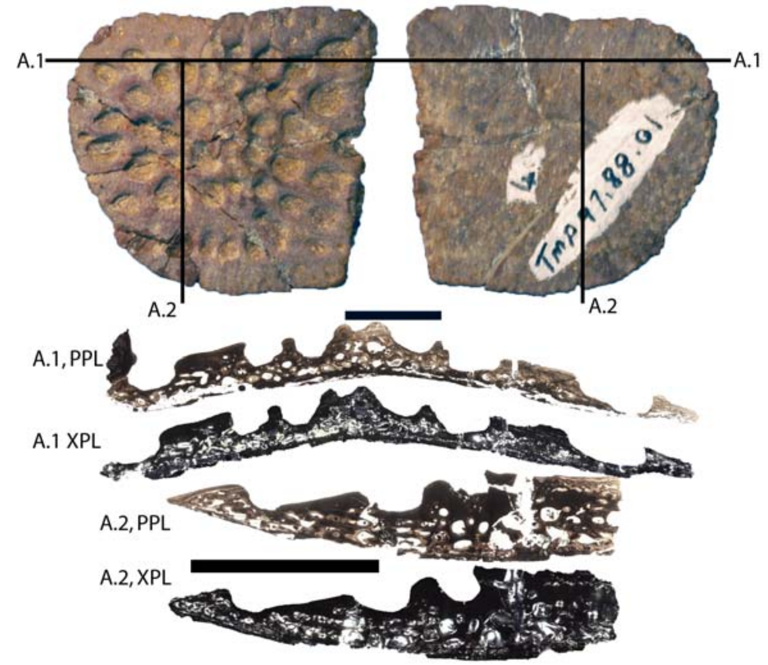


FIGURE 2.16. Dorsal square osteoderm of *Leidyosuchus* sp. (TMP 97.88.1.A) in superficial and deep views (anterior is up) and corresponding thin sections. A relatively thin fibrolamellar cortex surrounds a core consisting of Haversian bone and some trabeculae. Scale bars equal 1 cm.

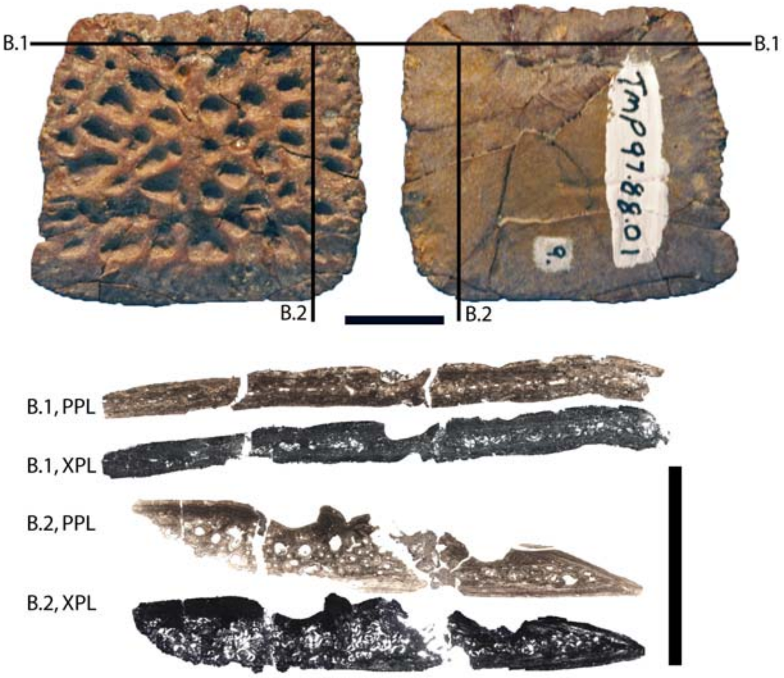


FIGURE 2.17. Dorsal square osteoderm of *Leidyosuchus* sp. (TMP 97.88.1.B) in superficial and deep views (anterior is up) and corresponding thin sections. A mixed Haversian/trabecular core is pinched out close to the margins by the fibrolamellar cortex. Scale bars equal 1 cm.

All fossil osteoderms were prepared via resin impregnation (using Buehler EpoThin Low Viscosity Resin and Hardener) and petrographic thin sectioning. Photographs of sections were taken using a Nikon ECLIPSE E400 POL Polarizing Microscope equipped with a digital camera and an ELMO P10 Visual Presenter.

2.3 Results

2.3.1 Modern specimens

Gross Examination—A specimen of extant *Caiman crocodilus* used in this study (ROM R6587) includes 21 postcervical rows of articulated osteoderms. They exhibit the characteristic crocodilian dorsal and dorsolateral osteoderms, from the cervical region to the distal end of the caudal region. Successive osteoderms in each row imbricate on the immediately posterior osteoderm row, forming a continuous sheet of osteoderms over the dorsum. The ventral surface of the body is also equipped with an uninterrupted expanse of osteoderms, including a complete caudal sheath. The number of osteoderms in each row ranges from four to ten. Each osteoderm displays a median, longitudinal keel. The lateralmost osteoderms in nine of the thoracic rows display a more sharply keeled morphology than those more medially situated in the same row. The immediately medial osteoderm in each of these cases (lateralmost in rows lacking a sharply keeled osteoderm) has a rounded lateral edge. The remainder of the osteoderms are roughly square.

Each osteoderm corresponds to an external keratinous scale of similar shape. The superficial surface of the osteoderms is characterized by sculpturing consisting of numerous round pits that radiate away from the keel. The lateral and medial edges are roughened for the fibrous attachments between articulated (but not fused) osteoderms in a transverse row; however, the rounded edges of lateral osteoderms are smooth. On the deep surface, a cross-hatch pattern (more prominent on some specimens than others) indicates the former attachment of deep fascia. There is a roughly transverse groove near the posterior edge, presumably for branches of the dorsal median artery ( ). Anterior to this, four to five foramina for passage of blood vessels and nerves mottle the center of the osteoderm. Posteriorly, the ventral surface slopes dorsally and is crossed by thin weakly developed transverse ridges.

Osteoderms chosen for thin sectioning (from ROM R6587 and ROM R7719) represent square and spine-like morphologies, allowing tests of variation in individuals. All of the osteoderms from both specimens exhibit a uniform pitted sculpturing characteristic of the Crocodylia. Neurovascular grooves and/or foramina are absent on the superficial surfaces of all the osteoderms.

Hard Tissue Histology—Specimens (*Caiman crocodilus*; ROM R6587 and ROM R7719; Figs. 2.1) were examined in histological and petrographic thin sections. In addition to histological description, several measurements of the different histological regions were obtained for each section for statistical analyses (Table 2.1). They are composed of a combination of fibrolamellar bone and calcified connective tissue. The structural design of the tissue, both mineralized and un-mineralized, is far from homogenous, but the osteoderms consist of a basic stratified structure.

In general, the specimens exhibit a circumferential fibrolamellar cortex surrounding a core. In places where the osteoderm is thinner, the core is absent, and the deep and superficial cortices come into contact with one another. The deep cortex is characterized by several prominent LAGs and densely packed, regularly arranged structural fibers. These fibers are oriented parallel to the deep surface in one set and at an oblique angle in another. In some osteoderms, the ordered fibrolamellar bone wraps around the lateral margins and may even merge with the superficial cortex. The superficial cortex is also composed of fibrolamellar bone, but exhibits less prominent LAGs and a looser arrangement of structural fibers.

TABLE 2.1. Summary of histological measurements used in analyses from two individuals of extant *Caiman crocodilus*. All measurements are in mm. Relative thicknesses are presented as a percentage of total osteoderm thickness. * indicates a spine-like rather than square morphology. Abbreviations: TT, total osteoderm thickness; TS, total superficial cortical thickness; Tcore, total core thickness; TD, total deep cortical thickness; %S, relative superficial cortical thickness; %Core, relative core thickness; %D, relative deep cortical thickness, %Cortex, relative thickness of the overall cortex.

Specimen	**Histological Measurements**								
	TT	**TS**	**Tcore**	**TD**	**Tcortex**	**%S**	**%Core**	**%D**	**%Cortex**
ROM R6587 A1	0.702	0.229	0.312	0.161	0.39	33	44	23	56
ROM R6587 A2	1.572	0.337	1.06	0.175	0.512	21	67	11	33
ROM R6587 B1*	0.573	0.109	0.391	0.073	0.182	19	68	13	32
ROM R6587 B2*	2.186	0.424	1.586	0.176	0.6	19	73	8	27
ROM R6587 B3*	3.688	1.224	2.306	0.158	1.382	33	63	4	37
ROM R6587 B4*	2.407	0.428	1.837	0.142	0.57	18	76	6	24
ROM R6587 C1*	1.006	0.106	0.816	0.084	0.19	11	81	8	19
ROM R6587 C2*	2.45	0.08	2.05	0.32	0.4	3	84	13	16
ROM R6587 C3*	4.577	0.202	4.22	0.155	0.357	4	92	3	8
ROM R6587 D2	0.81	0.142	0.561	0.107	0.249	18	69	13	31
ROM R6587 D3	0.509	0.147	0.191	0.171	0.318	29	38	34	62
ROM R7719 A2	2.121	0.287	1.338	0.496	0.783	14	63	23	37
ROM R7719 A3	2.689	0.211	1.88	0.598	0.809	8	70	22	30
ROM R7719 A4	3.616	0.549	2.3	0.767	1.316	15	64	21	36
ROM R7719 B1	1.05	0.406	0.335	0.309	0.715	39	32	29	68
ROM R7719 B2	1.534	0.597	0.57	0.367	0.964	39	37	24	63
ROM R7719 B3	1.164	0.398	0.442	0.324	0.722	34	38	28	62
ROM R7719 C1	1.027	0.38	0.383	0.264	0.644	37	37	26	63
ROM R7719 C2	0.746	0.133	0.332	0.281	0.414	18	45	38	55
ROM R7719 C3	1.668	0.284	1.026	0.358	0.642	17	62	21	38
ROM R7719 D1	1.389	0.437	0.344	0.608	1.045	31	25	44	75
ROM R7719 D2	1.044	0.192	0.281	0.571	0.763	18	27	55	73

The core differs between the two specimens. The core of ROM R7719 is predominantly compact and contains numerous Haversian canals (the term is used loosely as the canals have no regular orientation) and exhibits a high degree of vascularization. On the other hand, in ROM R6587, the core is completely made up of trabecular bone. On average, the cortices of ROM R7719 make up a greater component (i.e., are thicker, 34% avg.) of the total osteoderm thickness than the cortices of ROM R6587 (56% avg.), but this is not a significant difference (t=1.98, df=6, α=0.05) according to a two-tailed t-test assuming unequal variances.

Soft Tissue Histology—In the histological sections, a scalloped line indicating an erosional/resorptive surface separates this central region from an external region of unorganized fibrolamellar and woven bone combined with loosely mineralized dense irregular connective tissue. In this layer near and at the lateral margins of the osteoderm, a number of thick, unmineralized fibers cross the boundary of mineralization.

Histological Relationships—The relationship between osteoderm thickness and the thickness of the cortex was tested in both specimens. Multiple sections taken through a single osteoderm were treated as separate data points as total thickness changes in each osteoderm depending on where the section was taken. A plot of total osteoderm thickness versus total cortical thickness shows a logarithmically increasing trend (Fig. 2.18); however, a plot of total osteoderm thickness versus percent cortical thickness shows a decreasing trend (Fig. 2.19). Although

r^2 values are relatively low for these correlations (0.35 to 0.55), both individual specimens show similar trends.

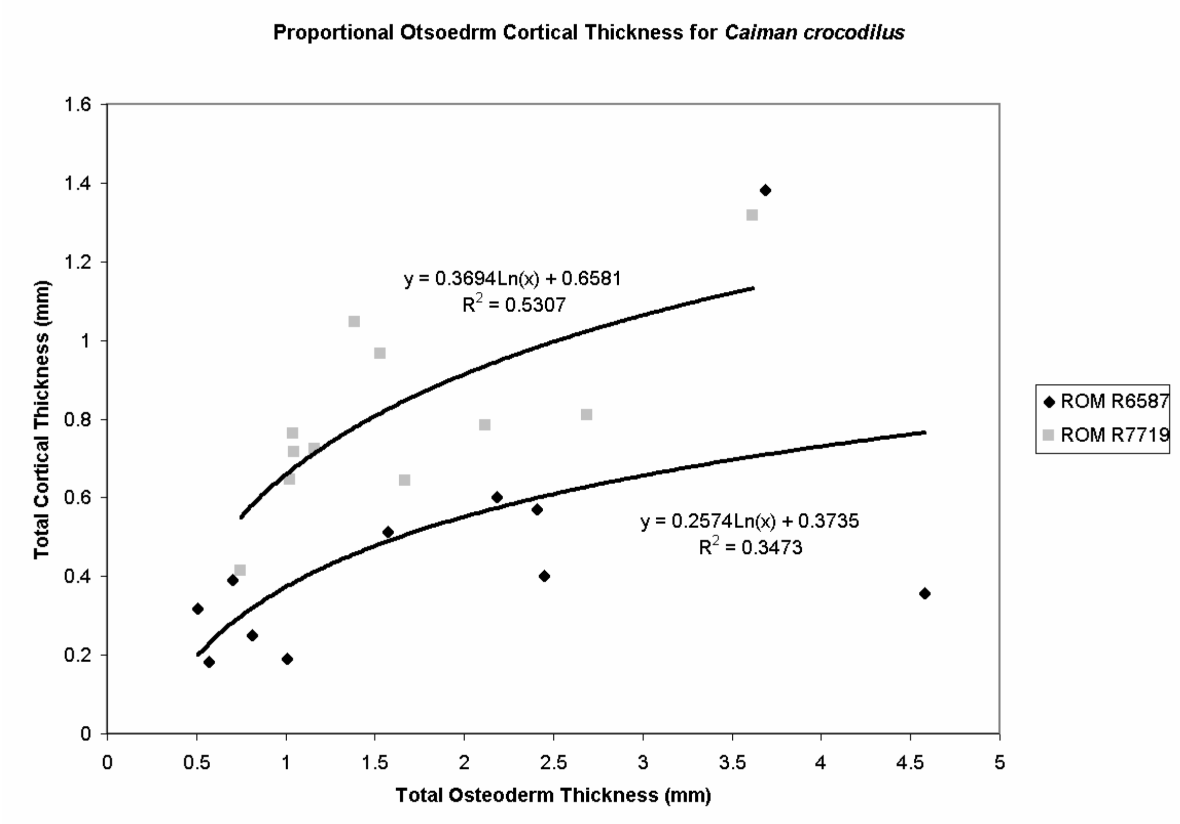


FIGURE 2.18. Absolute osteoderm cortical thickness for extant *Caiman crocodilus*. The total thickness (mm) of the cortex (superficial and deep combined) is plotted against the total thickness (mm) of the osteoderm. Data includes dorsal and dorsolateral osteoderms from two individuals (ROM R6587, ROM R7719).

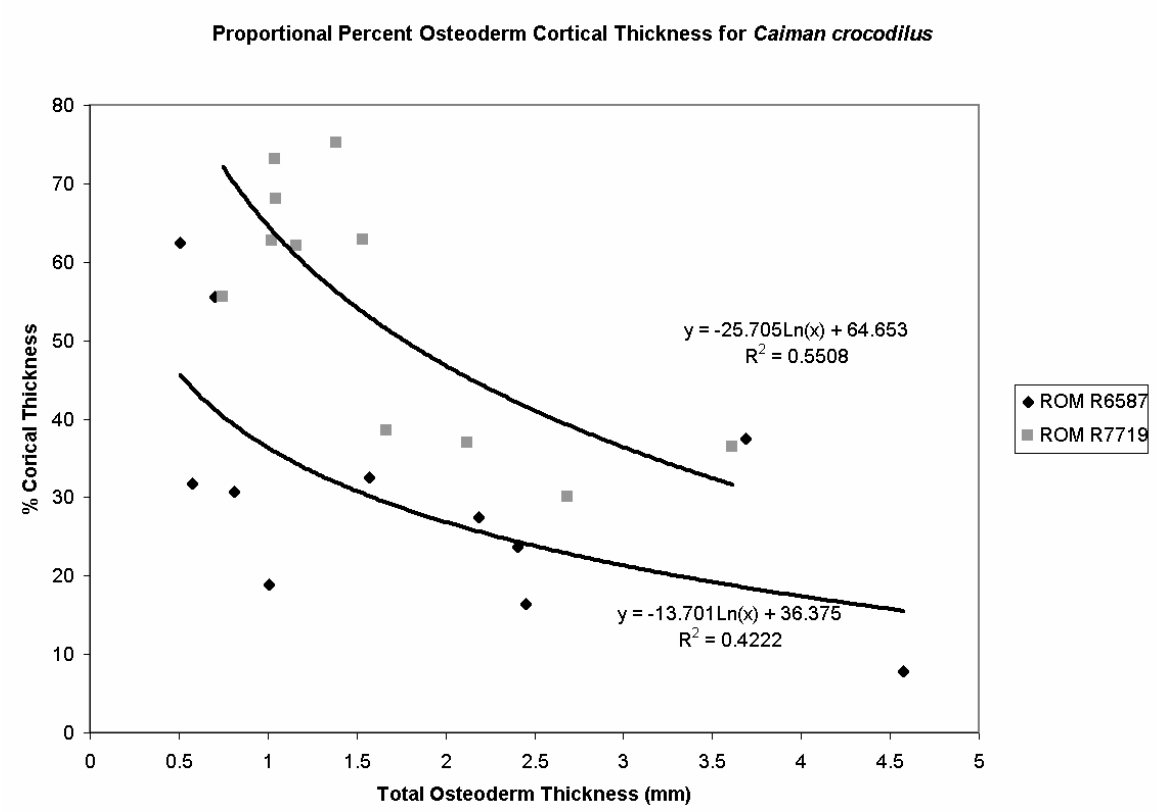


FIGURE 2.19. Relative osteoderm cortical thickness for extant *Caiman crocodilus*. The percent thickness (mm) of the cortex (proportion of combined thickness of the superficial and deep cortices versus total osteoderm thickness) is plotted against the total thickness (mm) of the osteoderm. Data includes dorsal and dorsolateral osteoderms from two individuals (ROM R6587, ROM R7719).

2.3.2 Fossil specimens

Gross Examination— All of the osteoderms from both specimens have the same characteristic uniform pitted sculpturing on the superficial surface. The lateral and medial edges are roughened on some of the osteoderms. A cross-hatch pattern is visible on the deep surface with varying prominence on each osteoderm. The posterior transverse groove and anterior neurovascular foramina (there are no neurovascular grooves) are visible on the deep surface as in the extant specimens. There are no neurovascular grooves or foramina present on the superficial surface.

Hard Tissue Histology—The histology of the fossil specimens examined is similar to that of the extant material. The cortex is made up of primary fibrolamellar bone. The core also tends to pinch out in areas where the osteoderm is thinner overall. The deep cortex is characterized by LAGs and Sharpey's fibres. The superficial cortex is also composed of fibrolamellar bone, but exhibits less prominent LAGs and fewer fibres. As in the extant specimens of *C. crocodylus*, the core may be composed of either highly vascular Haversian canals or trabecular bone. Also as in the extant specimens, osteoderms from a single individual are restricted to one core histology or the other. The same histological measurements were taken for the fossil material as for the extant osteoderms (Table 2.2).

2.3.3 Combined analyses

To examine the effects of osteoderm shape on histology, the percent cortical thickness (deep and superficial combined) was plotted separately for square and spine-like osteoderms for both recent and fossil specimens (Fig. 2.19). Those osteoderms exhibiting a spine-like morphology had consistently smaller relative cortical thicknesses (36% avg.) than square osteoderms (57% avg.). A two-sample t-test assuming unequal variance shows that this trend represents a statistically significant difference ($t=4.38$, $df=15$, $\alpha=0.05$). When plotted against total thickness, total cortical thickness showed no statistical difference ($t=0.72$, $df=13$, $\alpha=0.05$) between square and spine-like osteoderms (2.20).

TABLE 2.2. Summary of histological measurements used in analyses from several specimens of fossil crocodilian. All measurements are in mm. Relative thicknesses are presented as a percentage of total osteoderm thickness. * indicates a spine-like rather than square morphology. Abbreviations: TT, total osteoderm thickness; TS, total superficial cortical thickness; Tcore, total core thickness; TD, total deep cortical thickness; %S, relative superficial cortical thickness; %Core, relative core thickness; %D, relative deep cortical thickness, %Cortex, relative thickness of the overall cortex.

Specimen	**Taxon**	**Histological Measurements**								
		TT	**TS**	**Tcore**	**TD**	**Tcortex**	**%S**	**%Core**	**%D**	**%Cortex**
TMP 79.14.445 A.1	Crocodylidae indet.	2.77	1.036	0.782	0.952	1.988	37	28	34	72
TMP 79.14.446 A.2	"	2.23	0.84	0.597	0.793	1.633	38	27	36	73
TMP 79.14.447 B.2	"	3.142	1.399	0.536	1.207	2.606	45	17	38	83
TMP 79.14.448 C.1	"	2.76	0.785	1.196	0.779	1.564	28	43	28	57
TMP 79.14.449 C.2	"	1.99	0.679	0.887	0.424	1.103	34	45	21	55
TMP 84.39.13 A.1	*Leidyosuchus* sp.	2.51	0.683	0.656	1.171	1.854	27	26	47	74
TMP 84.39.14 A.2	"	3.488	1.248	1.301	0.939	2.187	36	37	27	63
TMP 87.48.54 A.1	"	1.76	0.835	0.313	0.612	1.447	47	18	35	82
TMP 87.48.55 A.2	"	1.088	0.425	0.253	0.41	0.835	39	23	38	77
TMP 87.48.56 B.1*	"	5.28	1.517	2.805	0.958	2.475	29	53	18	47
TMP 87.48.57 B.2*	"	2.965	1.185	1.544	0.236	1.421	40	52	8	48
TMP 91.36.105 A.1	"	2.15	0.326	0.88	0.944	1.27	15	41	44	59
TMP 91.36.106 A.2	Crocodylidae indet.	1.59	0.297	0.828	0.465	0.762	19	52	29	48
TMP 91.36.107 A.3	"	3.409	0.799	1.501	1.109	1.908	23	44	33	56
TMP 91.36.108 B.1	"	2.75	0.809	1.219	0.722	1.531	29	44	26	56
TMP 91.36.109 B.2	"	1.917	0.435	0.954	0.528	0.963	23	50	28	50
TMP 91.36.110 C.1	"	2.566	1.226	0.803	0.537	1.763	48	31	21	69
TMP 91.36.111 C.3	"	2.042	1.076	0.63	0.336	1.412	53	31	16	69
TMP 97.88.1 A.1	*Leidyosuchus* sp.	1.202	0.257	0.647	0.298	0.555	21	54	25	46
TMP 97.88.2 A.2	"	2.643	0.27	2.114	0.259	0.529	10	80	10	20
TMP 97.88.3 B.1	"	0.681	0.259	0.437	0.244	0.503	38	64	36	74
TMP 97.88.4 B.2	"	2.13	0.344	1.269	0.517	0.861	16	60	24	40

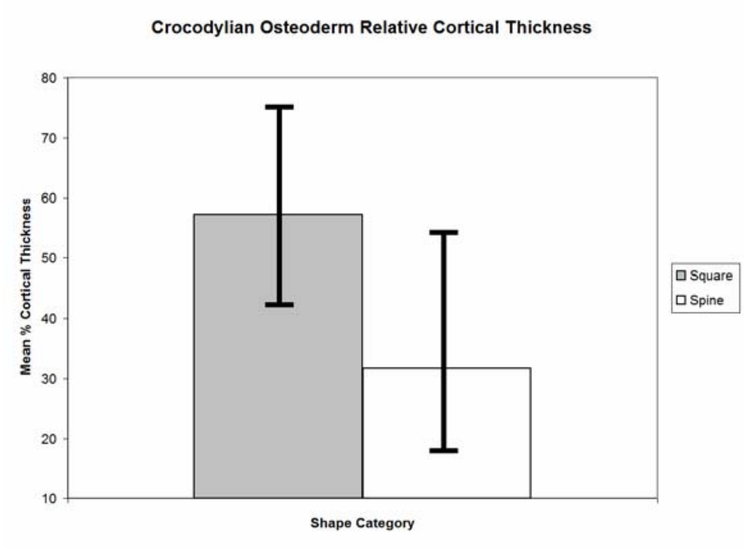


FIGURE 2.20. Osteoderm shape versus mean relative (%) cortical thickness for square and spine-like crocodilian osteoderms. Error bars represent standard deviation of the mean. Data includes dorsal and dorsolateral osteoderms from extant (ROM R6587, ROM R7719) and fossil (TMP 79.14.445, TMP 84.39.13, TMP 87.48.54, TMP 91.36.105, TMP 97.88.1) specimens.

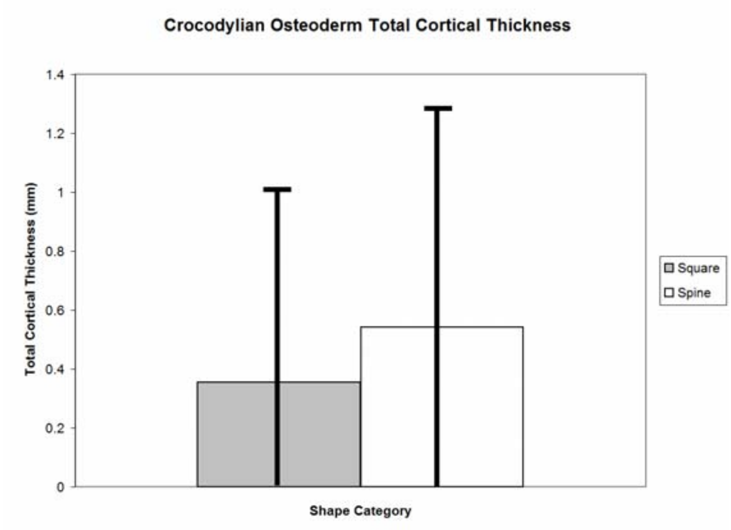


FIGURE 2.21. Osteoderm shape versus total cortical thickness for square and spine-like crocodilian osteoderms. Error bars represent standard deviation of the mean. Data includes dorsal and dorsolateral osteoderms from extant (ROM R6587, ROM R7719) and fossil (TMP 79.14.445, TMP 84.39.13, TMP 87.48.54, TMP 91.36.105, TMP 97.88.1) specimens.

2.4 Discussion

2.4.1 Plane of sectioning

Sections were cut in all three normal anatomical planes to test for discrepancies in histological interpretations due to viewing angle. Most soft-tissue histological sections are cut at right angles to the tissue surface, and incorrectly cut sections can often lead to misinterpretations. In this study, however, the three-dimensional structure of the osteoderms allows for accurate interpretations in any normal plane of sectioning. Unlike in other bone (e.g., long bones), there is either a random arrangement of mineralized structures such as osteons/Haversian canals or bony tissues are organized circumferentially, as is the case with fibrolamellar cortical bone. Therefore, unlike the case in long bones, osteoderm histological features are not directional, and therefore osteoderm histology does not appear different in different planes of sectioning.

2.4.2 Soft tissue correlates in hard tissue

The differences in structural fiber arrangement in the deep and superficial cortices is possibly due to the soft tissue layers of the dermis with which each cortex is interacting as the osteoderm forms. Crocodilian osteoderms are localized in the stratum superficiale, and only the deepest margins may contact the stratum compactum (Martill et al. 2000; Salisbury and Frey, 2000; Vickaryous and Hall, 2008; Vickaryous and Sire, 2009). The histology of each of these dermal regions is unique and matches the histological organization of the cortices. The stratum superficiale is characterized by loose irregular connective tissue whereas the stratum compactum, by contrast, is dominated by large bundles of collagen fibres. These fibres are regularly distributed, with the deepest layers of the stratum compactum (=reticular dermis of synapsids) forming lamellar and orthogonal arrangements (Sire et al., 2009).

2.4.3 Core histology

The data indicate that, in both the extant and fossil material specimens examined, core histology is variable, although not with respect to taxon or osteoderm morphology. In the extant specimens, both from the same species, there is a dichotomy between a mixed Haversian/trabecular core and a completely trabecular core. In the fossil specimens, most exhibit mixed cores with the exception of two osteoderms from TMP 87.48.54, both of which are trabecular despite their different morphologies (square versus spine-like). Despite the ontogenetic stages of the animals, which are not known, all of the osteoderms may all be at the same stage of skeletogenesis in a single individual. Or it is possible that the possession of trabecular bone indicates calcium resorption by females and that it is the result of sexual dimorphism. Whereas crocodilians are known to reabsorb structural femoral bone for egg production, it is unknown whether or not the same is true for the osteoderms (Elsey and Wink, 1985; Wink and Elsey, 1986). Either way, in both the extant and fossil specimens, although histology of the osteoderm core may vary, it is always consistent in a single individual.

2.4.4 Cortical Variation and Relationships

There is a continuous trend in overall relative cortical thickness versus total osteoderm thickness in the two extant *Caiman* specimens examined. As osteoderm thickness increases, cortical thickness increases logarithmically; however, the relative thickness of the cortex decreases, also logarithmically. Therefore, the cortex makes up less of the overall osteoderm as the element becomes thicker.

In the combined analysis of fossil and recent specimens, there was a significant difference in cortical thickness between square and spine-like osteoderms. Conversely, the total cortical thickness was the same between the two osteoderm morphologies. This suggests that, as the osteoderm grows, the keel becomes hypertrophied and the core remodels. The core region then expands to create the change in shape from a square osteoderm to a spine-like one while the cortical thickness remains constant.

There is a trend relating relative cortical thickness to absolute osteoderm thickness. As thickness increases, the relative thickness of the cortex decreases. In the case of lateral spines, which are modified versions of the basic square morphology, this trend also holds true. However, these osteoderms can also be distinguished on their low relative cortical thickness alone. Therefore, there is evidence to show that, whereas osteoderm histology may follow similar trends, there are significant differences between osteoderms of different shapes/functions. This is an important consideration for the taxonomic homologies of different osteoderm morphotypes as well as the assignment of osteoderms to specific taxa. It is necessary to keep in mind that, although one osteoderm of an individual has a given histology, not all will necessarily share that exact histology. Therefore, it is important when comparing osteoderms across individuals or taxa to ensure that they all share a similar function and/or similar placement on the body.

Chapter 3 Osteoderm Variation Across Tetrapoda

3.1 Introduction

Osteoderms are widespread throughout the Vertebrata (Vickaryous and Sire, 2009; Sire et al., 2009). In particular, in the Tetrapoda, these various osteodermal systems are highly variable, both morphologically and histologically (Goodrich, 1907; Francillon-Vieillot et al. 1990; Zylberberg et al. 1992; Sire & Huysseune, 2003; Vickaryous and Sire, 2009). Especially when assessing the taxonomic validity of osteodermal characters, it is important to understand what level of variation can be expected in and across taxa. For example, relative to ankylosaurs, the osteoderms of crocodilians tend to be morphologically conservative during the many millions of years the group has existed. In other lineages, however, this may not be the case. This chapter is a review of the variability of osteoderms in various tetrapod lineages for comparison with similar trends in the Ankylosauria.

3.2 Materials and Methods

As the primary focus of this work is variation in Archosauria, the extent to which other taxa were examined first-hand is limited. As a result, descriptions and comparisons are largely based on previously published information. Those taxa that were studied include members from Testudines and Xenarthra.

Two forelimb osteoderm specimens (TMP 80.16.1810, TMP 85.6.67) of the fossil turtle *Basilemys* were acquired for thin sectioning. Both specimens were impregnated with Buehler EpoThin synthetic resins under vacuum before grinding. The samples were then processed into thin sections with a thickness of about 60–80 μm, depending on the visibility of internal structures of interest instead of using a predetermined thickness. Finished slides were scanned with a Nikon Super Coolscan 5000 ED using polarized film.

Previously prepared histological sections and two dried, whole osteoderms from the nine-banded armadillo, *Dasypus novemcinctus* were also obtained for study. Histological sections were prepared by Vickaryous and Hall (2006) via decalcification in Tris-buffered (pH 7.0) 10% EDTA, dehydration in 100% ethanol, clearing in CitriSolv, and embedding in low melting paraffin at 54°C. Sections were cut on a microtome at 6–7 μm and mounted on 3-aminopropytriethoxy-silane-coated slides. Of four slides obtained one was unstained, one was stained with Mallory's trichrome, and two were stained with Masson's trichrome connective tissue stain (Witten and Hall, 2003). Sections were subsequently mounted with Di-n-butyl Phthalate in Xylene. All sectioned specimens were from adult individuals.

The whole *Dasypus* osteoderms were μCT scanned at the UALVP on a Skyscan 1174. CT slices were reconstructed into three-dimensional models using GeoMagic Studio 10 for examination.

3.3 Description and Comparisons

3.3.1 Basal Tetrapoda and “amphibians”

With respect to osteoderm histology, the basal tetrapod condition, that of a fibrolamellar cortex encircling a trabecular core, appeared early in the group’s evolution. Evolving from the crossopterygian cosmoid scale, the odontogenic component (retained in the scales in early sarcopterygians) is lost by the time of *Eusthenopteron* (Ørvig, 1957; Jarvik, 1980, Vickaryous and Sire, 2009). Osteoderm morphology can be highly variable and may range from small, granular ossicles to oval/spindle shaped osteoderms on a single individual (e.g., *Greererpeton*, Godfrey, 1989). Osteoderms were already present in the early larval stages of these animals, and during ontogeny both the morphology and histology of individual osteoderms change (Schoch, 2003; Witzman, 2007). A compact, fibrolamellar matrix remodeled into a compact cortex and trabecular core in the adults (Dias and Richter, 2002; Castanet et al., 2003). Osteoderms are also independently scattered among stem temnospondyl and anuran taxa (Trueb, 1973; Lynch, 1982; Fabrezi, 2006; Dilkes and Brown, 2007).

3.3.2 Testudines

The turtle carapace/plastron represents one of the most recognizable and dramatic manifestations of the vertebrate membrane skeleton in an extant organism. That notwithstanding, it is also a unique structure and does not exhibit development or evolution similar to the osteoderms of other tetrapods. Not completely confined to the dermis, the carapace instead receives direct contributions from the vertebrae and ribs during skeletogenesis. As a result, the carapace is excluded from the current study. Some turtle taxa, however, are known to have osteoderms on the limbs, which are developmentally and anatomically restricted to the dermis. From what is known, their histology is comparable to those of archosaurs: a compact cortex and a trabecular core, composed of woven and/or fibrolamellar bone and having evidence for some degree of remodelling (Barrett et al. 2002).

Descriptions of TMP 80.16.1810, TMP 85.6.67 (*Basilemys* sp.; Figs. 3.1, 3.2) are included together as they display similar morphology and histology. All *Basilemys* limb osteoderms examined have an elongate shape with a smooth deep surface. The superficial surface is characterized by two to three apices and a characteristic uniform hummocky sculpturing. No neurovascular grooves or foramina were observed on the superficial surface. Both show a thick superficial cortex (40% average) composed of fibrolamellar bone and a trabecular core (60% average). There is no deep cortex. The superficial cortex is thicker in TMP 85.6.67 (44%) than in 80.16.1810 (35%), although the sample size was too small to determine whether or not this difference was significant.

The cortical lamellae roughly follow the line of the superficial surface.

Some secondary osteons are sparsely scattered throughout the cortex.

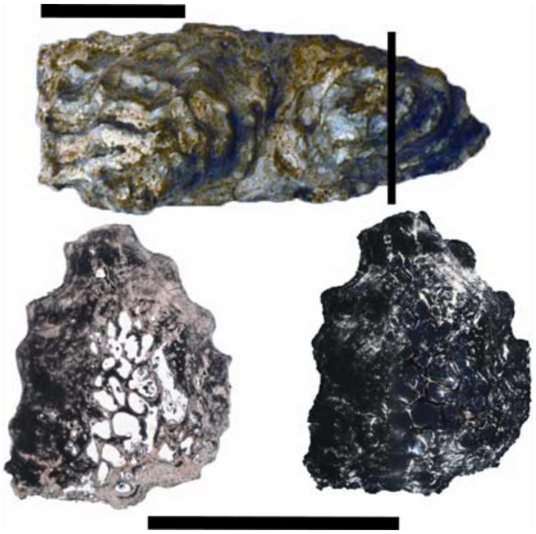


FIGURE 3.1. Forelimb osteoderm of *Basilemys* sp. (TMP 80.60.1810) in superficial view (orientation uncertain). The thin line indicates plane of thin section (below) in PPL and XPL (superficial is up). Scale bars equal 1 cm.

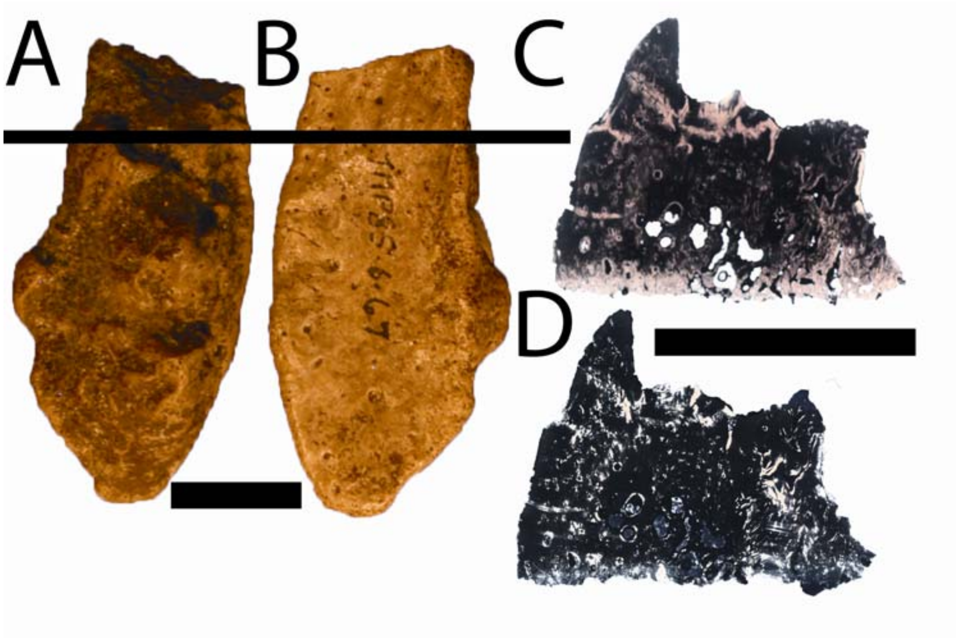


FIGURE 3.2. Forelimb osteoderm of *Basilemys* sp. (TMP 85.6.67) in superficial view (orientation uncertain). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). Scale bars equal 1 cm.

3.3.3 Pareiasauridae

The pareiasaurs exhibit a morphocline with respect to osteoderms covering the dorsum from a single pair of parasaggital rows in basal forms to an expansive mosaic of tightly interlocking elements in derived taxa. Despite the resulting morphological diversity of their osteoderms, their osteoderm histology is relatively consistent throughout the lineage and is distinct among tetrapods. Scheyer and Sander (2009) described the histology of three representative pareiasaurs: *Bradysaurus*, *Anthodon*, and *Pareiasaurus*. External cortices are highly vascular fibrolamellar bone invested with Sharpey's fibers. The core is trabecular. The deep cortex is similar in histology to the superficial cortex, although it tends to be thicker. LAGs are well-developed in both cortices but a fundamental system (indicative of slowing growth with old age) is not observed in any osteoderm.

3.3.4 Placodontia

Osteoderms are not plesiomorphic for placodonts as evidenced by their absence in the basal *Paraplacodus*. In the more derived *Placodus*, they appear as a single sagittal row of osteoderms dorsal to the spinal column. In the more highly-derived Cyamodontoidea, osteoderms fuse to create a solid carapace (superficially similar but not homologous to the turtle carapace). Despite their highly divergent morphologies, osteoderms are histologically consistent across placodont taxa. These elements are completely compact and incorporate Sharpey’s fibres into the superficial and deep cortices. The core is composed of woven bone. The few vascular spaces consist of scattered primary osteons. There is no evidence for a trabecular core or extensive secondary remodeling in any placodont osteoderm (Scheyer, 2007). Based on the few juvenile specimens, osteoderms developed post-embryonically and mineralized in an anterior-to-posterior progression (Vickaryous and Sire, 2009).

Scheyer (2007) reported the unique presence of cartilaginous tissue retained in placodont osteoderms. This is distinct from all other tetrapods, in which osteoderm formation occurs metaplastically or intramebranously without a cartilage precursor. This identification was based upon a tissue resembling fibrocartilage: large, spherical lacunae that, in some cases, aligned into isogenous groups. Vickaryous and Sire (2009) note that the loss of unmineralized tissues in fossil specimens could create the appearance of large lacunae. Therefore, it is also possible that these spaces represent former passages for unmineralized collage fiber bundles.

3.3.5 Lepidosauria

In the Lepidosauria, osteoderms are widespread in the anguimorphs, geckos, and skinks (Gadow, 1901; Camp, 1923; McDowell and Bogert, 1954; Read, 1986; Estes et al., 1988; Gao and Norell, 2000; Maisano et al., 2002; Barrett et al., 2002; Krause et al., 2003; Vickaryous and Sire, 2009). They are also highly variable in this group and can provide taxon-dependent characters.

Skink osteoderms exhibit superficial sculpturing that has been used in systematic and phylogenetic studies of that group. However, this feature can also vary in a single individual with ontogeny and/or according to location on the body (Oliver, 1951).

Dermal ossifications are rare among gekkotans, although they have been described for the head and body of several members of the subfamily Gekkoninae (Cartier, 1872, 1874; Leydig, 1876; Ficalbi, 1880; Otto, 1908; Schmidt, 1912, 1915; Kluge, 1967; Levrat-Calviac and Zylberberg, 1986; Bauer and Russell, 1989).In the gekkonid *Tarentola*, distributions of dermal ossifications on the body are variable among species. Two distinct histological layers, an acellular superficial layer and deep fibrolamellar layer, characterize these osteoderms (Leverat-Calviac and Zylerberg, 1986; Vickaryous and Sire, 2009). These layers correspond to and reflect the general histological structure of the dense and loose layers of the dermis in which they develop (Leverat-Calviac and Zylerberg, 1986).

In anguids, the superficial layer is composed of woven bone, and the thicker deep layer lamellar bone (Moss, 1969; Zylerberg and Castanet, 1985; Leverat-Claviac et al., 1986; Vickaryous and Sire, 2009). Collagen fibers in this deep layer exhibit highly organized orthogonal arrangements (Zylerberg and Castanet, 1985). Osteoderm growth and development has also been examined in some anguids. In particular, in the platynotan *Heloderma horridum* (Moss, 1969), mineralization in the integument begins medially in the cranial region and extends posteriorly and laterally throughout ontogeny. In helodermatids, osteoderm histology is a blend of woven to fibrolamellar bone and unmineralized dermal tissue, although they also possess a thin superficial layer (Moss, 1969; Smith and Hall, 1990).

3.3.6 Synapsida

With the exception of two Late Permian species, synapsids that have osteoderms are restricted to the Xenarthra (Reisz et al.,1998; Both-Brink and Modesto, 2007; Reisz and Modesto, 2007; Vickaryous and Hall, 2006) and are most prevalent in the Cingulata, which includes glyptodonts and armadillos (Vickaryous and Hall, 2006). For most of the Tertiary, the Xenarthra was a more diverse clade than it is today (Patterson and Pascual, 1968; Marshall and Cifelli, 1990; Fariña, 1995; McDonald, 2005; Croft et al., 2007). Still, the osteoderms of cingulates are generally of two morphs: interlocking polygonal osteoderms, and mobile, imbricating, rectangular osteoderms (Hill, 2006). The osteoderms of extinct pampatheres exhibit morphological trends similar to those of extant armadillos (Engelmann, 1985). The glyptodonts, on the other hand, had a rigid “carapace” made up solely of fused or tightly articulating polygonal osteoderms (Gillette and Ray, 1981; Engelmann, 1985).

Despite these broad taxonomic patterns, there is still a high degree of morphological and histological diversity in the osteoderms of xenarthran mammals. Osteoderms of different species exhibit unique surface textures. They are also often histologically variable to accommodate specialized associations with soft tissues. The histological structures described in fossil specimens are also diverse, ranging from compact, avascular tissue to heavily remodelled Haversian bone (Hill, 2006).

Osteoderms of the two morphologies from the extant *Dasypus novemcinctus* were examined. Band osteoderms (Fig. 3.3) are subrectangular and elongate with two distinct regions. The anterior portion is relatively smooth, with sparse, randomly distributed neurovascular grooves and foramina. The posterior portion, on the other hand, is ornamented with two pairs of foramina rows that diverge from the osteoderm midline posteriorly. Foramina in the outer row are specialized to support hair follicles in a 1:1 ratio. A series of large foramina along the posterior edge of the osteoderm also support one hair follicle each. In articulation, the posterior portion of the osteoderm overlaps the anterior portion of the osteoderm directly posterior to it. This is a mobile articulation, evidenced by the smooth deep surfaces of these osteoderms, allowing the elements to slide over one another and the animal a greater degree of movement. According to Vickaryous and Hall (2006), each osteoderm is overlain by a complex system of scales that allow for this degree of articulation.

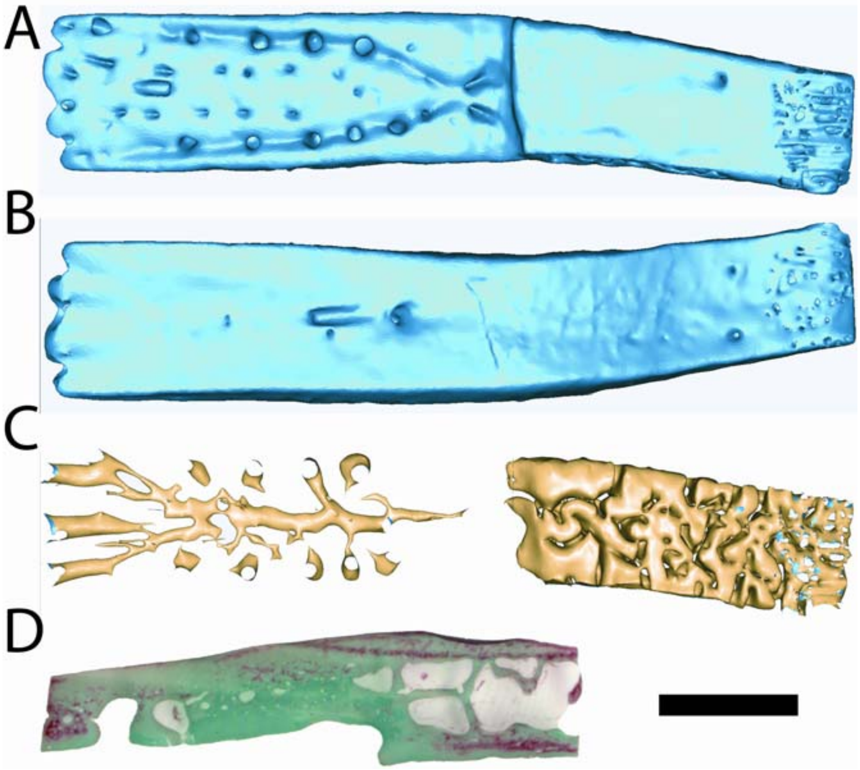


FIGURE 3.3. Elongate band osteoderm from adult nine-banded armadillo, *Dasypus novemcinctus*. Three dimensional computer models (GeoMagic Studio 10 derived from µCT scan data) in superficial (A) and articular (B) views. Internal spaces may be viewed by digitally removing the outer surface of the 3D model (C). A histological section was cut longitudinally (D) and stained with Masson's trichrome. Scale bar equals 5 mm.

The polygonal osteoderms (Fig. 3.4) of the pectoral and pelvic regions form mosaic, solid bony bucklers. The deep surfaces of these osteoderms are relatively smooth, with only a few neurovascular foramina perforating each surface. They are, however, superficially ornamented with several foramina connected by grooves, matching in shape the overall outline of the osteoderm itself. Osteoderms do not fuse to their neighbors, but rather contact each other in vertical, interdigitating sutural butt joints (the same is true for the articulating surfaces of adjoining band osteoderms). Overlying each osteoderm is a series of polygonal, keratinized, epidermal scales. These are aligned with the pattern of superficial grooves on the underlying osteoderm and are not aligned with the osteoderms themselves. In fact, superficial grooves may cross over to adjacent osteoderms, creating a pattern of smaller overlying scales that does not correspond to the polygonal pattern of osteoderms below.

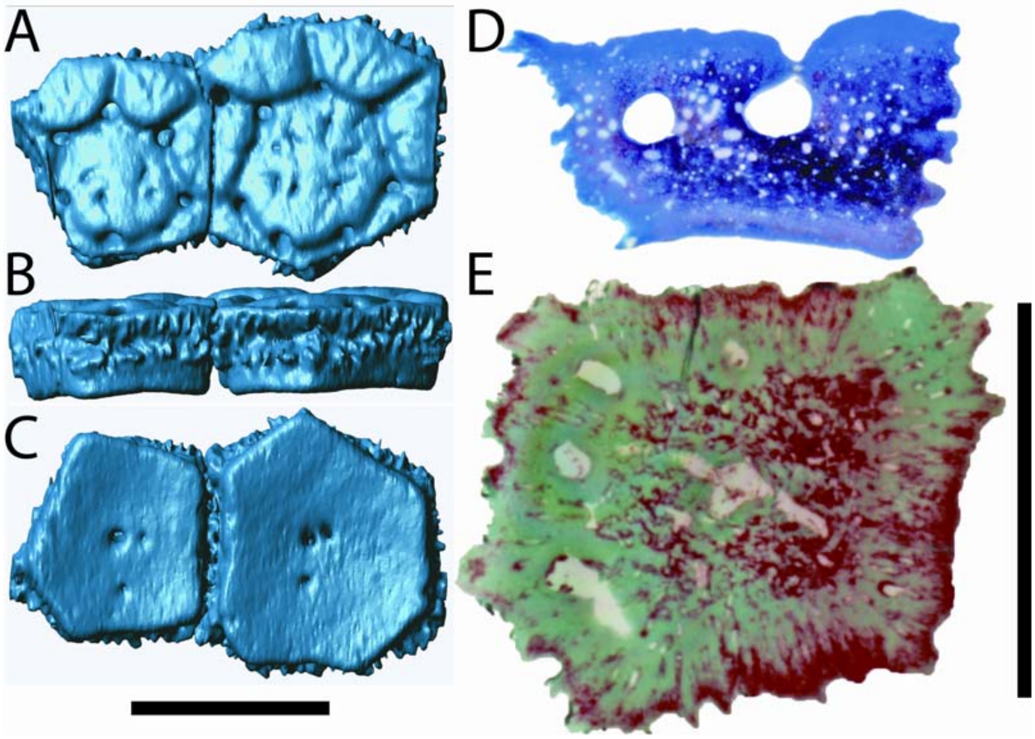


FIGURE 3.4. Polygonal pectoral or pelvic articulated osteoderms from adult nine-banded armadillo, *Dasypus novemcinctus*. Three dimensional computer models (GeoMagic Studio 10 derived from µCT scan data) in superficial (A), articular (B), and deep (C) views. Histological sections were cut longitudinally (D, Mallory's trichrome) and transversely (E, Masson's trichrome). Scale bars equal 5 mm.

Histological sections of polygonal osteoderms are composed almost entirely of fibrolamellar bone, with only a few primary and secondary osteons visible near the center of the element. The margins are characterized by dense concentrations of Sharpey's fibres, likely corresponding to ligamentous attachments to the adjoining osteoderms.

The posterior portion of band osteoderms shares a similar histology, exhibiting remodeling to accommodate the inclusion of hair follicles and blood vessels later in skeletogenesis (Vickaryous and Hall, 2006). The anterior portion, however, contains fibrolamellar bone only in a circumferential cortical region. The core of this portion is instead composed entirely of trabecular bone.

Skeletogenesis of osteoderms begins anteromedially and progresses posteriorly and laterally independently in each body section (Wilson, 1914). Also, Vickaryous and Hall (2006) note that there is no evidence of dermal collagen fiber incorporation into the mineralizing osteoderm. This would suggest that these elements do not form initially via tissue metaplasia, as is the case with the other taxa investigated in this study. However, Hill (2006) reported that many xenarthran osteoderms shared a high content of mineralized fibre bundles. This disparity is likely the result of confusion over the nature of Sharpey's fibres, which are classically defined as a collagenous interaction between a periosteum and bone lamellae (Dorland, 2003). As this usually applies to endochondral bones or those of the dermatocranium, the term is often associated with tendinous or ligamentous insertions into bone. In cases where similar mineralized tissues could not be correlated with such structures, other terms have been employed (e.g., "structural fibres" *sensu* Scheyer and Sander, 2004). Therefore, it is likely that the bundles observed by Hill

(2006) are analogous to the Sharpey’s fibres described by Vickaryous and Hall (2006).

3.4 Discussion

A broad comparison of osteoderm morphology and histology across disparate tetrapod taxa reveals several important trends. First, there is a tendency in some taxa to display distinct osteoderm morphologies in distinct body regions. In lepidosaurs, most body osteoderms have a relatively uniform morphology throughout the body, including cranial osteoderms. In crocodilians, osteoderms of the cervical region are distinct and identifiable to the species level (Chapter 2). Whereas all osteoderm-bearing cingulates possess polygonal osteoderms, some have a uniquely elongate morphology in the thoracic region. This is correlated with their specific and specialized defensive behaviour. For example, the Southern Three-Banded Armadillo, *Tolypeutes matacus*, is capable of rolling into a complete ball to defend itself.

In addition to exhibiting varied morphologies, osteoderms associated with different regions/functions also show different histology. Again, this is evident in the specialized band osteoderms of xenarthrans. Therefore, a unique or divergent histology may indicate a specialized function for that element. However, as evidenced by the uniqueness of a turtle carapace, it may also reflect a distinct developmental/evolutionary path. In some of these regions, namely pectoral and pelvic, there is a tendency for fusion or tighter articulation in which there is a reliance on osteoderms for defense. The testudine carapace demonstrates the extreme manifestation of this tendency. The mosaic of tightly interlocking osteoderms in xenarthrans also reflects this inclination, although the band osteoderms and absence of a plastron allow for the retention of more complex movement.

There is also a pattern of osteoderm development across all taxa examined: mineralization progressing in a lateral and posterior manner. In armadillos, this developmental pattern is roughly synchronized in the pectoral, thoracic, pelvic, and caudal regions. In lepidosaurs in which this has been examined, the pattern is not specific to region, but instead occurs across the entire body.

Chapter 4 Variation in Ankylosaur Osteoderms

4.1 Introduction

There have been many published descriptions of the gross morphology of ankylosaur osteoderms, most of which have not utilized standardized terminology or comparative material (see assessment by Coombs, 1971). A few studies have attempted to homogenize the way in which these elements are described. Blows (2001) categorized the dermal elements of polacanthids into 13 distinct morphological categories; however, this system was not adapted in other publications. Ford (2000) also presented a more concise terminology for ankylosaur osteoderms. This was adopted by Burns (2008) and is retained here with revisions (Chapter 1).

There has been a recent surge in studies examining the histology of ankylosaur osteoderms. Scheyer and Sander (2004) presented the first systematic way for investigating these elements and standardized shape categories for the various osteoderm morphologies, which is used here in part. Hayashi et al. (in press) followed the procedures of Scheyer and Sander (2004), increasing the sample size, and investigating differences between modified and unmodified osteoderms. Although these studies identified taxonomically useful characters, they used them to make inferences about ankylosaur systematics without phylogenetic testing.

The purpose of this study is to incorporate both external (morphological) and internal (histological) features into a comprehensive survey of ankylosaur osteoderms. In addition to increasing the available sample size, a large comparative sampling of extinct and extant outgroup taxa will be investigated. Tentative osteoderm characters will also be quantitatively evaluated for the first time.

4.2 Materials and Methods

Osteoderms were examined from North American and Asian nodosaurid, ankylosaurid, and polacanthid taxa as well as specimens of the basal thyreophoran *Scelidosaurus*. External variation in osteoderm shape and texture among these specimens was studied through measurements, observations, and photographs. For descriptions of surface textures, a standardized system was used that follows six categorical values established by Hieronymous et al. (2009, fig. 4).

When available, representative osteoderms were selected for palaeohistological 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 to a high gloss using CeO_2 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 for statistical analyses were taken from imaged slides using ImageJ 1.40g.

Due to the overwhelming number of osteoderm specimens available for observation, gross anatomy of these elements is not listed for each specimen. Instead, an overall description for individual taxa is given. For histological sections, each specimen is described in detail.

4.3 Results

4.3.1 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 an excavated base) and are superficially relatively smooth, exhibiting sparse pits. There are two cervical half rings, although osteoderms in this region are not fully fused but articulate via interdigitating sutures. There is no osteoderm fusion anywhere else on the body. Compared with derived ankylosaurs, osteoderm morphology is fairly homogenous across the body, conical in shape grading towards more elongate laterally and posteriorly. This produces dorsoventrally compressed, triangular lateral osteoderms. The caudal region is completely encircled by free-floating osteoderms.

UOP 03/TS2 is described by Scheyer and Sander (2004). It is a spine with an oval cross-section formed by a hypertrophied keel of the osteoderm. The base is strongly concave, making the osteoderm walls equally thick throughout. Although originally described as rugose (Scheyer and Sander, 2004), the superficial surface is actually smooth relative to more derived ankylosaur osteoderms, exhibiting only sparse pitting. The cortices are thin (both 6%) and composed of fibrolamellar bone invested with structural fibers arranged at regular angles to the osteoderm surface. The core is thick (87%) and entirely trabecular, containing no structural fibers or osteons.

4.3.2 Nodosauridae

***Edmontonia*—**The genus *Edmontonia* is represented by several well-preserved specimens of *E. rugosidens* and *E. longiceps*. Their osteoderm morphology differs in the cervical half rings. Medial osteoderms of the first and second half ring in *E. rugosidens* are square to polygonal and have posteriorly divergent keels. Those of *E. longiceps* have more rounded edges and their shape in superficial view is more laterally skewed. Distal osteoderms of the second half ring are modified into anterolaterally-drected spines. Similar spines are found in the distal position on the third half ring that exhibit various degrees of bifurcation in different specimens, but they project more laterally in *E. longiceps*. Posterior to this is a pair of distal thoracic spines, one anteriorly and one posteriorly projecting. This pair of osteoderms may be fused together or not depending on the individual specimen. Over the dorsum of the thoracic region, osteoderms are circular with low keels. This changes to transversely oval osteoderms, also with low keels, over the pelvic region.

TMP 98.98.1, includes a well-preserved skull so it is unequivocally identifiable as *Edmontonia rugosidens* (Vickaryous, 2006; Fig. 4.1). Along with the first cervical half ring, which is attached to the back of the skull, much of the postcrania is preserved, including dermal spines and osteoderms. Several ossicles and one osteoderm (oval and flat) were selected for analysis from this specimen. All osteoderms possess the same surface texture: a strong, uniform, pitted rugosity with sparse, reticular neurovascular grooves, and normal to obliquely oriented neurovascular foramina.

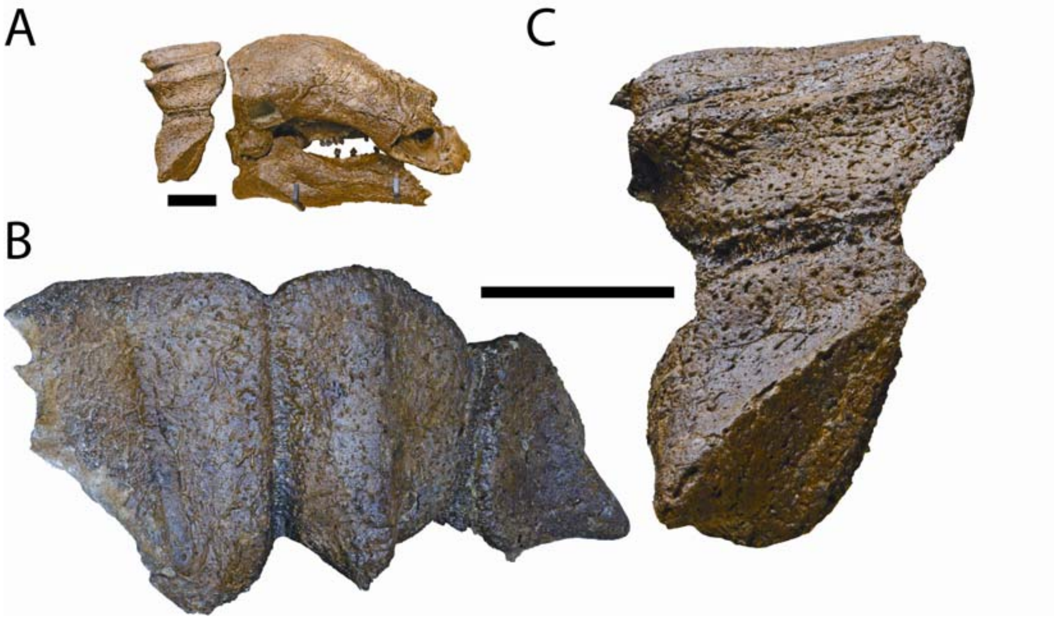


FIGURE 4.1. Skull, mandible, and first cervical half ring of *Edmontonia rugosidens* (TMP 98.98.1). A, mounted skull, mandible, and first cervical half ring in right lateral view(anterior is to the right); B, detail of first cervical half ring in dorsal view; C, detail of first cervical half ring in right lateral view. Scale bars equal 5 cm.

The sectioned osteoderm (Fig. 4.2 A) is of a flat morphology with an oval shape. It has both a superficial and deep cortex. The superficial cortex is relatively thick (52%) whereas the deep cortex is thin (13%). Both consist of woven bone with highly ordered, dense structural fibers. The thin (36%) core is composed of a mixture of Haversian and trabecular bone. The two cortices merge near the margins of the osteoderm and pinch out the cortex. A section taken near the anterior/posterior margin shows only woven bone where remodeling has not created a core region. The smaller ossicles (Fig. 4.2 B, C, D) associated with this specimen show varying histologies in thin section. Only two are differentiated into three regions. Their superficial cortices are composed largely of fibrolamellar bone with many observable LAGs, although this organization becomes less regular in one region (=?deep) on both ossicles. These ossicles also possess a Haversian core that grades into a woven deep cortex. The deep cortex is of a similar thickness in both (17% and 18%); however, the superficial cortex is relatively thick and differs between the two (35% and 60%). The third ossicle displays a different histology, consisting of undifferentiated woven bone and a dense network of orthogonally-oriented structural fibres.

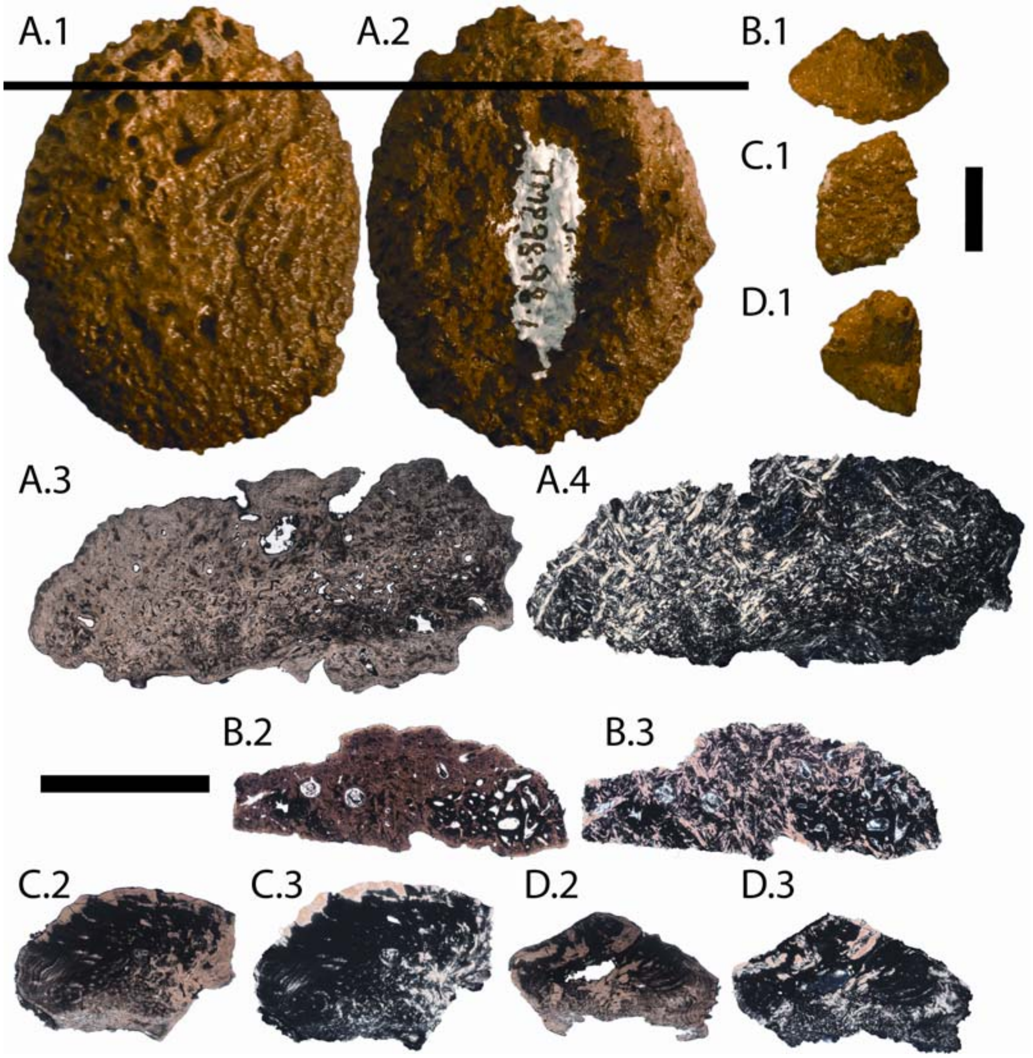


FIGURE 4.2. Thoracic osteoderm (A) and interstitial ossicles (B–D) of *Edmontonia rugosidens*. Osteoderm is shown in superficial (A.1) and deep (A.2) views. Orientation of ossicles uncertain. The thin line in A indicates plane of thin section in PPL (A.3) and XPL (A.4). Ossicle sections are shown in PPL (B.2, C.2, D.2) and XPL (B.3, C.3, D.3) Superficial is up in all sections. Ossicle histology in some cases (B) matches the woven bone in the larger unmodified osteoderms (A). In others, however, ossicles histology is different (C and D display fibrolamellar and Haversian bone). Scale bars equal 1 cm.

Two nodosaur lateral spines, identified as *Edmontonia* sp. (DMNH 2452 and TMP 79.147.94), are described by Hayashi et al. (in press). DMNH 2452 is characterized by a smooth superficial surface with a sparse reticular pattern of neurovascular grooves. The base is flat. The superficial cortex is woven, comprises 14% of the total osteoderm thickness, and lacks visible LAGs. The deep cortex is poorly developed (2%). The thick (84%) core is trabecular and invested with large vascular canals that connect neurovascular openings on the osteoderm base with the grooves on the superficial surface. In the superficial cortex, two distinct systems of dense orthogonally arranged structural fibres are observable under XPL. Some secondary osteons are visible where the superficial cortex contacts the core.

TMP 79.147.94 was sectioned in four locations along its length by Hayashi et al. (in press). The surface is ornamented with sparse, uniformly distributed pits. Only one neurovascular groove/foramen is visible near the apex. Histologically, it resembles other nodosaur osteoderms in the lack of a deep cortex and the presence of a thick trabecular core. The spine is produced by the hypertrophied growth and remodeling of the osteoderm keel or apex. The cortex is relatively thinner near the base (10%) than at the apex (17%).

***Panoplosaurus*—**Whereas no specimens of *Panoplosaurus* have been sectioned, diagnostic morphological characters may be derived from several specimens namely the holotype (CMN 2759) and ROM 1215, which includes a skull, postcrania, and numerous disarticulated osteoderms. Superficial osteoderm texture is pitted with a relatively dense reticular pattern of neurovascular grooves. Medial osteoderms of the cervical half rings are suboval and the posteriorly diverging keels curve laterally. Lateral and distal osteoderms are transversely elongate and have relatively high, sharp keels. The arrangement of the osteoderms on the remainder of the body is not known.

***Glyptodontopelta mimus*—**Three osteoderms from SMP VP-1580 (C, D, and E; Figs. 4.3–4.5) were obtained from a referred specimen of *Glyptodontopelta*. C is a portion of a keeled osteoderm (Morphotype A or B, *sensu* Burns, 2008) whereas D and E are flat, although superficially concave (Morphotype D). The texture of each of the three is characterized by a relatively smooth surface and a dense pattern of reticular neurovascular grooves, which is a diagnostic character for the genus. Neurovascular foramina are oriented obliquely to the surface. This specific dense pattern of superficial grooves is not observed in other ankylosaur taxa and is diagnostic for this genus and species (Burns, 2008). The woven superficial cortex is of average thickness (14%) and the core is composed of compact Haversian bone. A deep cortex is absent from specimens C and E but is present in D as a poorly-developed thin (2%) layer of woven bone.

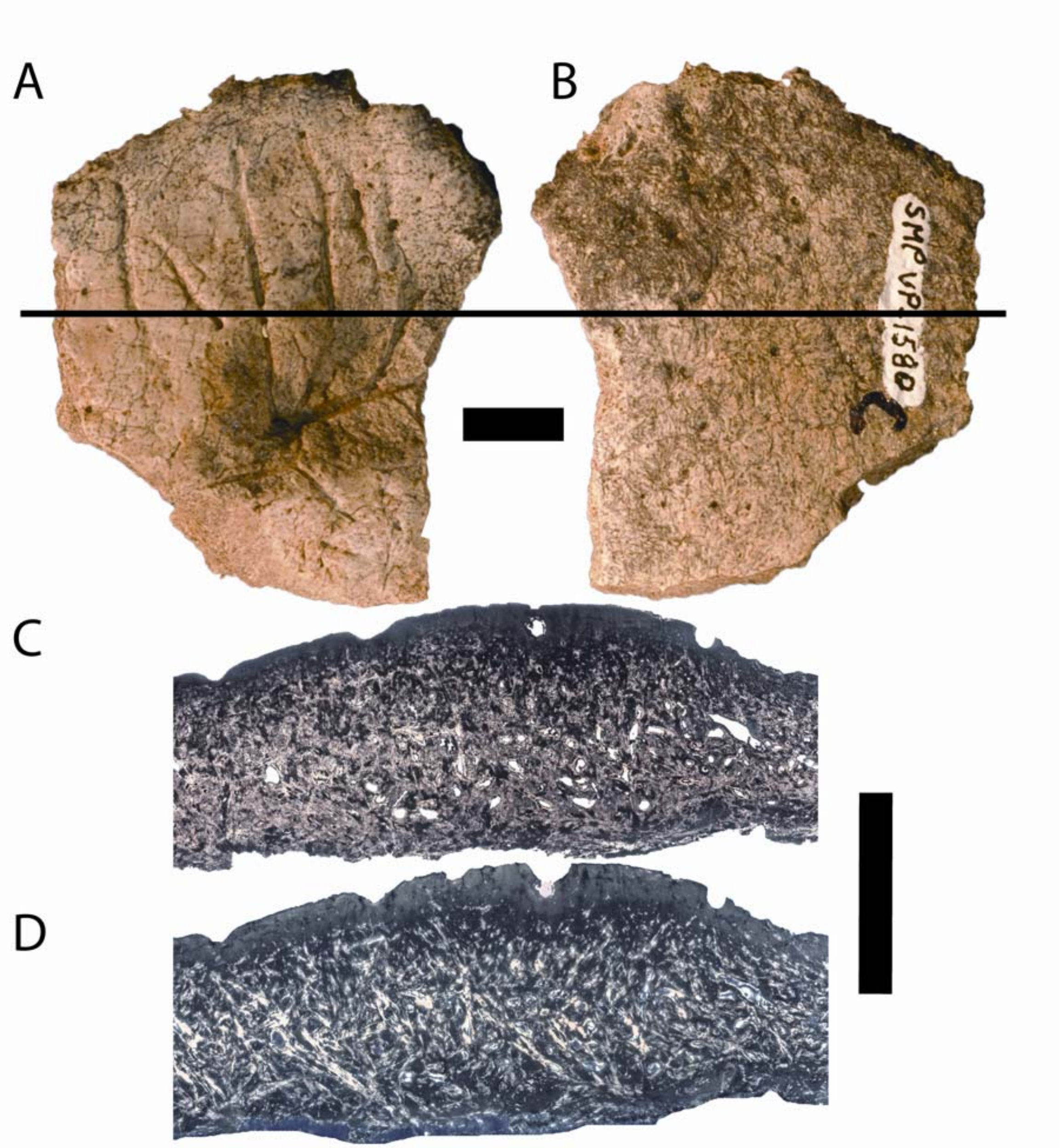


FIGURE 4.3. Thoracic osteoderm of *Glyptodontopelta mimus* (SMP VP 1580 C) in superficial (A) and deep (B) views (orientation uncertain). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). Numerous, prominent structural fibers are visible in a regular arrangement in PPL in D. Scale bars equal 1 cm.

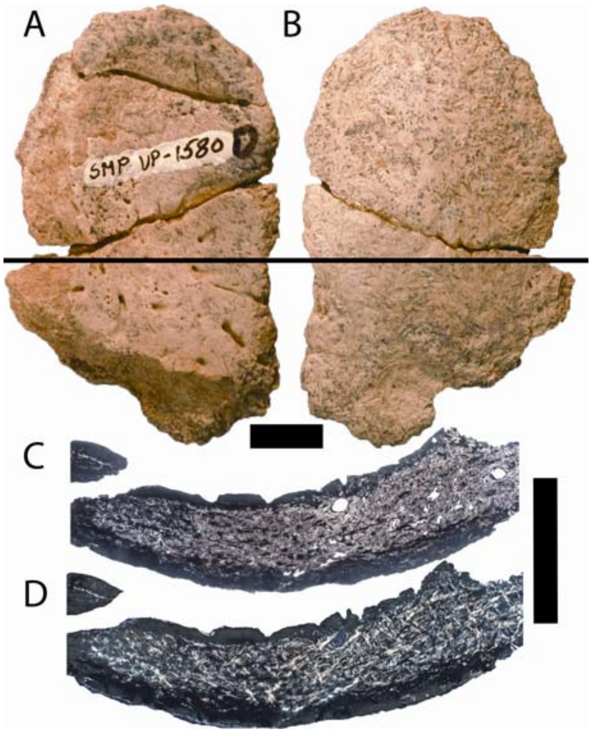


FIGURE 4.4. Thoracic osteoderm of *Glyptodontopelta mimus* (SMP VP 1580 D) in superficial (A) and deep (B) views (orientation uncertain). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). An orthogonal array of structural fibers is visible throughout the osteoderm core. Scale bars equal 1 cm.

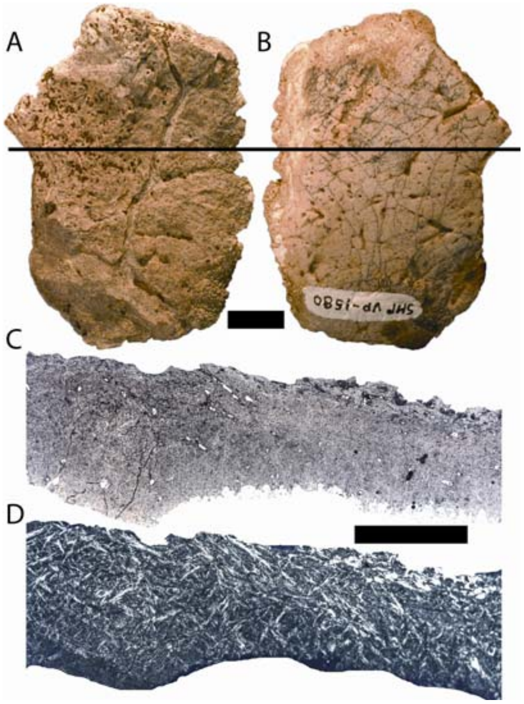


FIGURE 4.5. Thoracic osteoderm of *Glyptodontopelta mimus* (SMP VP 1580 E) in superficial (A) and deep (B) views (orientation uncertain). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). Structural fibers are pronounced in the superficial cortex (D). Scale bars equal 1 cm.

***Sauropelta*—**A skeleton of *Sauropelta*, AMNH 3036 is the most complete nodosaur specimen yet found and preserves a complete series of articulated postcervical osteoderms. AMNH 3035 completes the cervical series and has a partial *in situ* skull. All three cervical half rings have two paired osteoderms: medial and lateral. Medial osteoderms are oval with a rounded posterior apex. Lateral osteoderms are modified into transversely elongate triangular spines that project posterolaterally with a sharp anterior 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* sp. (DMNH 18206) were sectioned by Hayashi et al. (in press). One is keeled whereas the other, smaller (roughly one quarter the size) is circular with an offset apex. Both exhibit a uniform, pitted surface rugosity and a sparse, reticular pattern of neurovascular grooves. The base is slightly concave in each. Also, neither specimen has a deep cortex, the thick (86% average) trabecular core instead being exposed at the base. The superficial cortex is, by contrast, well-developed and of average thickness (14% average) and is composed of woven bone without observable LAGs. Secondary osteons are found at the border between cortex and core. There are several, however, near the base, in the trabeculae. Structural fibers are dense in the superficial cortex an arranged either perpendicular or parallel to the surface.

Nodosauridae indet.—TMP 67.10.29 is an isolated, keeled nodosaurid osteoderm from the Upper Cretaceous Dinosaur Park Formation, Alberta, Canada, that was sectioned by Scheyer and Sander (2004). Based on provenance, it is assignable to either *Edmontonia* or *Panoplosaurus*. It is circular with an off-center apex. The superficial cortex is made of fibrolamellar bone and several LAGs, although faint, are visible. Structural fibres in this region are dense and highly ordered and arranged in two sets of orthogonal meshwork set at 45° to one another. The core is thick (92%) and entirely trabecular. There is a remnant of secondary compact bone on the deep margin of the osteoderm, but it makes up less than 1% of the overall element thickness. Few scattered secondary osteons are also found deeper in the superficial cortex.

4.3.3 Ankylosauridae

***Ankylosaurus*—**There are few specimens of *Ankylosaurus* itself (less than 10), resulting in a lack of osteoderms available for thin sectioning. Osteoderms of this taxon are diagnostically smooth (more so than any other ankylosaur) and have a distinctive pattern of prominent but sparse neurovascular grooves. The size and depth of these grooves approach the texture seen on many ceratopsian frill and craniofacial bones. Most of the osteoderms are flat, only sometimes exhibiting a low keel near the lateral margin. Others are similar to contemporaneous taxa and include medially keeled and flatter, circular osteoderms.

***Euoplocephalus*—** The osteoderms of *Euoplocephalus* are the most variable of any ankylosaur taxa. This has been in the past attributed to different sources, including the possibility of taxonomic differences (Carpenter, 1982; Penkalski, 2000; Arbour et al., 2009). Despite this, in all referred specimens, two cervical half rings have varying numbers of paired osteoderms fused to an underlying band of bone. These osteoderms are roughly circular with apices of varying heights. Thoracic osteoderms are similar in morphology, becoming more compressed in lateral positions. Osteoderms of the pelvic region are similar to that of *Sauropleta*, consisting of transverse bands of circular, apical osteoderms interspersed with a polygonal mosaic, also situated in the bands. These bands are repeated in the caudal region, but contain osteoderms with prominent keels.

Although there is confusion currently surrounding the status of some specimens referred to *E. tutus* (Arbour et al., 2009), TMP 96.75.1 (Fig. 4.6) is associated with a skull and can be unequivocally assigned to the taxon based on discreet cranial characters (Vickaryous and Russell, 2001). The osteoderm sectioned is not of definite body placement nor, as it is incomplete, can its overall shape be determined. The superficial surface is characterized by projecting, uniformly distributed rugosity and an absence of neurovascular grooves and foramina. The superficial and deep cortices are relatively thin (13% and 9%, respectively) and are composed of woven bone. The core is principally formed by compact Haversian bone.

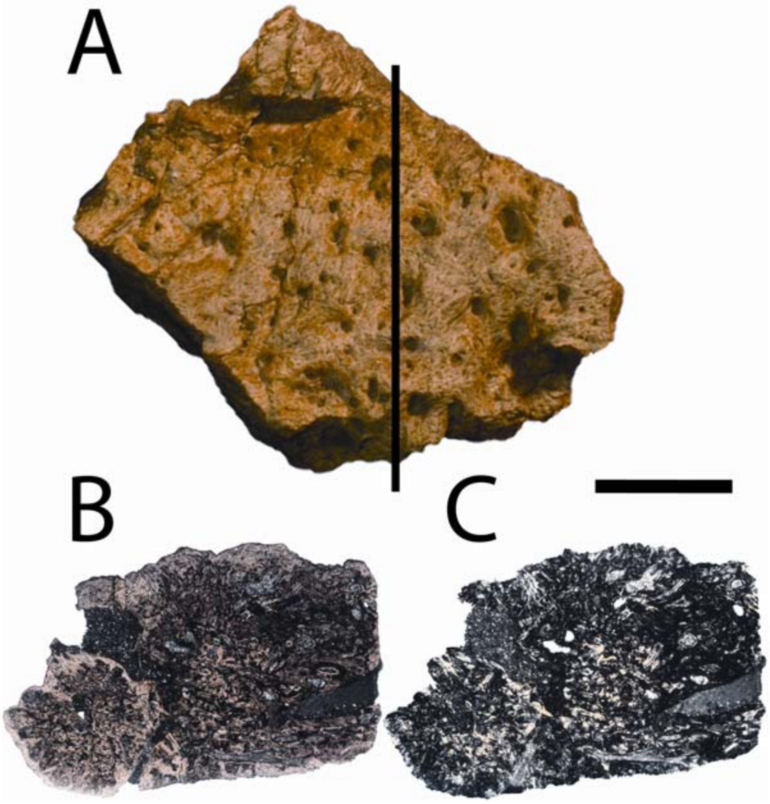


FIGURE 4.6. Osteoderm of *Euoplocephalus tutus* (TMP 96.75.1) in superficial (A) view (orientation uncertain). The thin line indicates plane of thin section in PPL (B) and XPL (C) (superficial is up). Structural fibers are diffuse throughout the osteoderm, which is largely composed of Haversian bone. Scale bar equals 1 cm.

UALVP 31 (Fig. 4.7) is associated with a complete skull and incomplete postcrania. Whereas its body placement is not known, the osteoderm studied was recovered in association with the pelvic region. The surface is smooth with no neurovascular grooves or foramina. The cortex is of average thickness (superficial 20%, deep 16%) and composed of woven bone, with dense structural fibres approaching orthogonal arrangement near the superficial and deep bone surfaces. The core grades smoothly into the cortex and consists predominantly of trabecular bone.

Several small, interstitial ossicles of the same specimen were also sectioned. Their superficial cortices are fibrolamellar bone complete with visible LAGs, although the cores are compact, composed of Haversian bone, and poorly-developed deep cortices are visible as thin layers of woven bone.

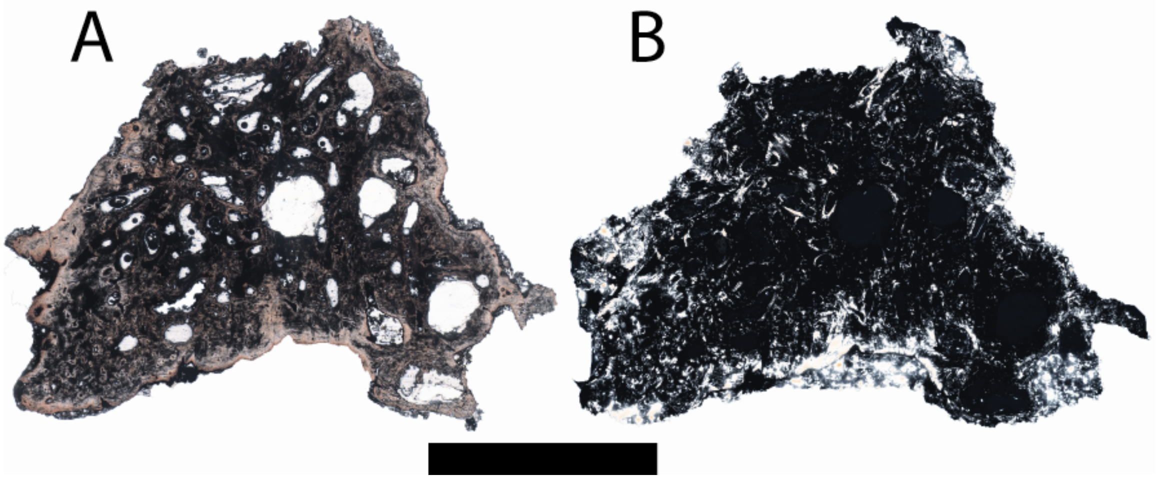


FIGURE 4.7. Thin section through an osteoderm of *Euoplocephalus tutus* (UALVP 31) in PPL (A) and XPL (B) (superficial is up). Several diffuse structural fibers are visible in the cortex but do not penetrate into the trabecular core. Scale bar equals 1 cm.

Nodocephalosaurus kirtlandensis**—**SMP VP 2067 is a referred specimen (Fig. 4.8) that was found near the same locality as other definitive specimens of *Nodocephalosaurus kirtlandensis*. As a fragment, the overall shape is unknown. The superficial surface has a uniformly distributed, projecting rugosity and sparse distribution of reticular neurovascular grooves. Neurovascular foramina are normally to obliquely inserted.

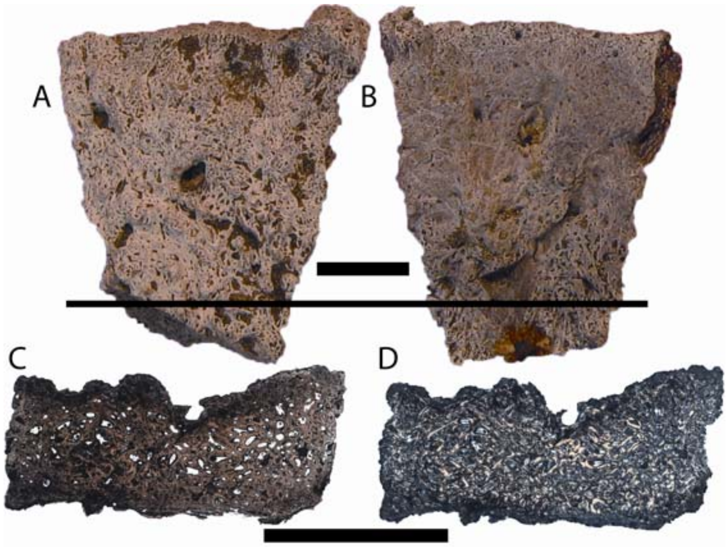


FIGURE 4.8. Thoracic osteoderm fragment of *Nodocephalosaurus kirtlandensis* (SMP VP 2067) in superficial (A) and deep (B) views (orientation uncertain). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). A few structural fibers are visible, scattered throughout the compact core. Scale bars equal 1 cm.

***Pinacosaurus grangeri*—**TMP 92.302.22 is a cranial osteoderm (Fig. 4.9) of *Pinacosaurus*, likely one of the supraorbital osteoderms, and was chosen because of a lack of availability of postcranial osteoderms from this taxon. Its superficial surface texture is unique and may or may not reflect the corresponding texture of postcranial osteoderms. It is smooth with an ordered pattern of grooves radiating away from the apex, although they are not neurovascular grooves. Internally, there has been extensive taphonomic alteration in the form of remineralization, and the cortex is not distinguishable. The original composition of the core is visible and consists of ordered Haversian bone. This is different from the largely random arrangement of Haversian canals seen in the postcranial osteoderms of other taxa.

Despite the lack of information provided by TMP 92.302.22, Scheyer and Sander (2004) also sectioned an osteoderm fragment from *P. grangeri* (ZPAL MgD-II/27). Its overall morphology cannot be determined, but the surface is completely smooth, lacking neurovascular foramina and grooves. The superficial (6%) and deep (17%) cortices are fibrolamellar. The core (77%) is composed of trabecular bone, although Haversian bone does occur at the junction of the core and cortex. Structural fibres are extensive throughout the osteoderm.

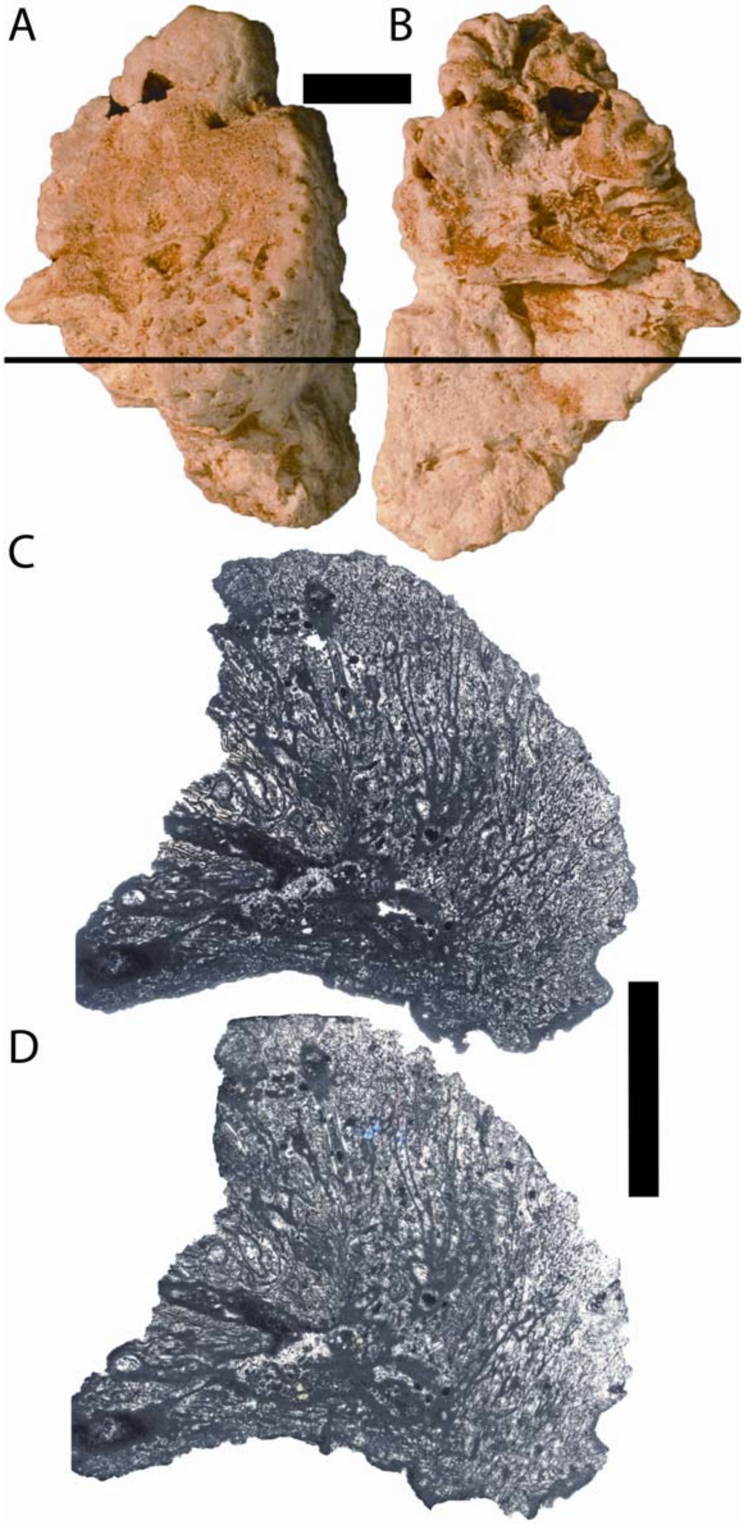


FIGURE 4.9. Cranial osteoderm of *Pinacosaurus grnageri*(TMP 92.302.22) in superficial (A) and deep (B) views (orientation uncertain). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). Although external morphology is well-preserved, the ostdoerm has been internally remineralized, taphonomically altering the histology of the element. Scale bars equal 1 cm.

4.3.4 Polacanthid-grade ankylosaurs

***Gargoyleosaurus parpkinorum*—** Two cervical half rings of *Gargoyleosaurus* are composed of six partially fused, paired keeled osteoderms (an unfused median osteoderm has been reported by Kilbourne and Carpenter, 2005, but is reinterpreted here as an odd number of osteoderms in unknown in any thyreophoran cervical band). Flat and keeled oval osteoderms characterize the thoracic region. Laterally, osteoderms of this region become elongate to triangular with deeply excavated bases. Pelvic osteoderms consists of larger and smaller osteoderms of a flat to apical circular morphology fused into a continuous buckler covering the pelvis.

One keeled osteoderm was described by Hayashi et al. (in press) and is associated with the holotype of *G. parkpinorum* (DMNH 27726). The superficial surface is smooth and lacks neurovascular grooves and foramina. The base is flat. Internally, the superficial and deep cortices are relatively thin (7% and 11% respectively) and consist of woven compact bone lacking LAGs. Few secondary osteons are scattered throughout the cortex, but are concentrated near the border with the core. The core is entirely trabecular. Structural fibers are dense throughout the cortex and exhibit an orthogonal arrangement.

***Gastonia*—**Two cervical half rings of *Gastonia* have triangular plates laterally, although there are not complete or articulated half rings preserved. Posteriorly, *Gastonia* possesses the same osteoderm morphologies as seen in *Gargoyleosaurus*. Osteoderms in the pelvic region are similarly fused into a continuous buckler. One unique osteoderm morphology displays a radially fluted texture not seen in other polacanthids but does occur in some specimens of *Euoplocephalus*. These are elongate spines that twist ~90° towards their apex.

Three specimens from DMNH 53206 were collected from a monospecific bonebed assemblage and, as such, can be confidently assigned to *Gastonia* sp. (they are labeled A, B, and C for convenience). DMNH 53206 A is a lateral spine, whereas DMNH 53206 B (Fig. 4.10) and C are both circular osteoderms with central apices. Each of the three specimens is characterized by a smooth superficial surface and a lack of neurovascular grooves and foramina. DMNH 53206 A possesses a thin cortex (8–10%) of woven bone. The thick (81%) core is composed of trabecular bone. The few osteons preserved in the cortex are secondary. The other two osteoderms also exhibit trabecular cores; however, the cortices are relatively thicker in both B (superficial 14%, deep 15%) and C (superficial 26%, deep 25%) to the point where the cores are pinched out laterally. The cortex in each is composed of woven bone consisting of prominent, orthogonally-arranged structural fibres. A single neurovascular foramen is visible in cross-section in DMNH 53206 C. It shows no bone modification surrounding it and cross-cuts the structural fibers in the osteoderm.

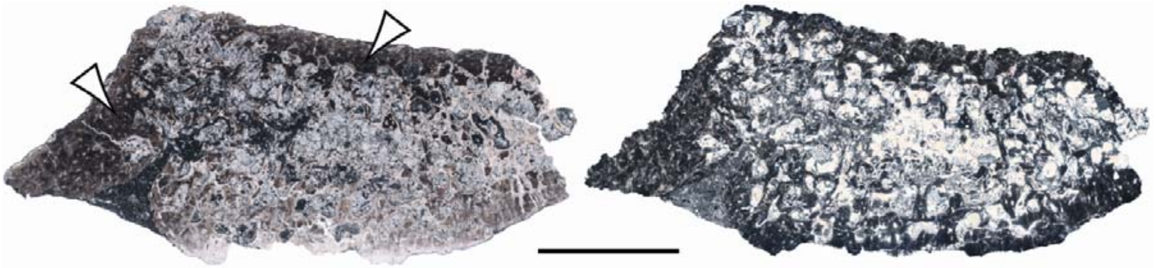


FIGURE 4.10. Transverse thin section through an osteoderm of *Gastonia* sp. (DMNH 53206 B) in PPL and XLP. Arrows indicate the superficial cortex. The core is trabecular and marked by numerous, large vacuities that have become infilled with mineral deposits. Superficial is up. Scale bar equals 1 cm.

DMNH 49754-1, DMNH 49754-4, and IPB R481 are osteoderms from the same monospecific bonebed assemblage as those described in the previous paragraph. DMNH 49754-1 and 2 were sectioned by Hayashi et al. (in press) and IPB R481 is described by Scheyer and Sander (2004). DMNH 49754-1 is a circular osteoderm with an offset apex whereas DMNH 49754-4 represents a spine. Most of the surface texture previously described for these specimens occurs on the margins and deep surfaces. The superficial surface is smooth and lacks neurovascular grooves and foramina. The deep and superficial cortices in both are composed of woven bone with the same orthogonal structural fibres seen in other specimens of *Gastonia*. Secondary osteons are rare throughout the osteoderms but, when present, occur at the transition between the cortex and core. The cortex is relatively thicker in DMNH 49754-1 (19%) than it is in DMNH 49754-4 (17%); however, the cortical thickness in the spine (DMNH 49754-4) varies from 22% at the base to 18% to 16% closer to the tip.

***Mymoorapelta*—**The hypodigm material of *Mymoorapelta* preserves five distinct osteoderm types similar to those of *Gastonia* and

Gargoyleosaurus: elongate spines with deeply excavated bases, dorsoventrally compressed lateral triangular osteoderms, also basally excavated, a smaller solid spine, flat and keeled thoracic osteoderms, and fused pelvic osteoderms.

MWC 211 (Fig. 4.11) represents a circular osteoderm with an off-center apex and a weakly excavated base, is from the Mygatt-Moore (middle Bushy Basin Mbr., Morrison Fm.) along with all other published material of *M. maysi*. The superficial surface is characterized by uniform, weak pitting and an absence of neurovascular grooves and foramina. Internally, the superficial and deep cortices are equally thick (21% and 23% respectively) and consist of woven compact bone lacking LAGs. No primary osteons are observed but several secondary osteons are scattered throughout the cortex. The core consists of trabecular bone. Structural fibers are dense and are found in both the core and cortex, comprising almost the entirety of the latter. In the cortex, these fibers are arranged orthogonally to the osteoderm surface and relative to one another.

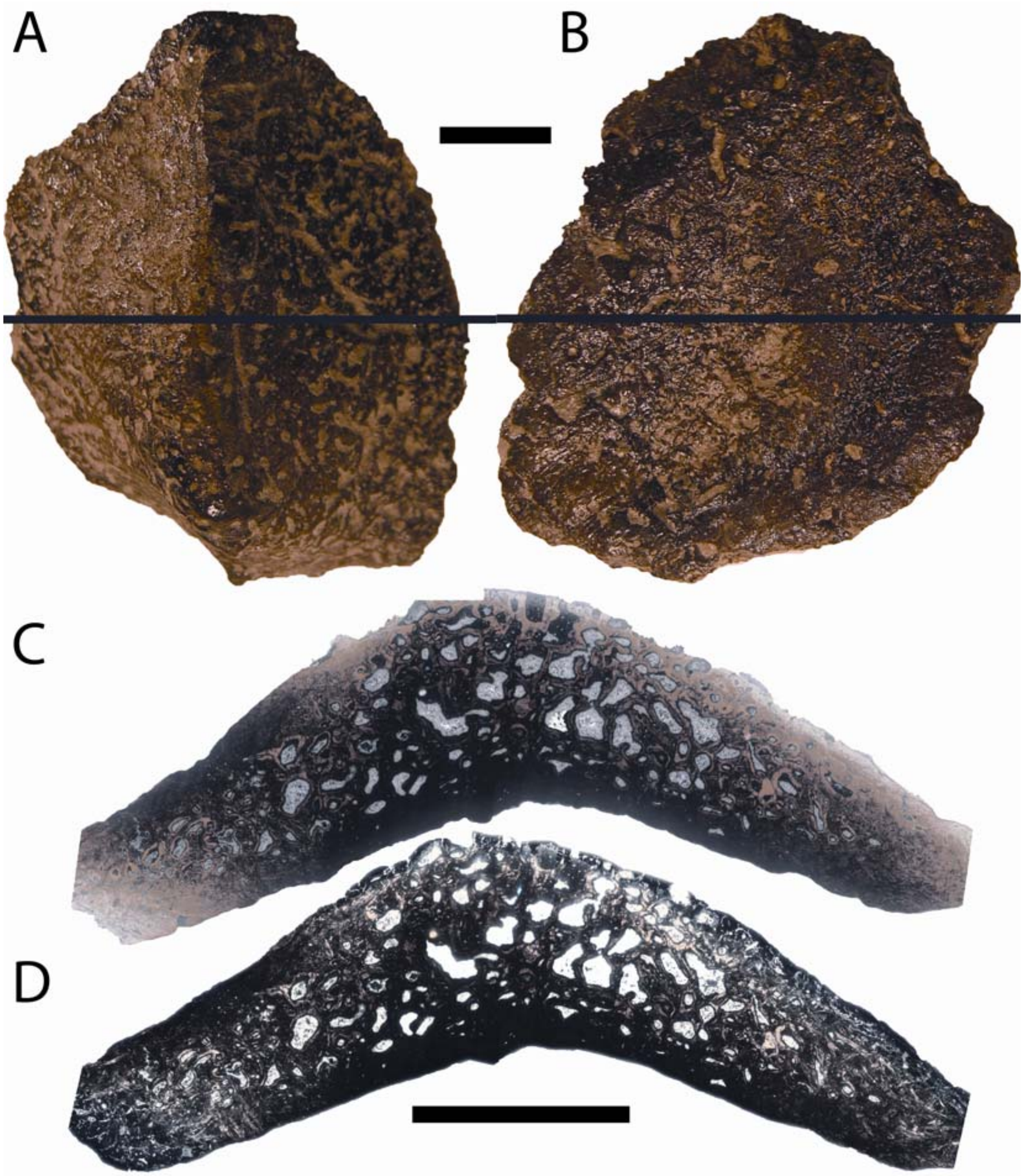


FIGURE 4.11. Thoracic osteoderm of *Mymoorapelta maysi* in superficial (A) and deep (B) views (anterior is up). The thin line indicates plane of thin section in PPL (C) and XPL (D) (superficial is up). Trabecular bone makes up the core (with thicker trabeculae than in osteoderms of Gastonia, Fig. 4.10). Scale bars equal 1 cm.

***Polacanthus*—**Cervical half rings in *Polacanthus* are composed of separated keeled osteoderms fused to an underlying band of bone. Spines of the anterior thoracic region and dorsoventrally compressed lateral osteoderms are similar to those of *Gastonia* and *Mymoorapelta*. A continuous buckler of fused osteoderms also existed in the pelvic region.

One osteoderm from *Polacanthus foxii* (BMNH R9293) was sectioned and is described by Scheyer and Sander (2004). It is circular with an off-center apex and a slightly convex base. The superficial and deep cortices are equally thick (both 14%) and composed of fibrolamellar bone. Structural fibers are denser in the deep than superficial cortex and approach an orthogonal arrangement closer to the deep margin of the osteoderm. In the superficial cortex, the fibers are mostly arranged perpendicularly to the surface. The core is composed of trabecular bone, but a few secondary osteons are visible where the core contacts the cortex. Interstitial primary bone in the core retains the structural fibers visible throughout the cortex.

4.3.5 Ankylosauria indet.

Several osteoderm fragments from the Hell Creek Fm. of Montana (TMP 87.113.4) probably represent a specimen of *Edmontonia longiceps* (Fig. 4.12), which is known to occur there. Two of the larger fragments indicate that this is a thoracic osteoderm with a weakly developed keel and a flat base. The superficial surface is smooth with a sparse reticular pattern of neurovascular grooves and obliquely to normally oriented neurovascular foramina. It is capped with a thick (36%) superficial cortex composed of woven bone. Structural fibers in this cortex are orthogonally arranged. The core is made up entirely of trabecular bone. There is no deep cortex as a layer distinct from the core. This is not a taphonomic artifact as the specimen is complete.

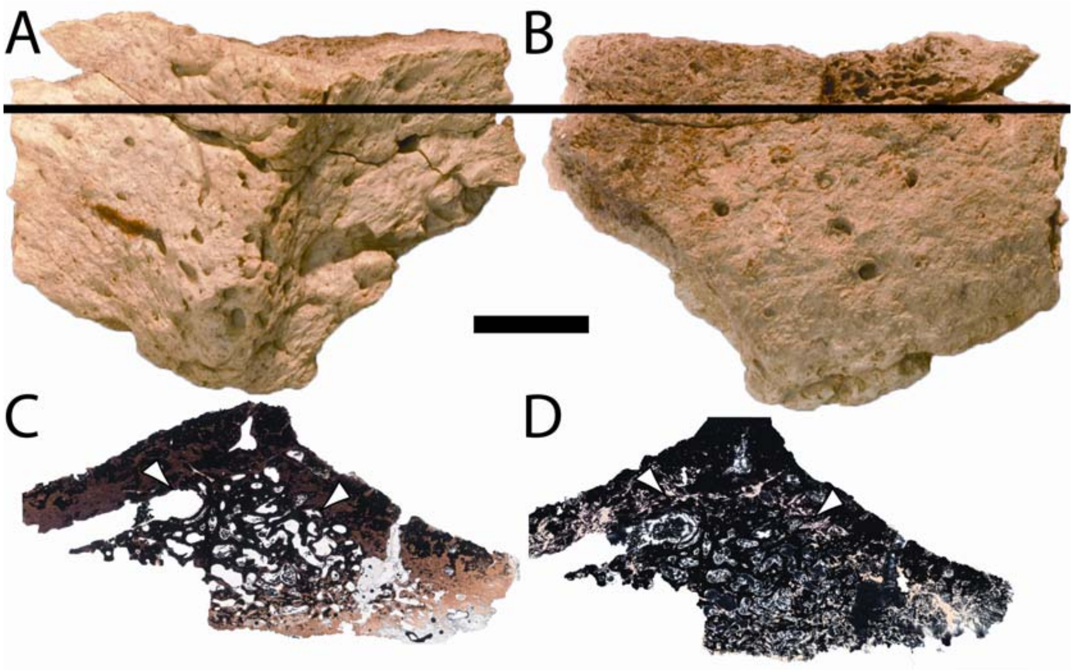


FIGURE 4.12. Thoracic osteoderm of Ankylosauria indet. (probably *Edmontonia longiceps*; TMP 87.113.4) in superficial (A) and deep (B) views (orientation uncertain). The thin line indicates transverse plane of thin section in PPL (C) and XPL (D) (superficial is up). Arrows indicate border of superficial cortex and core. The deep cortex is absent from this osteoderm. Scale bar equals 1 cm.

UALVP 47865 (Fig. 4.13) from Dinosaur Provincial Park can be tentatively assigned to Ankylosauridae indet. (probably *Euoplocephalus tutus*). It is a keeled thoracic osteoderm with a flat base. The superficial surface is uniformly pitted with a sparse pattern of reticular neurovascular grooves. The superficial and deep cortices are thick (28% and 26%, respectively). They are made up of woven bone, which consists of dense, regularly arranged structural fibres. The thin core (47%) is entirely trabecular bone, with a few secondary osteons between the core and cortex.

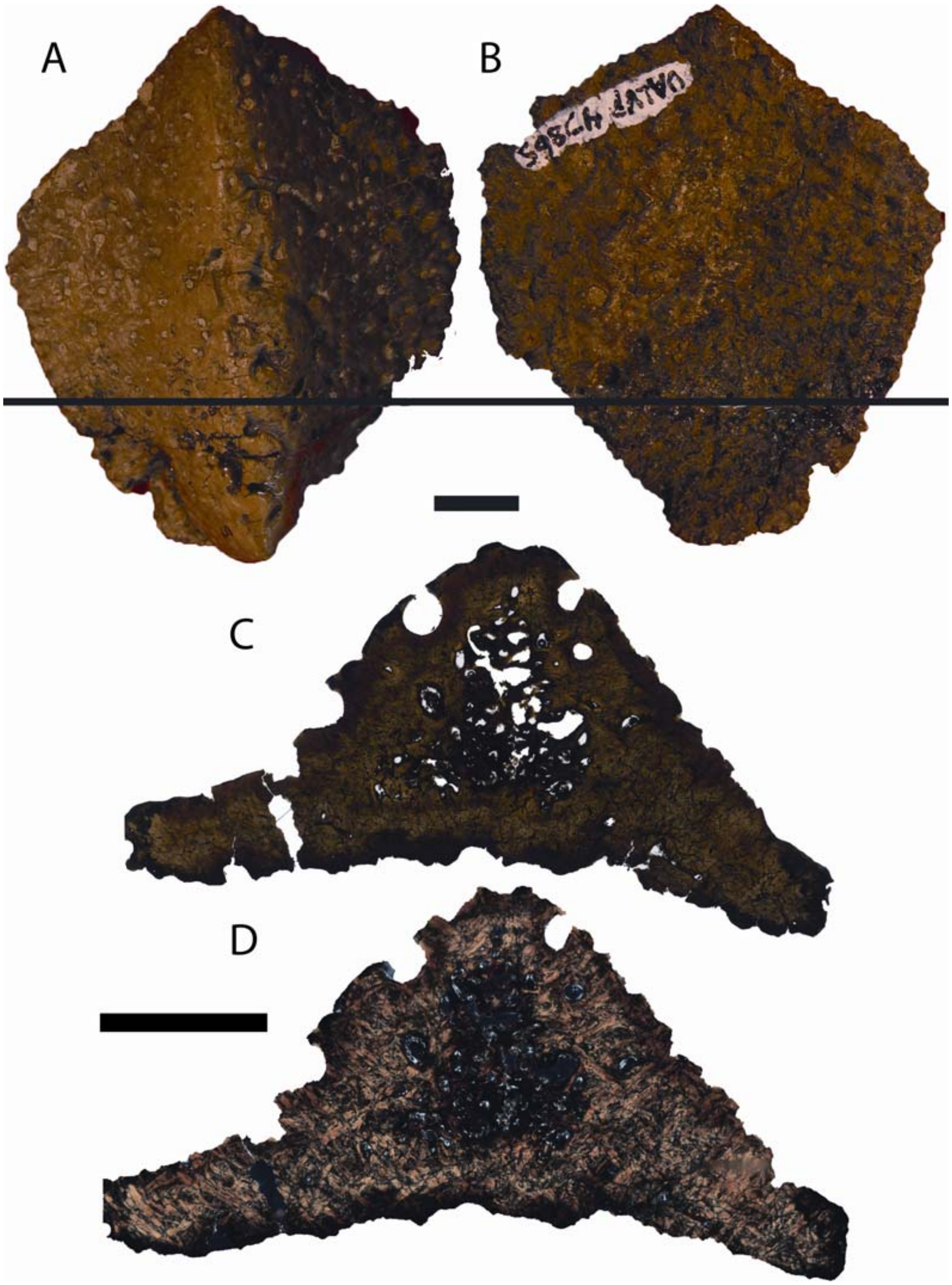


FIGURE 4.13. Thoracic osteoderm of Ankylosauria indet. (probably Ankylosauridae indet.; UALVP 47865) in superficial (A) and deep (B) views (anterior is up). The thin line indicates transverse plane of thin section in PPL (C) and XPL (D) (superficial is up). A thick woven cortex completely encircles the trabecular core. In the cortex, XPL allows for viewing of the regular, orthogonally-arranged network of mineralized collagen structural fibers. Scale bars equal 1 cm.

4.3.6 Quantitative Analyses

To quantitatively test previously identified subjective characters, several statistical tests were done on osteoderm measurements (Table 4.1). The relative thickness of different histological layers was evaluated via a two-sample t-test assuming unequal variances, comparing each of the three ankylosaur groups against one another. As they diverge histologically from the condition seen in unmodified body osteoderms, small interstitial ossicles and lateral spines were excluded from these analyses. Osteoderms of indeterminate taxa (although likely assignable based on subjective characters) 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.

There was no significant difference among any group with respect to relative core thickness (ankylosaur/polacanthids $t=0.64$, $df=16$, $\alpha=0.05$; ankylosaur/nodosaur $=1.25$, $df=9$, $\alpha=0.05$; polacanthid/nodosaur $=0.89$, $df=10$, $\alpha=0.05$). A comparison of relative deep cortical thickness showed a significant difference separating nodosaurids from ankylosaurids ($t=5.80$, $df=6$, $\alpha=0.05$) and polacanthids ($t=4.59$, $df=7$, $\alpha=0.05$). Conversely, there was no similar difference between ankylosaurids and polacanthids ($t=0.25$, $df=12$, $\alpha=0.05$). With respect to total osteoderm thickness, ankylosaurids showed a significant difference relative to nodosaurids ($t=2.24$, $df=17$, $\alpha=0.05$) and polacanthids ($t=2.49$, $df=13$, $\alpha=0.05$). There was no such difference between nodosaurids and polacanthids ($t=1.08$, $df=21$, $\alpha=0.05$).

TABLE 4.1. Summary of histological measurements used in analyses arranged by group (Ankylosaurid, Nodosaurid, and Polacanthid). All measurements are in mm. Relative thicknesses are presented as a percentage of total osteoderm thickness. Abbreviations: TT, total osteoderm thickness; TS, total superficial cortical thickness; Tcore, total core thickness; TD, total deep cortical thickness; %S, relative superficial cortical thickness; %Core, relative core thickness; %D, relative deep cortical thickness, %Cortex, relative thickness of the overall cortex.

Specimen	**Taxon**	**Histological Measurements**								
		TT	**TS**	**Tcore**	**TD**	**Tcortex**	**%S**	**%Core**	**%D**	**%Cortex**
TMP 85.36.218 1	Ankylosauridae indet.	7.959	0.333	7.021	0.605	0.938	4	88	8	12
TMP 85.36.218 2	Ankylosauridae indet.	9.579	0.844	7.89	0.845	1.689	9	82	9	18
TMP 96.75.1 A.1	*Euoplocephalus tutus*	8.426	0.729	6.714	0.983	1.712	9	80	12	20
TMP 96.75.1 A.2	*Euoplocephalus tutus*	10.512	1.797	8.1	0.615	2.412	17	77	6	23
UALVP 31 A.1	*Euoplocephalus tutus*	8.257	1.947	4.696	1.614	3.561	24	57	20	43
ZPAL MgD-1/188	Ankylosauridae indet.	12.932	1.244	10.184	1.504	2.748	10	79	12	21
ZPAL MgD-II/27 A	*Pinacosaurus grangeri*	14.529	0.802	11.222	2.505	3.307	6	77	17	23
DMNH 2452	*Edmontonia* sp.	52.395	7.286	43.812	1.297	8.583	14	84	2	16
DMNH 18206 1	*Sauropelta edwardsorum*	39.587	4.916	34.671	0	4.916	12	88	0	12
DMNH 18206 2	*Sauropelta edwardsorum*	9.629	1.588	8.041	0	1.588	16	84	0	16
SMP VP 1580 C.1	*Glyptodontopelta mimus*	10.991	1.852	9.139	0	1.852	17	83	0	17
SMP VP 1580 D.1	*Glyptodontopelta mimus*	5.736	0.788	4.84	0.108	0.896	14	84	2	16
SMP VP 1580 E.1	*Glyptodontopelta mimus*	10.826	1.335	9.491	0	1.335	12	88	0	12
TMP 1967.10.29	Nodosauridae indet.	32.834	2.483	30.351	0	2.483	8	92	0	8
TMP 87.113.4 A.1	Ankylosauria indet.	11.931	4.317	7.614	0	4.317	36	64	0	36
TMP 98.98.1 A.2	Ankylosauria indet.	6.633	3.398	2.38	0.855	4.253	51	36	13	64
BMNH R9293 1	*Polacanthus foxii*	13.533	1.956	9.696	1.881	3.837	14	72	14	28
DMNH 27726	*Gargoyleosaurus parkpini*	18.661	1.306	15.306	2.049	3.355	7	82	11	18
DMNH 49754 1	*Gastonia* sp.	20.154	2.193	16.66	1.301	3.494	11	83	6	17
DMNH 53206 A.1	*Gastonia* sp.	17.236	0.912	15.911	0.177	1.325	5	92	1	8
DMNH 53206 B.1	*Gastonia* sp.	8.253	1.181	5.799	1.273	2.454	14	70	15	30
DMNH 53206 C.1	*Gastonia* sp.	5.687	1.493	2.798	1.396	2.889	26	49	25	51
IPB R481	*Gastonia* sp.	14.924	3.322	10.201	1.401	4.723	22	68	9	32
MWC 210 A.1	*Mymoorapelta maysi*	6.764	2.101	3.384	1.279	3.38	31	50	19	50

A plot of relative (%) osteoderm cortical thickness versus total osteoderm thickness (Fig. 4.14) revealed a similar trend (logarithmic) to what is observed in osteoderms of *Caiman crocodylus* (Chapter 2). All three groups of ankylosaurs plotted separately but showed a decrease in the contribution of the cortex to overall thickness as the osteoderm thickness increased.

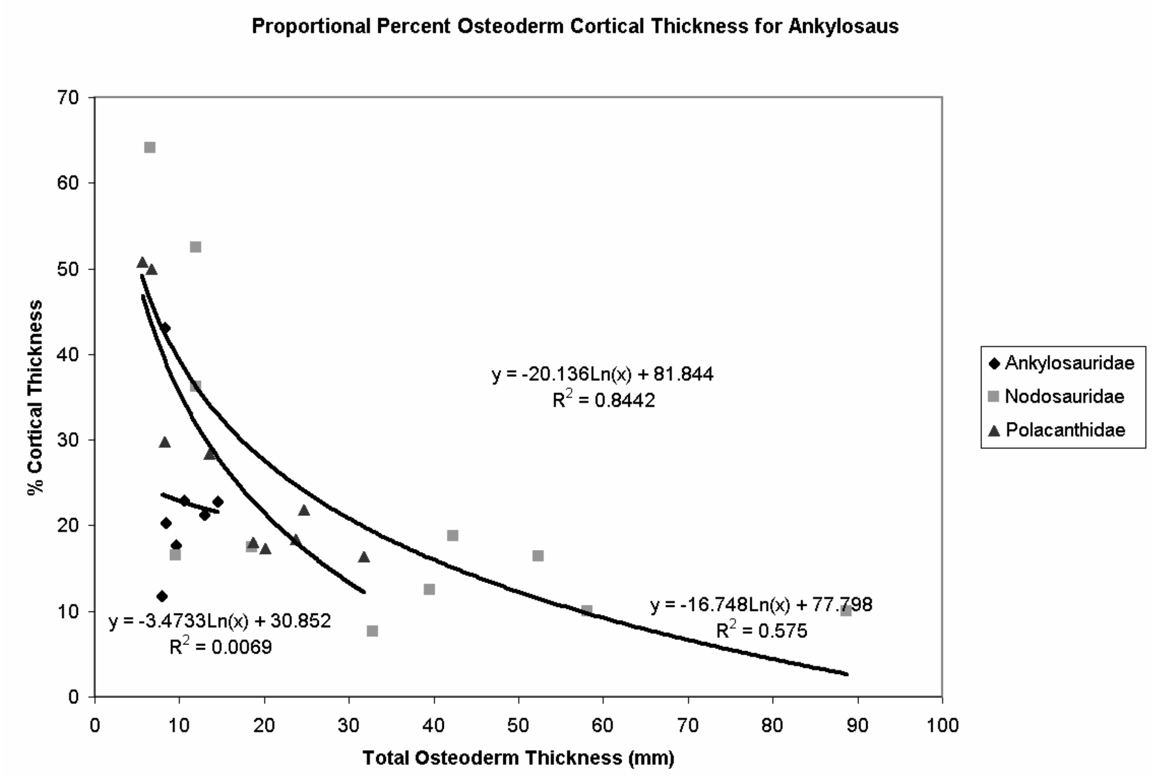


FIGURE 4.14. Proportional osteoderm cortical thickness for three groups in the Ankylosauria. The percent thickness (mm) of the cortex (proportion of combined thickness of the superficial and deep cortices versus total osteoderm thickness) is plotted against the total thickness (mm) of the osteoderm.

4.4 Discussion of Osteodermal Variation and Characters

The following characters are shared among all ankylosaurs for unmodified postcranial osteoderms: (1) they possess a superficial cortex that is distinguishable from the underlying core, (2) they lack observable Sharpey's fibres in both the deep and superficial cortices, and (3) they posses mineralized structural collagen fibres in at least part of the osteoderm.

Nododsaurid osteoderms can be distinguished on the basis of a poorly-developed or absent deep cortex. Most of the osteoderms examined had a trabecular core, but a few exhibited compact Haversian bone as well. Likewise, a woven superficial cortex is common, although some specimens had fibrolamellar bone there. This layer is complete with a dense pattern of orthogonal structural fibers as demonstrated by Scheyer and Sander (2004) and Hayashi et al. (in press).

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.

Of the polacanthids examined, only *Polacanthus* itself possessed fibrolamellar bone in the osteoderm cortex. All other taxa had woven bone in the cortex, but all polacanthids have relatively thick trabecular cores. No specimens exhibit Haversian bone, although occasional secondary osteons may be found at the contact between the cortex and core.

4.4.1 Ossicles

Small interstitial ossicles can show varying histologies even in a single individual, although they do have a few similarities. They all show two distinct regions: one dense and organized (either fibrolamellar or densely packed structural fibers) the other less dense (non-lamellar or trabecular bone). Fully mature osteoderms show the same polarization: a compact superficial cortex and trabecular core. It is possible that these ossicles represent different stages of osteoderm skeletogenesis (see discussion on skeletogenesis). In addition, these elements show no difference between ankylosaurids and nodosaurids. Both specimens examined (TMP 98.98.1 and UALVP 31) show fibrolamellar and Haversian bone as well as orthogonal structural fibers. Ossicles may represent incipient osteoderms that stopped mineralizing before reaching maturity or they may be *de novo* structures, developmentally histologically distinct from larger body osteoderms. Either way, as they do not exhibit the taxon-specific characters seen in the larger osteoderms, they are not useful providers of taxonomic information.

4.4.2 Modified versus unmodified osteoderms

Hayashi et al. (in press) examined osteoderms (tail club knob osteoderms and nodosaur lateral spines) that have been modified to perform specific functions. They concluded that spines and clubs maintain the same characteristic features for each group despite the differences in shapes and sizes. According to this study, however, the opposite seems to be true, and modified osteoderms display a corresponding modified histology. This is supported by evidence from extant *Caiman* osteoderms, in which even minor changes in shape can produce significant changes in histology even in a single individual. The same can be seen in specimens of ankylosaurs. Polacanthid and nodosaur spines exhibit lower relative cortical thicknesses than unmodified osteoderms (this is consistent with the tests done on *Caiman* osteoderms). In ankylosaurids, although the unmodified body osteoderms may be relatively thin and contain Haversian bone, those of the tail club knob are thick and have trabecular cores (see Hayashi et al., in press, fig. 10). Therefore, osteoderms that have been histologically and morphologically modified to perform specific functions do not provide taxonomic characters.

4.4.3 Structural fibers

The presence, density, and arrangement of mineralized structural fibers have been previously identified by Scheyer and Sander (2004) as characteristic for the three ankylosaur groups. Their conclusions are supported here. In nodosaurids, there are two three-dimensional sets of structural fibres in the superficial cortex, one that is parallel and perpendicular to the surface, and one arranged 45° to the first. Ankylosaurids also possess structural fibres in the cortex that insert perpendicularly into the osteoderm, but become more diffuse in the core as the woven bone has been remodelled. In polacanthids, whereas fibres in the core are randomly distributed, they attain a more regular arrangement near the margins, although they are never as highly organized as in nodosaurids.

4.4.4 Cortical relationships

The division of ankylosaur groups (notably ankylosaurids and polacanthids) based on the development (thickness) of the cortex (Scheyer and Sander, 2004) is not supported here. Statistical tests show that there is significant overlap in the overall thickness of the cortex, so much so that these two groups cannot be confidently distinguished based on this character. This change is likely based on the larger sample size used in this study as well as the inclusion of polacanthids spines, which have relatively thinner cortices.

In all nodosaur specimens examined the deep cortex contributed 2% or less to the overall osteoderm thickness. This is consistent with the conclusions of Scheyer and Sander (2004) and Hayashi et al. (in press), but is the first time this character has been quantitatively analyzed. When present, this cortical layer is made up of woven bone. As this represents a significant difference between nodosaurs and all other ankylosaurs, it is treated here as a synapomorphy for the group.

4.4.5 Core histology

There is more overlap in the histological makeup of the core of osteoderms than previously thought. Scheyer and Sander (2004) were able to distinguish ankylosaurids from other ankylosaurs based on a compact, Haversian core. Hayashi et al. (in press), on the other hand, called the core trabecular, in one case even examining the exact same thin section (TMP 85.36.218/1). The discrepancy is here attributed to the highly vascular nature of the compact bone in ankylosaur osteoderms and their random arrangement of Haversian canals. This study supports a mixture of histologies in ankylosaurid osteoderms: whereas some are Haversian, others may remodel to a trabecular state. This may be based on the fact that core histology is more dependent on osteoderm shape and function than on taxon. Nodosaurs, although their cores are largely trabecular, can have Haversian bone present. Only the polacanthids examined exhibited consistent core histology. Therefore, the retention of compact bone in the osteoderm core is a characteristic of derived nodosaurids and ankylosaurids. Due to the overlap among taxa, however, it is not a good basis on which to distinguish ankylosaur groups.

4.4.6 Osteoderm thickness

Osteoderms of ankylosaurids have been often been described as "thin-walled" or having "excavated" bases. This description has been alternately used as a distinguishing character (Coombs, 1971) or as a subjective assessment, with too much overlap between ankylosaurids and nodosaurids to be of real taxonomic value (Burns, 2008). Based on the statistical analyses here, there is support for ankylosaurid osteoderms being significantly thinner than nodosaurid osteoderms. This difference in thickness corresponds to a difference in histology: a higher overall occurrence of Haversian bone in the cores of ankylosaurid osteoderms. Whereas polacanthid osteoderms were also found to be significantly thicker than ankylosaurid osteoderms, measurements from one or more hollow, triangular lateral osteoderms from polacanthids were not included. Therefore, there is not enough confidence in this difference to be used as a distinguishing character. Nonetheless, based on the samples examined, the difference is valid for ankylosaurids and nodosaurids.

4.4.7 Superficial surface texture

Burns (2008) devised a method for differentiating North American ankylosaurids and nodosaurids and the species based on the surface texture of the superficial osteoderm surface. This scheme is in need of revision based on the increased sample size and more rigorous descriptive technique employed here. It now appears 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.

Polacanthid osteoderms are consistently smooth and lack (for the most part) neurovascular grooves and foramina. Nodosaurs may have smooth or uniformly pitted osteoderms and can develop a reticular pattern of neurovascular grooves and foramina. As an autapomorphy, *Glyptodontopelta* has a dense pattern of neurovascular grooves as opposed to the sparse pattern seen in other nodosaurids. Ankylosaurids may also retain smooth osteoderms but can develop a strong projecting surface rugosity. This is a distinguishing feature of some specimens referred to *Euoplocephalus* and *Nodocephalosaurus* and may represent a taxonomic difference or variation in epidermal covering (see discussion on ankylosaur integument below). In addition, the characteristic pattern of prominent yet sparse neurovascular grooves in *Ankylosaurus* (Burns, 2008) is supported as an autapomorphy as it was not observed in other ankylosaur specimens.

4.5 Osteoderm Skeletogenesis

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) we must rely on comparative material to hypothesize the mode(s) of osteoderm skeletogenesis. In crocodilians, osteoderms develop via the direct transformation of pre-existing dense irregular connective tissue in the dermis (=tissue metaplasia; Vickaryous and Hall, 2008). Evidence of extensive mineralized inclusions from the dermis suggests that is also the case in the osteoderms of ankylosaurs. In crocodilians and synapsids, the metaplastic initiation of mineralization is followed by intramembranous ossification and remodelling (Vickaryous and Sire, 2009). The extensive networks of mineralized tissues characteristic for ankylosaurs suggests that metaplasia may play a more dominant (or longer-lived) role in the skeletogenesis of these elements. Their high level of organization in the fully mineralized element suggests some manner of pre-mineralization reorganization of collagen in the stratum compactum, which generally display a random arrangement. To date, there has been no description of similar tissue reorganization in other tetrapods, although osteoderm histological development has been investigated in relatively few, scattered taxa (see Vickaryous and Sire, 2009).

The cortices of many ankylosaur osteoderms show primary woven or structural fibre bone with extensive vascularity. This is a strong indicator of relatively rapid growth in modern vertebrates (Young and Heath, 2000) as well as juvenile dinosaurs (Sander, 2000). In other ankylosaur osteoderms, however, primary fibrolamellar bone with LAGs suggests slower annual growth or remodelling. It is likely that histology changes throughout ontogeny as suggested by Hayashi et al. (in press), at least in derived nodosaurids and ankylosaurids. This is also the case in *Stegosaurus*, where woven bone is remodelled into lamellar bone during skeletogenesis (Hayashi et al., 2009). Primitively, the osteoderm core will remodel rapidly into trabecular bone while the cortex remains woven (as observed here in polacanthids).

Ankylosaur osteoderms also exhibit a delayed onset of osteoderm 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*, Currie, pers. comm., 2009) do not exhibit osteoderms beyond the cervical half rings. It is presumed, therefore, that their osteoderms exhibited a similarly delayed skeletogenesis to other sauropsid groups.

4.6 Ankylosaur Integument

In most crown gnathostomes, the dermis is bilaminar with a superficial stratum superficiale and a deeper stratum compactum (Sire et al., 2009). The stratum superficiale is characterized by loose irregular connective tissue whereas the stratum compactum, by contrast, is dominated by large bundles of collagen fibres. These fibres are regularly distributed, with the deepest layers of the stratum compactum (=reticular dermis of synapsids) forming lamellar and orthogonal arrangements. This structural configuration of the stratum compactum provides the integument with stress resistance (Sire et al., 2009).

Osteoderms, prior to bone remodelling if it occurs, represent a mineralization of soft tissue, in essence an *in vivo* mineralization of the dermis of an animal. Therefore, these structures present a unique opportunity to comment on the soft-tissue histology of extinct organisms. In ankylosaur osteoderms that have not remodelled to Haversian or trabecular bone, there exists a dense network of orthogonally-arranged collagenous structural fibres. This network suggests that the mineralized connective fibre network of osteoderms represents inclusions from the stratum compactum of the dermis. In all taxa thus far examined, tetrapod osteoderms primitively share a common site of origin: at the interface between the stratum superficiale and stratum compactum in the dermis. In some cases, the osteoderm may extend into the stratum compactum itself. It appears that, given the density of structural fibres in ankylosaur osteoderms, that 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 deepest 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, such as sauropods).

This is unsurprising given the great thickness of dinosaur osteoderms relative to other tetrapod groups. 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).

Hieronymus et al. (2009) performed an extensive examination of osteological correlates of various integumentary coverings using 96 specimens from 84 taxa and applied the results to the craniofacial coverings of Centrosaurine ceratopsids. Their criteria for describing surface textures were used here to describe the superficial (epidermal) surface of ankylosaur osteoderms. We can therefore use their correlations to hypothesize what type of integument covered osteoderms more accurately than in previous studies.

Although there is some variation in this surface textures, all of the specimens in this study can be best correlated with having a cornified sheath as described by Hieronymus et al. (2009). This suggests that, whereas there would have been some soft epidermal component covering the osteoderm, it was relatively minor compared to the keratinized structure overlying it. In extant correlates (e.g., the bovid horn) the bony attachment of these structures is characterized by densely concentrated metaplastic dermal collagen fibres (analogous to the structural fibres observed in ankylosaur osteoderms). These fibres also interact obliquely with the bone surface and may approach an orthogonally arranged network. Therefore, ankylosaurs most likely had a relatively thick, keratinized sheath covering their osteoderms and only minimal contributions from other layers of the epidermis.

4.7 Osteoderm Function(s)

The hypothesis that ankylosaur osteoderms were optimized for a mechanically defensive role is well-supported and is further corroborated by this study. The unique arrangement of structural fibres in all members of the Ankylosauria suggests that they were adapted to absorb stresses. The conclusion of Scheyer and Sander (2004) that ankylosaur osteoderms served as efficient lightweight armour is supported here. Their high vascularity may indicate the ability to heal rapidly in the case of physical damage. It should be noted, however, that no ankylosaur osteoderm has yet shown evidence of fracture or physical damage during life (Blows, 2000).

By comparison, crocodilian osteoderms do not share these same structural fibres in their cortices, which are instead fibrolamellar, although they do share highly vascularized cores. It is likely, then, that crocodilian osteoderms perform something other than a mechanically defensive function, which, has been often suggested but not demonstrated. Work on *Alligator mississippiensis* has suggested that multiple functions are likely for these structures (Seidel, 1979). These range from the usual protective function to a more specific protection of the blood vessels housed by the osteoderms. A role in locomotion has also been proposed based on the osteoderms acting as an anchor for epaxial musculature (only in the regions of the body used in swimming) and a stabilizing property for the keels. Additionally, thermoregulation has also been suggested, although it is important to remember that these hypotheses lack experimental evidence.

Given their structure, ankylosaur osteoderms appear optimized towards a protective function. This does not, however, preclude other possible uses. For example, in stegosaurs, the primary evolutionary force creating the vast diversity of osteoderms and spikes may have been species individuation and recognition as indicated by Main et al. (2005). This study on their function(s) could not exclude the possibility that other secondary roles, such as thermoregulation and intraspecific display, also played a part (perhaps a species-specific one) in the evolution of these unique strictures. Therefore, it is probable that ankylosaur osteoderms also performed various secondary functions, given their dense vascularity and incredible morphological diversity.

4.8 The Homology and Evolution of Ankylosaur Osteoderms

Osteoderms are plesiomorphic for Tetrapoda. In the various tetrapod groups, they have either disappeared or become modified and reduced (Vickaryous and Sire, 2009). All osteoderm-bearing archosaurs share a common primitive osteoderm histology: 1) a periodically-growing superficial cortex of compact bone (fibrolamellar and/or lamellar) with numerous Sharpey’s fibres, and; 2) a central core of trabecular bone demonstrating evidence of localized resorption and secondary remodelling (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; Hill and Lucas, 2006; Vickaryous and Sire, 2009).

The histological condition in *Scelidosaurus* can be considered the basal condition for that in the Ankylosauria as *Scelidosaurus* is likely the sister to all ankylosaurs (Carpenter, 2001). These osteoderms also exhibit histology that allies them with the basal archosaurian condition, namely a circumferential fibrolamellar cortex enclosing a trabecular core (Vickaryous and Sire, 2009). In most other osteoderm-bearing archosaurian lineages (e.g., parasuchians, aetosaurs, crocodylomorphs, etc.) a conservative yet distinct pattern of superficial pitting is common. In basal-most thyreophorans, this is not the case. Instead, the osteoderm surface, even on modified spines, is relatively smooth, and the few pits that are observed are small neurovascular foramina. This is different than most other archosaurian osteoderms, which exhibit a characteristic pattern of ornamental pitting. This smooth texturing is retained in the polacanthids. Only in the derived nodosaurs and ankylosaurs does it become highly modified and divergent.

Histological similarities among ankylosaur osteoderms from each of the three groups examined indicate similar development and evolution as hypothesized by Hayashi et al. (in press). Morphologically distinct (modified) osteoderms were elaborated by both modification of the external morphology and internal histology of unmodified osteoderms (*contra* Hayashi et al., in press). Based on certain characters, it is possible to identify isolated osteoderms to family via histology. Primitively, basal thyreophorans lack extensive structural fibres in their osteoderm cortices (de Buffrénil et al. 1986; Scheyer and Sander 2004; Main et al. 2005; Hayashi et al. 2009; Hayashi et al., in press). Hayashi et al. (in press) concluded that the presence of such systems in ankylosaurs indicate that either their osteoderms evolved differently or their skin differed from that of other thyreophorans. This study lends support to the former hypothesis, as it demonstrates that the integument does not need to be different in order to produce these divergent histologies. It is likely that a greater contribution from the dense connective tissues of the stratum compactum was involved in osteoderm skeletogenesis. Therefore, ankylosaurs simply utilized different developmental pathways to achieve the diversity we observe in their osteoderms.

Chapter 5 Phylogenetic Analyses of the Ankylosauria

5.1 Introduction

There are several problems with our current understanding of ankylosaur phylogeny. The addition of osteodermal characters identified through this study may help to resolve some of these issues. First, there has been contention over the status of the polacanthid ankylosaurs. Past phylogenetic analyses have variously placed this group as members of a grade of primitive ankylosaurids (Vickaryous et al., 2004), members of the ankylosaurid subfamily Polacanthinae (Kirkland, 1998), or in their own family, the Polacanthidae (Carpenter, 2001). The two former studies (Kirkland, 1998; Vickaryous et al., 2004) examined the Ankylosauria using traditional global parsimony methods. The latter (Carpenter, 2001) employed the controversial method of compartmentalization, which includes constraining the monophyly of clades viewed as stable *a priori*. It remains the only published study to recover a monophyletic Polacanthidae.

Two comprehensive overviews of ankylosaur osteoderm histology (Scheyer and Sander, 2004; Hayashi et al., in press) have offered evidence to suggest that polacanthids are a clade distinct from nodosaurids and ankylosaurids. Although they recovered diagnostic histological characters for the three groups, these studies did not analyze them in a phylogenetic context. So it is unknown whether or not these characters support such an arrangement, or whether they show that polacanthids actually have an affinity with either the ankylosaurids or nodosaurids. Also, if these characters do suggest a monophyletic group, would they still support it in light of other morphological characters?

The purposes of the following analyses are to (1) determine whether or not osteodermal characters show enough directionality to increase the resolution of a phylogenetic hypothesis of the Ankylosauria, (2) look for indications that such characters are useful at higher taxonomic levels (subfamily, family, etc.), lower taxonomic levels (genus and species), or both, and (3) to test the validity of a monophyletic Polacanthidae/Polacanthinae using this new suite of data independent of and in combination with other sets of previously identified character sets.

5.2 Materials and Methods

Data was taken from three previous studies and modified in two separate phylogenetic analyses. One includes only postcranial and cranial characters and the other incorporates osteodermal characters coded for this study.

For the first test, 21 ingroup and two outgroup taxa were used, the latter of which included the basal stegosaur *Huayangosaurus* and basal thyreophoran *Scelidosaurus*. A total of 63 characters and taxa were obtained from previous studies: fifty cranial characters were modified from Hill et al. (2003) and thirteen postcranial characters were modified from Vickaryous et al. (2004). The cranial characters were chosen from Hill et al. (2003) as they not only included and revised some of the characters of Vickaryous (2001), but also incorporated data from other studies. In addition, preliminary searches revealed that this combination of the two datasets produced trees with higher branch support than either set run separately. Both of these tests recovered the polacanthids as a polyphyletic grade of primitive ankylosaurs. The scorings for *Scelidosaurus* were taken from Parsons and Parsons (2009) and *Nodocephalosaurus* was coded by the author. The osteoderm characters used in the tests were adapted to the new data matrix and new taxa were coded for those characters to create the final character-taxon matrix (Appendix 1). All characters and character states for this set of tests are described in Appendix 2, and similarities/overlap of the new osteodermal characters with those of previous analyses is noted.

The second test involved *Scelidosaurus* as the one outgroup taxon and 16 ingroup taxa. Data (Appendix 3, 4) was from Kirkland (1998), an analysis that recovered a monophyletic Polacanthinae. A search was run first on the data with osteodermal characters removed. Character 24 (Appendix 3; Kirkland, 1998 # 23) included an a priori assumption about the secondary loss of a jugal/quadratojugal osteoderm. That state was recoded as absent.

All data were analyzed using winPAUP* 4.0b10 (Swofford, 1999) with the tree bisection reconnection (TBR) swapping algorithm with 1000 repetitions for each search. All characters were treated as unordered and of equal weight. Branch and bound and heuristic parsimony searches using a random addition sequence were performed. The frequency distribution of a random search of the data matrix was performed with 1000000 repetitions to evaluate the quality of the three datasets. Bootstrap values were found using a heuristic parsimony search with a random addition sequence. For Bremer support analysis, heuristic searches were run retaining suboptimal tree lengths to collapse the ingroup. These are listed in the results as (Bootstrap/Bremer).

Tree editing was performed in MacClade 4.08 OSX (Maddison and Maddison, 2000). For each test, a 50% majority rule consensus tree was created from the MPTs for comparisons.

5.3 Results

5.3.1 Test Set 1

The first search examined 62 cranial and postcranial characters (56 parsimony informative), returned twenty MPTs (TL=148, CI=0.480, RI=0.672). The frequency distribution of random trees returned a mean TL of 262 with a SD of 10. The resulting consensus (Fig. 5.1) was almost fully resolved, exhibiting one polytomy in the Nodosauridae and one deeply nested in Ankylosaurinae. The polacanthid-grade ankylosaurs are polyphyletic, with *Gargoyleosaurus* as the most basal member of the Ankylosauria. The remainder - *Gastonia*, *Gobisaurus*, and *Minmi* - plot as a grade of primitive ankylosaurs at the base of Ankylosauridae. A monophyletic Ankylosauria is strongly supported (100/3+). There is relatively strong support for the Nodosauridae (60/2) and relationships in that clade, including the monophyly of the genus *Edmontonia* (62/1). There is a soft polytomy among *Silvisaurus*, *Sauropelta*, and the more derived nodosaurids. There is also relative support for close relationship of polacanthids to the Ankylosauridae (72/2), but less support for the monophyly of the Ankylosauridae itself. *Pinacosaurus* is the most basal member of the Ankylosauridae and its monophyly is strongly supported (75/2). There is less support for other relationships in Ankylosauridae and Ankylosaurinae. Deeply nested in the latter, the relationships among *Tianzhenosaurus*, *Nodocephalosaurus*, and *Ankylosaurus* could not be resolved.

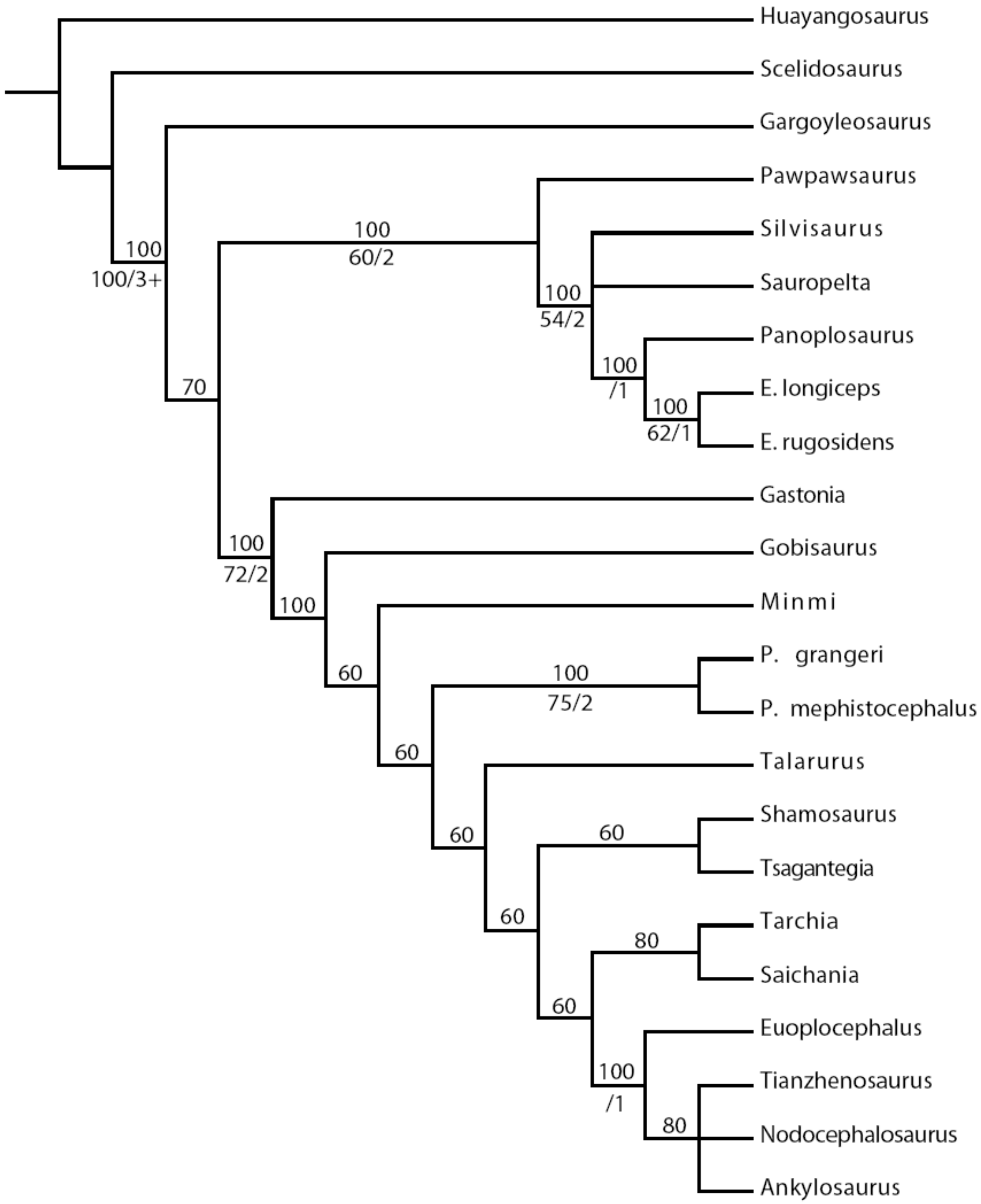


FIGURE 5.1. 50% Majority-rule consensus of 20 MPTs for Ankylosauria found via branch and bound and heuristic parsimony searches of 56 parsimony informative characters (TL=148, CI=0.480, RI=0.672). Across each clade-supporting branch, majority rule percentages are displayed above line with bootstrap/Bremer support values below. Outgroups are *Huayangosaurus* and *Scelidosaurus*. Data include cranial and postcranial characters only.

The second search for this set used 90 combined cranial, postcranial, and osteoderm characters (77 parsimony informative), returned 6 MPTs (TL=199, CI=0.538, RI=0.687). The frequency distribution of random trees returned a mean TL of 346 with a SD of 14. The resulting consensus (Fig. 5.2) shares the topology with the tree from the first search. Most branches show a trend of increased support from the first search and both CI and RI show an increase. Overall, there is more Bremer support in this tree. There is an increase in support for the two multispecific genera *Edmontonia* (69/1) and *Pinacosaurus* (78/2). Support for the relationship between polacanthid-grade taxa and the Ankylosauridae is reduced (61/2), corresponding to a change in the position of *Gargoyleosaurus* its former basal position in the Ankylosauria. The taxon is now the most basal in the clade polacanthids+Ankylosauridae. There is still strong support for a monophyletic Ankylosauria (100/3+) and Nodosauridae (83/2). Topologically, two soft polytomies were not resolved by the addition of the osteodermal characters.

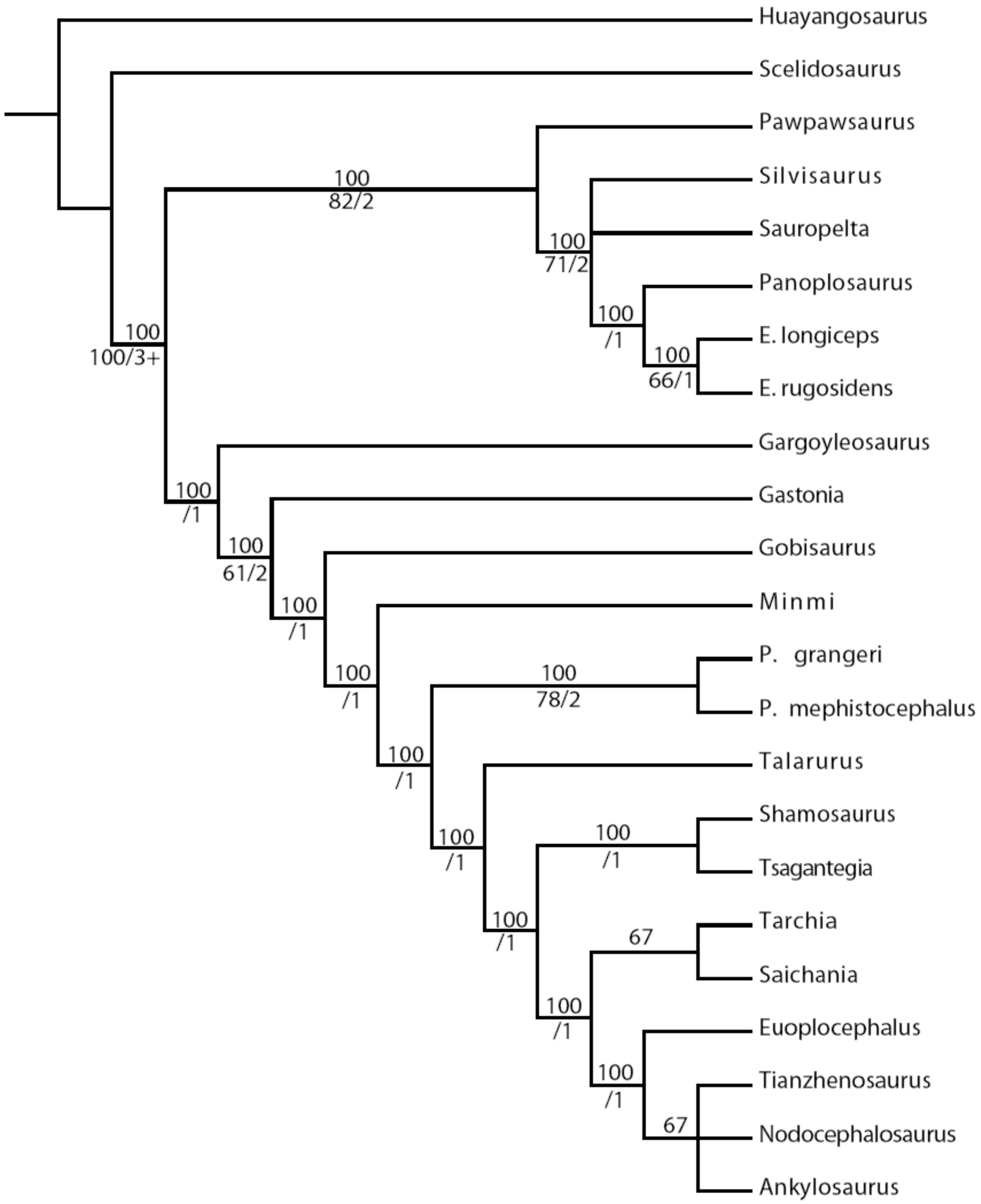


FIGURE 5.2. 50% Majority-rule consensus of 6 MPTs for Ankylosauria found via branch and bound and heuristic parsimony searches of 77 parsimony informative characters (TL=199, CI=0.538, RI=0.687). Across each clade-supporting branch, majority rule percentages are displayed above line with bootstrap/Bremer support values below. Outgroups are *Huayangosaurus* and *Scelidosaurus*. Data include cranial, postcranial, and osteoderm characters.

5.3.2 Test Set 2

The first search examined 38 total characters (31 parsimony-informative) and returned 76 MPTs (TL=79, CI=0.729, RI=0.846). The frequency distribution of random trees returned a mean TL of 129 with a SD of 10. The resulting consensus (Fig. 5.3) contains several soft polytomies. The positions of *Sauropelta*, *Gastonia*, and *Ankylosaurus* are unresolved. As is the case with Test Set 1, *Edmontonia* forms a supported clade with *Panoplosaurus* as do *Saichania* and *Tarchia*. Here, *Shamosaurus* and *Tsagantegia* do not form a clade, but instead they are separated by Gastonia and Polacanthus, the latter of which was not included in Test Set 1. *Minmi* falls out as the most basal member of Ankylosauria

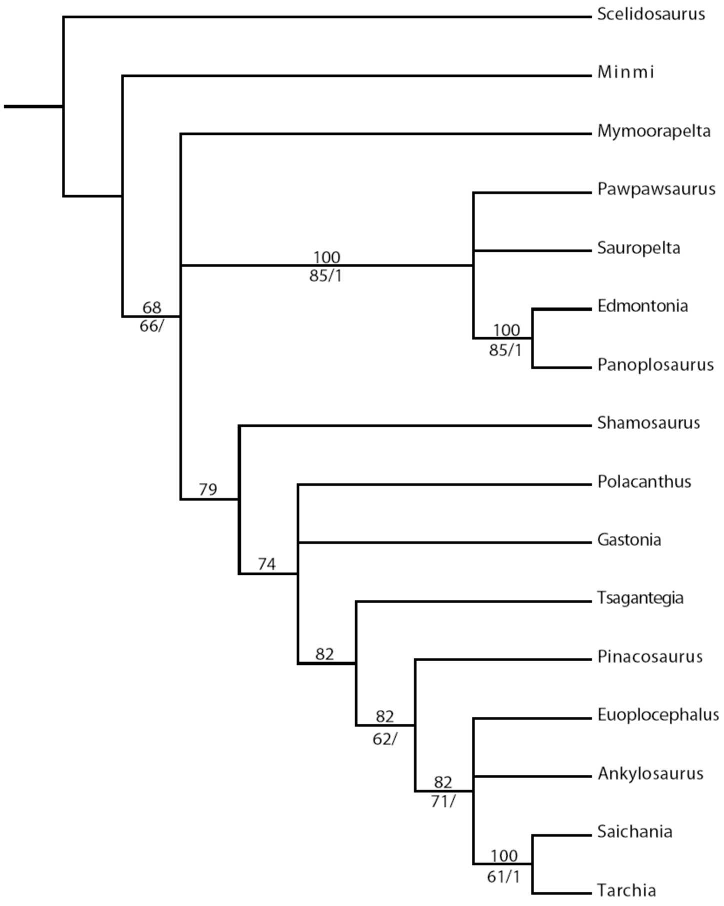
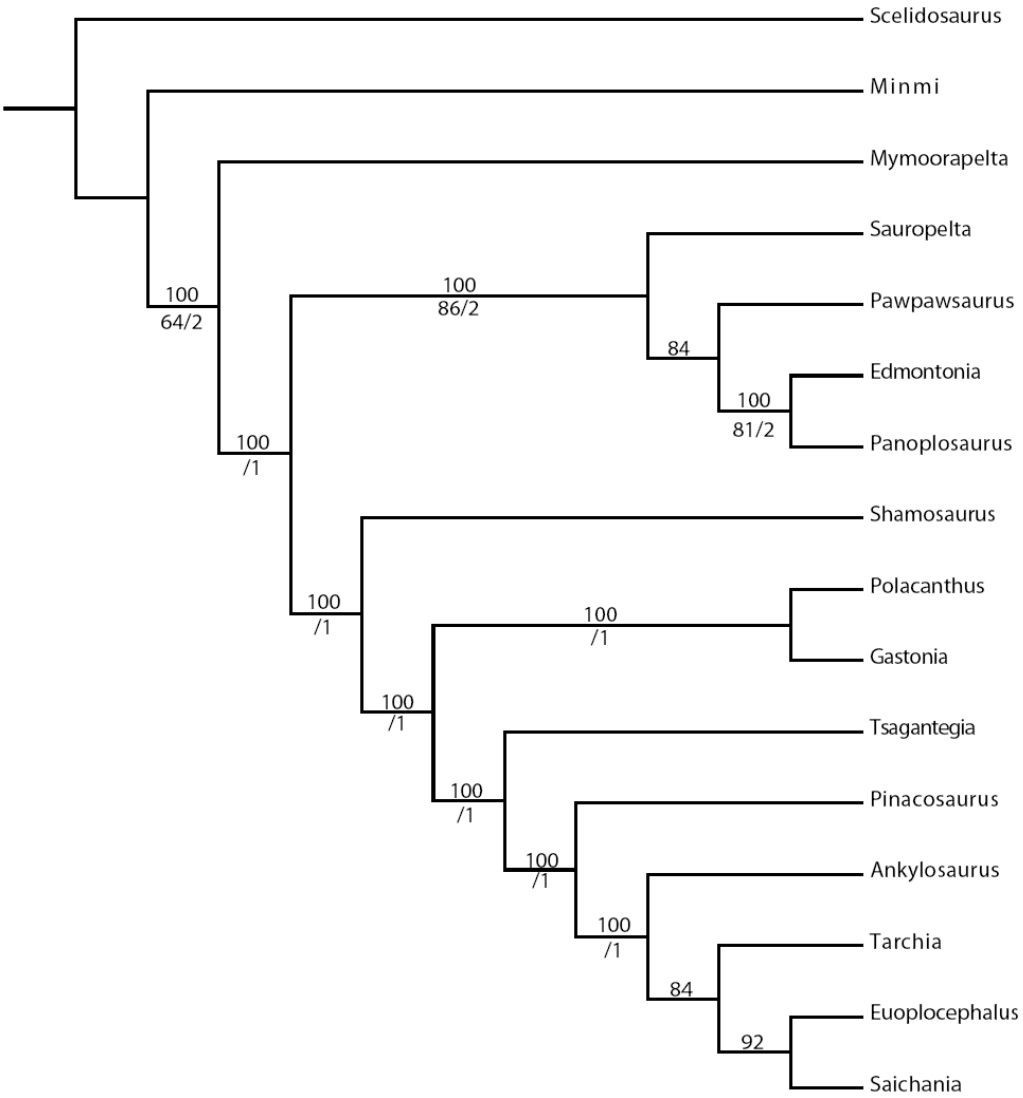


FIGURE 5.3. 50% Majority-rule consensus of 76 MPTs for Ankylosauria found via branch and bound and heuristic parsimony searches of 31 parsimony informative characters (TL=79, CI=0.729, RI=0.846). Across each clade-supporting branch, majority rule

percentages are displayed above line with bootstrap/Bremer support values below. Outgroup is *Scelidosaurus*. Data include cranial and postcranial characters.

The second search incorporated new osteodermal characters into the data matrix and examined 66 total characters (48 parsimony-informative) and returned 25 MPTs (TL=113, CI=0.628, RI=0.702). The frequency distribution of random trees returned a mean TL of 187 with a SD of 11. The resulting consensus (Fig. 5.4) shows a marked increase in resolution over the tree from the first search. Changes in branch support are more equivocal: bootstrap support has decreased overall whereas Bremer support now shows an increase. The exclusion of *Minmi* and *Mymoorapelta* from more highly derived ankylosaurs is more strongly supported. Support for the Nodosauridae is greater and taxon relationships within the clade are fully resolved. *Polacanthus* and *Gastonia* now form a clade near the base of Ankylosauridae. Support within the highly derived ankylosaurines has decreased, and *Saichania* now forms a clade with *Euoplocephalus* instead of *Tarchia*. *Ankylosaurus* occupies a more basal position within the deeply nested Ankylosaurinae.

FIGURE 5.3 (next page). 50% Majority-rule consensus of 25 MPTs for Ankylosauria found via branch and bound and heuristic parsimony searches of 48 parsimony informative characters (TL=187, CI=0.628, RI=0.702). Across each clade-supporting branch, majority rule percentages are displayed above line with bootstrap/Bremer support values below. Outgroup is *Scelidosaurus*. Data include cranial, postcranial, and osteodermal characters.



5.4 Discussion

5.4.1 Comparing the Test Sets

In Test Set 1, the addition of osteodermal characters increase the CI, RI, and overall branch support. Support for the monophyly of the multispecific genera *Edmontonia* and *Pinacosaurus* also increased. In contrast to an increase in branch support for the Nodosauridae and

Ankylosauridae, the Ankylosaurinae saw a decrease in support. Coupled with the placement of *Gargoyleosaurus* as more deeply nested than the Nodosauridae, this suggests that osteodermal characters imply a stronger polacanthid affinity to the Ankylosaurinae, prompting their placement in the Ankylosauridae with *Gargoyleosaurus* as its most basal member.

The results from Test Set 2 are not as definitive as those from the first set. In this case, the addition of osteodermal characters produced a decrease in support overall; however, it also increased the resolution of the tree. This discrepancy is likely due to a difference in taxon and character selection with Test Set 1. The data from Kirkland (1998) includes fewer taxa and characters than that from Vickaryous et al. (2004). It is unsurprising that removing the osteodermal characters from that set (Test Set 2, first search) would produce a tree with very little support and that the subsequent 75% increase in the number of characters would have a marked impact on topology and branch support. This search produced a polacanthine clade supported by a character of the pelvic shield: a characteristic pattern of larger osteoderms surrounded by rosettes of smaller, polygonal osteoderms. *Mymoorapelta* is excluded from this clade even though it shares this presumably diagnostic character. Several other unorthodox relationships also emerge, such as a *Euoplocephalus*+*Saichania* clade and basal positions for *Sauropelta* and *Ankylosaurus*. This is likely due to insufficient cranial/postcranial characters in this analysis.

5.4.2 Does a monophyletic Polacanthidae or Polacanthinae exist?

Previous studies on ankylosaur osteoderms (Scheyer and Sander, 2004; Hayashi et al., in Press) have suggested that osteodermal characters support the Polacanthidae as distinguishable from both nodosaurids and ankylosaurids. This study, however, does not support this. It is possible that such a group would appear distinct from other ankylosaurs based on characters of the osteoderms alone. However, these previous studies did not actually test their characters using global parsimony analyses, and could therefore only tentatively adopt such a clade. The cranial/postcranial-based tree from Test Set 1 (Fig. 5.1) does not show a monophyletic relationship for these animals. As hypothesized, the inclusion of osteodermal characters, which show some characters possibly diagnostic for the polacanthids, should have suggested monophyly for such a clade. This, however, was not the case. A decrease in branch support for the Ankylosauridae (correlated with an increase in support for Ankylosaurine) with the addition of the osteoderm characters may suggest that, given more data, the polacanthids may form a supported group. It may also mean, however, that they have more of an affinity for nodosaurids (as evidence by some of the results from Test Set 2) or that they posses a mixture of nodosaurid and ankylosaurid characters. Only the availability of more anatomical data can add support to one of these possibilities.

The second test recovered a monophyletic Polacanthinae, although not as classically defined due to the exclusion of *Mymoorapelta*. This clade was based upon the presence of a rosette pattern of osteoderms forming a pelvic shield. *Mymoorapelta* also has this character so its utility in diagnosing this clade is equivocal in the context of this analysis. Test Set 1 included more taxa and characters, but only two polacanthids, whereas Test Set 2 had fewer taxa overall but three polacanthids. This suggests that these taxa would give off a stronger phylogenetic signal in this case, possibly influencing their grouping.

Based on the results of this study, there is potential evidence to suggest a monophyletic clade of polacanthid ankylosaurs based on osteoderm characters alone, especially pelvic shield morphology. This is an interesting structure that requires further investigation. Neither this nor any other study has yet demonstrated unequivocally the existence of a polacanthid clade.

5.4.3 Are osteoderm characters useful in ankylosaur phylogenies?

It is often difficult to identify patterns of evolution based on the histology and/or morphology of osteoderms in Amniota. This is due to their plastic nature, and when plotted against traditional phylogeny, the many reversals and parallelisms are observable (see Vickaryous and Sire, 2009). Given this lack of directionality, it would seem difficult to imagine that characters derived from such a skeletal system would be of use in determining phylogenies. Despite this, the study by Hill (2005) and the work presented here show that this is not the case, and in fact the addition of osteodermal characters can serve to increase branch support and/or reinforce. In addition, osteoderms have been used successfully in other groups to infer phylogenies (e.g., glyptodonts, Croft et al., 2007). Therefore, it is probable that their utility depends on the amount of variation and directionality in distinct groups.

For ankylosaurs, osteoderms are most useful at the familial level as determined by Scheyer and Sander (2004) and reiterated by Hayashi et al. (in press). Despite this, diagnostic characters should still be tested by parsimony analyses to determine if the taxonomic divisions they suggest actually have statistical support. Furthermore, it may be important to examine whether or not osteoderm characters confirm, refute, or modify phylogenetic hypotheses derived from other character sets (cranial and postcranial).

In Test Set 1 of this study, the incorporation of osteodermal characters into the analysis caused in increase in CI, RI, and branch support. In addition, branch support increased for the Nodosauridae and Ankylosaurinae as well as for the species-level relationships in *Edmontonia* and *Pinacosaurus*. Results from Test Set 2 are more equivocal and actually show a decrease in support with the addition of osteodermal characters. Despite this, the tree becomes fully resolved only with the addition of these characters. What this test does demonstrate is the importance of not only informative osteodermal characters, but also cranial and postcranial characters in analyses of the Ankylosauria. Future analyses should increase taxonomic sampling as well as the number of characters. Many postcranial characters have been utilized over the years in systematic studies of the Ankylosauria and have proven to be informative (Hill et al., 2003; Vickaryous et al., 2004). The postcrania, 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 traditional cranial characters, the osteodermal characters identified herein, and a new suite of postcranial characters should be included in such a study. If all known ankylosaur taxa were included, this would resolve ankylosaurian evolutionary relationships as well as current data allows.

Chapter 6 Conclusions

This study demonstrates the utility if including integumentary skeletal characters in systematic studies if the Ankylosauria. It also provides a consistent and comprehensive way for describing the morphology, histology, and surface texture of these elements so that they may be used comparatively across taxa. This allows the identification of new characters and the reassessment of previously proposed characters.

Osteoderm morphology is systematically useful at the familial, generic, and specific levels. The distal cervical and thoracic spines of nodosaurids are strongly 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 statistically thinner osteoderms. Polacanthid-grade ankylosaurs share a mixture of derived characters from nodosaurids and ankylosaurids including lateral/distal spines (nodosaurids) and distal basally excavated dorsoventrally compressed triangular osteoderms (ankylosaurids). They also exhibit some primitive thyreophoran characters, such as similar cervical half ring morphology. A fusion of osteoderms into solid bucklers over the pelvic region is a character shared by most if not all ankylosaurs, reflecting an overall lack of mobility in the integument of this region. The general pattern of transverse bands of osteoderms embedded in a matrix of smaller interstitial osteoderms, sometimes considered diagnostic for polacanthids, is also seen in some ankylosaurids (e.g., *Euoplocephalus*) and nodosaurids (*Sauropelta*).

The histology of ankylosaur osteoderms is largely dependent on the specific function(s) of the element itself; however, there are several characters that are diagnostic for higher-level taxonomy. Only unmodified body osteoderms are useful as taxonomic indicators, and then only to the level of family. Small, interstitial ossicles are relatively homogenous across ankylosaur taxa and provide no taxonomic information. Modified osteoderms that perform specific functions (e.g., major tail club knob osteoderms) do not always retain the basic histology of unmodified osteoderms, and may in fact be divergent from this basal condition. The overall thickness of the cortex (absolute or relative) is a character that overlaps considerably among ankylosaurs and is not diagnostic to any particular group. The retention of compact bone in the osteoderm core is a characteristic of derived nodosaurids and ankylosaurids; however, it is not a basis on which to distinguish ankylosaur groups due to overlap among disparate taxa. An osteoderm that retains a Haversian core can be positively identified only as a derived taxon. An osteoderm with a trabecular core cannot be assigned to any particular group on this character alone.

The deep cortex of nodosaurid osteoderms is characteristically either absent or poorly developed. Mineralized fiber arrangement is also a useful character. Nodosaurids have two three-dimensional sets of structural fibres in the superficial cortex. Ankylosaurids have perpendicularly-inserting fibres in their osteoderm cortices, but they become more diffuse in the core. Fibres can attain a more regular arrangement near the margins in polacanthid osteoderms.

The superficial surface texture of ankylosaur osteoderms exhibits more variability than previously thought. Also, there are no evolutionary trends that correspond with phylogenetic patterns. Nonetheless, certain textures are observable only in isolated taxa and can be considered autapomorphic for them. The primitive thyreophoran condition (also retained in primitive ankylosaurs) is that of relatively smooth osteoderms, with only isolated or sparse surficial rugosity, foramina, or grooves. A relatively smooth surface coupled with dense reticular neurovascular grooves is diagnostic for the nodosaurid *Glyptodontopelta mimus*. Smooth osteoderms with sparse but prominent neurovascular grooves are characteristic of *Ankylosaurus magniventris*. The osteoderms of *Euoplocephalus* exhibit a wide variety of superficial surface textures that may indicate intraspecific polymorphism or a taxonomic difference.

Evidence of extensive mineralized inclusions from the stratum compactum and superficiale suggests that direct metaplasia of the dermis is responsible for (at least initial) osteoderm skeletogenesis in ankylosaurs. The occurrence of these fibres also suggests that metaplasia played a greater role in osteoderm formation than in other groups, such as crocodilians. The stratum compactum was likely thick in ankylosaurs, providing a greater contribution to the osteoderms relative to other archosaurs and resulting in their characteristic dense array of mineralized collagen fibres. Ankylosaur osteoderms exhibit a delayed onset of osteoderm skeletogenesis relative to the remainder of the body skeleton, although whether they grew relatively fast or slow cannot be determined. The timing and nature of skeletogenesis of ankylosaur osteoderms requires a correlation with LAGs from endochondral postcranial elements and is an area for further investigation.

Osteological correlates for integumentary coverings in extant taxa can be used to more accurately assess osteoderm coverings than has been previously possible. Whereas there would have been some soft tissue epidermal component covering the osteoderm, it was relatively minor compared to the keratinized structure overlying it. Ankylosaurs had a relatively thick, keratinized sheath covering their osteoderms similar to the modern horn of bovids.

Given their structure, ankylosaur osteoderms appear optimized towards a primary protective function. The osteoderms of crocodilians do not likely have a primary protective function, and their lack of mineralized structural fibres 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 for other, secondary osteoderm functions for ankylosaurs. These may include species individuation, thermoregulation, intraspecific display, etc.

The addition of osteodermal/integumentary characters has been shown here and elsewhere to increase the support of phylogenetic hypotheses for many different tetrapod and amniote groups. In ankylosaurs, these characters can add or subtract support for various ankylosaur clade and taxon relationships, depending on the quality and nature of other incorporated data. Osteoderm characters have been used to suggest a monophyletic Polacanthidae (or Polacanthinae), but when they are included in a global parsimony analysis this topology is not strongly supported. Whereas use of the term “polacanthid” is acceptable based on its frequent appearance in the literature, it should implicitly refer to a primitive grade of ankylosaurs (specifically, a stem group of ankylosaurids) and not its own monophyletic clade. Future analyses of the Ankylosauria should include the osteodermal characters identified here, revised postcranial characters, and increased taxonomic sampling.

Except 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. In addition, by mineralizing soft tissue *in vivo*, the integumentary skeleton can provide information about the biology, of a fossil organism. Far from homogenous elements, ankylosaur osteoderms were physiologically active tissues that were morphologically and histologically optimized for specific functional roles.

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Appendix 1

Character-taxon matrix used in phylogenetic analysis of Ankylosauria and two outgroup taxa, *Scelidosaurus* and *Huayangosaurus*. Cranial and dental characters (1 through 50) are modified from Hill et al. (2003). Postcranial characters (51 through 66) are modified from Vickaryous et al. (2004; characters 48 through 63). "P" denotes a polymorphic character with states 0 and 1.

										1										2									
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Scelidosaurus	0	0	?	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?	?	0	?	?	0	0	?	?	0	0	?
Huayangosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	1	?	?	?	0	?	0	0	?	0	1	0	1
Gargoyleosaurus	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	?	1	0	0	0	?	?	?	1	?	1	1	1	1
Gastonia	0	1	1	1	0	0	0	1	1	1	0	1	0	?	1	?	1	?	?	1	1	?	?	1	?	?	0	1	0
Gobisaurus	0	1	0	1	1	1	0	1	0	1	1	1	0	1	1	?	1	?	1	2	?	0	1	0	1	1	1	1	0
Shamosaurus	0	1	0	1	0	?	0	0	2	1	1	1	0	?	1	?	?	?	?	1	?	?	?	?	?	1	1	1	0
Tsagantegia	0	1	1	1	1	?	0	0	2	1	1	1	0	1	1	?	1	?	?	?	?	1	?	1	?	1	0	1	0
Talarurus	0	1	?	1	1	?	?	?	0	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Minmi	1	1	?	?	?	?	?	?	?	?	0	1	0	?	1	?	?	?	?	?	?	?	?	0	?	?	0	1	0
P. grangeri	0	2	1	1	1	1	0	1	0	1	1	1	0	1	1	0	1	1	1	1	1	0	1	0	1	0	0	1	1
P. mephistocephalus	0	2	1	1	1	1	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	0	1	0	1	0	0	1	1
Tarchia	1	1	1	1	1	?	0	0	2	1	1	1	0	?	1	0	1	1	1	2	1	1	1	0	1	0	0	1	0
Saichania	1	1	1	1	1	1	1	0	2	1	0	1	0	1	1	1	1	1	1	2	1	1	1	1	?	1	0	1	0
Tianzhenosaurus	1	1	1	1	1	0	0	?	2	1	1	1	0	?	1	?	1	?	?	?	?	?	?	?	?	0	0	1	0
Nodocephalosaurus	?	1	?	1	?	?	1	?	?	1	?	1	0	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	1
Ankylosaurus	1	2	1	1	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	0	0	0	1	0
Euoplocephalus	1	2	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	0	1	0	1	0

Pawpawsaurus	0	0	0	0	0	0	0	0	0	0	0	1	1	?	1	0	1	0	?	0	1	0	1	1	1	1	1	1	1
Silvisaurus	0	0	0	0	0	0	?	?	1	0	0	1	0	?	1	1	?	2	?	0	?	1	1	1	1	?	1	1	?
Sauropelta	0	0	?	1	0	0	?	?	?	?	0	1	?	?	1	1	?	2	?	0	?	1	1	1	1	1	1	1	1
Panoplosaurus	0	0	0	1	0	0	0	0	0	0	0	1	1	?	1	1	?	2	?	1	?	1	1	1	1	1	1	1	1
E. longiceps	0	0	0	1	0	0	?	0	0	0	0	1	1	?	1	1	?	2	?	1	?	1	1	1	1	1	1	1	1
E. rugosidens	0	0	0	1	0	0	?	0	0	0	0	1	1	?	1	1	?	2	?	2	?	1	1	1	1	1	1	1	1

	3										4										5									
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Scelidosaurus	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	1	1	?	0	0	0	0	0	0	0
Huayangosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0	1	?	0
Gargoyleosaurus	?	0	1	0	1	0	0	0	0	0	0	2	2	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?
Gastonia	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	?	?	?	?	?	?	?	2	?	1	1	1	1	?
Gobisaurus	?	1	1	0	1	1	1	0	0	0	0	1	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Shamosaurus	?	?	?	1	1	1	1	0	0	0	0	1	1	0	0	?	1	1	0	?	?	?	?	2	1	1	?	?	?	?
Tsagantegia	1	?	1	1	1	1	1	0	0	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Talarurus	?	?	1	0	1	1	1	0	0	0	0	2	1	0	0	1	1	?	1	?	?	2	1	2	?	1	2	1	0	1
Minmi	1	0	0	0	1	1	0	0	0	0	0	2	1	0	0	1	1	0	0	?	?	?	?	?	?	0	?	?	0	?
P. grangeri	1	0	1	0	1	1	1	0	0	0	0	2	1	0	1	1	1	1	0	1	0	2	1	2	0	1	2	1	0	0
P. mephistocephalus	1	0	1	0	1	1	1	0	0	0	0	2	3	0	1	1	1	1	0	1	?	?	1	?	?	1	1	?	?	?
Tarchia	1	0	0	0	1	1	1	0	0	1	1	2	3	0	0	0	1	1	0	1	?	?	0	2	?	1	2	1	0	1
Saichania	1	0	1	1	1	1	1	0	0	1	1	2	3	0	0	1	1	1	0	1	1	2	1	2	?	1	2	1	0	1
Tianzhenosaurus	0	0	1	1	1	1	1	0	0	1	1	2	2	1	1	1	?	?	?	?	0	?	1	?	?	?	1	?	0	?
Nodocephalosaurus	1	0	?	?	1	1	1	0	0	0	1	2	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ankylosaurus	1	0	1	1	1	1	1	0	0	0	0	2	2	1	1	0	1	1	0	?	?	1	1	1	?	1	?	1	0	?
Euoplocephalus	1	0	1	1	1	1	1	0	0	0	0	2	2	0	1	1	1	1	0	1	0	?	1	1	1	1	2	1	0	1
Pawpawsaurus	1	1	1	0	1	0	1	0	1	0	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Silvisaurus	1	1	1	0	1	1	1	?	?	0	0	1	0	?	?	1	1	?	1	?	?	1	0	?	?	?	?	?	?	0
Sauropelta	1	1	1	0	1	0	1	1	1	0	0	1	0	?	0	1	1	0	1	?	0	?	0	3	0	0	1	1	1	?
Panoplosaurus	1	1	1	0	1	1	1	1	1	0	0	1	0	1	0	1	1	1	0	1	1	?	?	3	0	0	?	1	1	?
E. longiceps	1	0	1	0	1	0	1	1	0	0	0	1	0	1	0	1	1	0	1	?	1	?	?	?	?	?	?	?	?	?

E. rugosidens	1	0	1	0	1	0	1	1	0	0	0	1	0	1	0	1	1	0	1	?	1	1	1	?	1	?	?	?	?	?

	6										7										8										9
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Scelidosaurus	0	?	0	0	0	1	2	0	4	0	P	1	0	0	1	0	3	1	0	1	0	1	2	0	0	0	2	0	1	0	0
Huayangosaurus	0	?	0	0	0	0	1	1	0	?	1	2	0	0	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	?
Gargoyleosaurus	?	?	?	1	0	0	?	0	?	0	P	P	1	0	?	?	1	1	1	1	0	1	2	0	0	1	1	1	1	?	1
Gastonia	?	?	1	1	0	0	1	0	?	0	?	P	1	0	?	?	?	1	1	1	0	1	2	0	0	1	1	1	1	?	1
Gobisaurus	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Shamosaurus	1	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Tsagantegia	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Talarurus	1	1	1	1	0	0	?	0	?	0	1	1	?	0	?	?	?	?	?	?	?	?	?	0	?	1	?	?	?	1	?
Minmi	1	?	?	1	0	1	1	0	4	0	P	?	1	0	1	1	1	1	?	?	?	?	?	0	0	1	1	1	1	?	?
P. grangeri	0	0	0	1	0	0	1	0	?	0	0	0	0	0	?	?	2	1	?	?	?	?	2	0	0	1	1	1	1	1	0
P. mephistocephalus	1	?	1	1	0	?	?	0	?	?	0	?	0	0	?	?	2	1	?	?	?	?	?	?	0	1	1	?	1	1	?
Tarchia	1	?	?	1	0	?	?	P	?	0	P	1	0	0	?	?	2	1	?	?	?	?	?	0	0	1	2	1	1	1	?
Saichania	1	1	1	1	0	?	1	0	3	0	P	1	0	0	1	0	2	1	?	?	?	?	?	0	0	1	2	1	1	1	?
Tianzhenosaurus	?	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	?
Nodocephalosaurus	?	?	?	1	0	?	?	?	?	0	P	P	?	0	?	?	?	?	?	1	1	1	?	0	?	1	?	?	?	1	0
Ankylosaurus	?	?	?	1	0	0	?	P	?	1	0	P	0	0	?	?	2	1	?	?	?	?	2	1	0	1	1	1	1	1	?
Euoplocephalus	?	0	1	1	0	1	1	0	3	0	P	P	0	0	1	0	2	1	0	1	1	1	3	0	0	1	2	1	1	1	1
Pawpawsaurus	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Silvisaurus	1	?	1	1	0	?	?	P	?	?	P	0	2	0	?	?	1	2	?	1	?	?	?	?	?	0	1	?	1	?	?
Sauropelta	1	?	?	1	0	0	1	P	4	1	P	0	2	0	0	0	1	2	0	?	0	2	1	1	2	0	1	1	1	0	2
Panoplosaurus	1	0	1	1	1	0	?	P	?	1	P	0	2	0	?	?	1	2	?	?	?	?	1	1	1	0	1	1	1	0	?
E. longiceps	?	?	1	1	0	0	?	P	?	1	P	0	2	0	?	?	1	2	?	?	?	?	1	1	1	0	1	1	1	?	?
E. rugosidens	?	?	1	1	0	0	?	P	4	1	P	0	2	0	?	?	1	2	?	1	1	2	1	1	1	0	1	1	1	?	2

Appendix 2

Description of characters used in phylogenetic analysis of Ankylosauria and two outgroup taxa, *Scelidosaurus* and *Huayangosaurus*. Cranial and dental characters (1 through 50) are modified from Hill et al. (2003). Postcranial characters (51 through 66) are modified from Vickaryous et al. (2004; characters 48 through 63). Similarities in osteoderm characters (64 through 90) with those of other analyses are noted after their descriptions.

1. Maximum skull width relative to maximum skull length: less than (0); greater than (1).
2. Highest point of skull roof: posterior to orbits (0); above orbits (1); anterior to orbits (2).
3. Premaxillary palate wider than long: absent (0); present (1).
4. Premaxillary teeth: present (0); absent (1).
5. External nares facing anteriorly: absent (0); present (1).
6. Accessory openings in the narial region: absent (0); present (1).
7. Fused osteoderms present on premaxilla: absent (0); present (1).
8. Anterior edge of premaxilla with broad ventrally concave notch in anterior view absent (0); present (1).
9. Ventral margin of premaxilla in lateral view: flat (0); concave (1); convex, resulting in a sharp premaxillary beak (2).

10. Continuous edge formed by the premaxillary beak and maxillary tooth rows: present (0); absent (1).
11. Anteriormost maxillary teeth obscured in lateral view by processes of the premaxilla: absent (0); present (1).
12. Maxillary tooth rows deeply inset from lateral edge of skull: absent (0); present (1).
13. Maxillary tooth rows deeply concave laterally, outlining and hourglass shape: absent (0); present (1).
14. Nasal septum dividing the respiratory passage into two separate bony canals: absent (0); present (1).
15. Closure of antorbital fenestra: absent (0); present (1).
16. Accessory antorbital ossification(s) completely separating orbit and antorbital cavity: absent (0); present (1).
17. Median palatal keel composed of the vomer and pterygoid: absent or weakly developed (0); extending ventrally to the level of the maxillary tooth crowns (1).
18. Extension of the vomerine septum: incomplete (0); extending to palatal shelves (1); extending to skull roof (2).
19. Paired premaxillary, maxillary, and nasal sinuses: absent (0); present (1).
20. Secondary palate: incomplete or absent (0); present and flat, reaching as far as the second or third maxillary tooth (1); present

and composed of two palatal shelves, describing S-shaped respiratory route (2).

21. Pterygoid foramen: absent (0); present (1).
22. Space between palate and braincase (interpterygoid vacuity): open (0); closed (1).
23. Dorsoventrally narrow pterygoids ramus of the quadrate: absent (0); present (1).
24. Quadrate shaft angled strongly rostroventrally: absent (0); present (1).
25. Quadrate excavated anteriorly: absent (0); present (1).
26. Quadrate fused to paroccipital process: absent (0); present (1).
27. Paroccipital process projecting posterolaterally: absent (0); present (1).
28. Occiput rectangular and wider than high: absent (0); present (1).
29. Hemispherical occipital condyle: absent (0); present (1).
30. Occipital condyle formed exclusively by the basioccipital: absent (0); present (1).
31. Occipital condyle set off from the ventral braincase by a distinct neck: absent (0); present (1).
32. Occipital condyle angled ventrally from place of maxillary tooth rows: absent (0); present (1).
33. Occipital condyle and paroccipital processes obscured in dorsal view by overhanging skull roof: absent (0); present (1).

34. Closure of supratemporal fenestra: absent (0); present (1).
35. Lateral temporal fenestra: open (0); closed (1).
36. Obliteration of cranial sutures in adults, involving fusion and dermal sculpturing of the outer surfaces of most of the dermal skull roof: absent (0); present (1).
37. Large subcircular dermal ossification covering most of the skull roof between the orbits: absent (0); present (1).
38. Anteroposteriorly narrow dermal ossification along the posterior border of the skull roof: absent (0); present (1).
39. Pair of large, subrectangular osteoderms at posterior edge of skull roof: absent (0); present (1).
40. Raised, polyhedral dermal ossifications on skull roof: absent (0); present (1).
41. Secondary dermal ossification, projecting ventrolaterally from the quadratojugal region: absent (0); present and rounded(1); present and wedge-shaped (2).
42. Secondary dermal ossification, projecting posterolaterally from the squamosal region: absent (0); present as weakly developed pyramid(1); present as prominent, wedge-shaped or pyramidal structure (2); present as narrow, elongated spines (3).
43. Median dermal ossification overlying dorsum of nasal region: absent (0); present (1).

44. Two pairs of dermal ossifications bordering the external nares: absent (0); present (1).
45. Tooth crown with cingulum: absent (0); present (1).
46. Closure of external mandibular fenestra: absent (0); present (1).
47. Coronoid process low and rounded, projecting only slightly above the level of the dentary tooth row: absent (0); present (1).
48. Sinuous ventral margin of mandible, which parallels the sinuosity of the dorsal margin in lateral view: absent (0); present (1).
49. Predentary ventral process short (relative to other thyreophorans): absent (0); present (1).
50. Atlas and axis fused to form a syncervical: absent (0); present (1).
51. One or more postaxial cervical centra in profile: anterior and posterior ends parallel and aligned (0); anterior and posterior ends parallel, anterior end dorsal to posterior end (1); anterior and posterior ends parallel, posterior end dorsal to anterior end (2).
52. Fusion of dorsal ribs to centra: absent (0); present (1).
53. Acrominon: absent (0); present, crest at anterior margin (1); present, bladelike flange perpendicular to long axis (2); present, knoblike process (3).
54. Ventral border of coracoid in profile: rounded (0); straight (1).
55. Length of deltopectoral crest relative to humerus: less than 50% (0); approximately equal to or greater than 50% (1).

56. Distal margin of ilium: oriented vertically (0); forms a horizontal shelf dorsal to the acetabulum (1); partially encircles the acetabulum laterally (2).
57. Acetabulum: open (0); closed (1).
58. Shaft of ischium: little to no curvature (0); pronounced curvature (1).
59. Pubis contribution to acetabulum: one-quarter or more (0); virtually excluded (1).
60. Ossified tendons in region of tail: absent (0); present (1).
61. Bilateral sternal element contact: not fused (0); fused (1).
62. Synsacrum of co-ossified dorsal, sacral and caudal vertebrae: absent (0); present (1).
63. Cranial osteoderms: (0) absent; (1) present. Estes et al., 1988 #128; Hill, 2005 #302.
64. Gular osteoderms: (0) absent; (1) present; Hill, 2005 #305.
65. Osteoderms on proximal limb segments: (0) absent; (1) present. deBraga and Rieppel, 1997 #167; Lee, 1997 # 127; Heckert and Lucas, 1999 #60; Hill, 2005 #306.
66. Caudal osteoderms: (0) absent; (1) present on dorsal or dorsolateral surfaces of tail only; (2) completely surrounding tail; Hill, 2005 #307.
67. Osteoderm dimensions: (0) smaller than a dorsal centrum; (1) equal to or larger than a dorsal centrum. Lee, 1997 #125; Hill, 2005 #309.

68. Maximum number of contiguous dorsal osteoderms per transverse row: (0) two; (1) four; (2) six; (3) eight; (4) ten or more. Modified from Brochu, 1997 #37; Hill, 2005 #313.
69. Neurovascular grooves on osteoderms: (0) absent or faint; (1) present and random; (2) present and parallel or radiate; Modified from Hill, 2005 #316.
70. Keel or boss height: (0) shorter than transverse width of osteoderm; (1) taller than transverse width of osteoderm; Hill, 2005 #320.
71. Deep surface of osteoderms: (0) flat or gently concave; (1) deeply excavated; (2) strongly convex; Modified from Carpenter, 2001 #34; Hill, 2005 #331.
72. Lateral thoracic osteodermal spines: (0) absent; (1) present as triangular, flattened elements, (2) present as solid, conical spines; Carpenter, 2001 #36; Hill, 2005 #336.
73. Edge of osteoderms: (0) smoothly tapering or rounded; (1) finely crenulated (“splintery”); (2) vertical with sutural boundary; Hill, 2005 #340.
74. Triangular caudal osteoderms with deep internal concavity: (0) absent; (1) present; Hill, 2005 #342.
75. Peaked caudal keel (heightened relative to dorsal keels): (0) absent (keels equal), (1) present; Hill, 2005 #343.
76. Multiple parasagittal rows of osteoderms on dorsal surface of cervical region: absent (0); present, fused together (1); present,

fused to half ring (2); present, unfused (3); Vickaryous et al., 2004 #49.

77. Parasagittal rows of fused osteoderms on dorsal surface of cervical region: absent (0), two present (1), three present (2); Carpenter, 2001 #35.
78. Pelvic osteoderms: (0) not coossified; (1) coossified into a mosaic of small osteoderms surrounding several larger osteoderms; (2) coossified into a solid mosaic of polygonal osteoderms.
79. Superficial cortex in skeletally mature osteoderms: (0)Fibrolamellar bone; (1) Woven bone.
80. Haversian bone: (0) absent in core of skeletally mature osteoderms; (1) may be present in in core of skeletally mature osteoderms.
81. Deep cortex in skeletally mature osteoderms: (0)fibrolamellar bone; (1) woven bone; (2) absent.
82. Superficial rugosity profile of skeletally mature osteoderms: (0) hummocky; (1) pitted; (2) smooth; (3) projecting.
83. Superficial neurovascular grooves on skeletally mature osteoderms: (0) absent; (1) present.
84. Lateral spines on cervical half ring: (0) absent; (1) present, projecting dorsoposteriorly; (2) present, projecting anteriorly; Carpenter, 2001 #83.

85. Osteoderms form posterior cranial “horns”: (0) absent; (1) present; Carpenter, 2001 # 59.
86. Median osteoderms of the cervical half rings: absent (0); present, flat with a low keel (1); present, tall and conical (2).
87. Elongate osteoderm fused to the ventrolateral side of the mandible in adults: absent (0); present (1); Hill et al. 2001 #48.
88. Multiple parasagittal rows of post cervical osteoderms: absent (0); present (1); Vickaryous et al., 2004 #50.
89. Tail club: absent (0); present (1); Vickaryous et al., 2004 #51.
90. Structural fiber arrangement in osteoderms: reaches orthoganoal arrangment near osteoderm surfaces (0); diffuse throughout (1); highly ordered sets of orthoganally arranged fibers in the superficial cortex (2).

Appendix 3

Character-taxon matrix used in phylogenetic analysis of Ankylosauria and one outgroup taxon, *Scelidosaurus*. Cranial and postcranial characters (1 through 46) are modified from Kirkland (1998) with osteoderm characters from that study removed. “P” denotes a polymorphic character with states 0 and 1.

									1										2										3			
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Scelidosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Minmi	1	0	0	?	?	?	0	0	0	0	0	0	1	0	0	0	0	0	1	?	1	?	1	1	0	0	0	0	0	0	0	0	?
Mymoorapelta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1	0
Pawpawsaurus	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	0	0	0	0	1
Sauropelta	0	0	0	?	?	0	?	0	1	?	0	0	1	1	1	1	1	0	1	0	1	?	1	1	0	1	2	1	0	0	0	0	1
Edmontonia	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	1	1	0	1	1	1	1	1	0	0	1	2	1	0	0	0	0	1
Panoplosaurus	0	0	0	0	0	0	2	0	1	0	0	0	0	1	1	1	1	0	1	1	1	1	1	0	0	1	2	1	0	0	0	0	1
Polacanthus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	0
Shamosaurus	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	?	0	0	0	0	0	0	0
Tsagantegia	1	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	?	?
Pinacosaurus	1	1	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0
Euoplocephalus	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	2	1	0	0	0	1	0	0	0	0
Saichania	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	2	1	0	0	0	1	1	1	0	0
Tarchia	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	2	1	0	0	0	1	0	1	0	0
Ankylosaurus	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	1	1	2	2	1	0	0	0	0	0	0	0	0
Gastonia	1	0	1	1	1	1	1	1	0	1	0	0	0	1	1	0	0	1	2	1	0	0	1	1	0	0	1	1	0	0	0	0	0

							4										5										6						
	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Scelidosaurus	0	0	0	0	0	1	0	0	?	P	?	1	0	P	0	0	?	?	2	1	0	?	?	?	2	1	0	1	1	1	1	1	?
Minmi	0	0	0	1	0	1	0	1	1	0	1	?	0	?	0	0	?	1	2	1	0	?	?	?	?	?	0	0	0	?	1	?	?
Mymoorapelta	0	?	?	1	?	1	0	0	1	0	3	0	P	P	1	0	1	0	2	1	1	1	1	1	3	0	0	1	2	1	1	1	1
Pawpawsaurus	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Sauropelta	0	1	1	1	1	1	0	1	1	0	4	0	P	?	2	0	1	1	1	1	0	?	?	?	?	0	0	1	1	1	1	?	?
Edmontonia	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Panoplosaurus	0	1	1	1	1	1	1	0	?	P	?	1	P	0	2	0	?	?	1	2	?	?	?	?	1	1	1	0	1	1	1	0	?
Polacanthus	1	1	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	0	?	?	?	?	?
Shamosaurus	?	?	?	1	1	1	0	0	1	0	?	0	0	0	0	0	?	?	2	1	?	?	?	?	2	0	0	1	1	1	1	1	0
Tsagantegia	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pinacosaurus	1	1	1	1	1	1	0	?	1	0	3	0	P	1	0	0	1	0	2	1	?	?	?	?	?	0	0	1	2	1	1	1	?
Euoplocephalus	1	1	1	1	1	1	0	1	1	P	4	1	P	0	1	0	0	0	1	2	0	?	0	2	1	1	2	0	1	1	1	0	2
Saichania	1	1	1	1	1	0	0	1	2	0	4	0	P	1	0	0	1	0	3	1	?	1	0	1	2	0	0	0	2	0	1	0	0
Tarchia	1	1	1	1	1	1	0	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Ankylosaurus	1	1	1	1	1	1	0	?	?	P	?	0	P	1	0	0	?	?	2	1	?	?	?	?	?	0	0	1	2	1	1	1	?
Gastonia	1	1	1	1	1	1	0	?	?	?	?	?	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	1	?	?	?	?	?

Appendix 4.

Description of characters used in phylogenetic analysis of Ankylosauria and one outgroup taxa, *Scelidosaurus*. Cranial and postcranial characters (1 through 46) are modified from Kirkland (1998) with osteoderm characters from that study removed. Similarities in osteoderm characters (47 through 74) with those of other analyses are noted after their descriptions.

1. Skull roof wider at rear of skull: absent (0); present (1).
2. Skull wider than long: absent (0); present (1).
3. Skull highest above and in front of orbits: absent (0); present (1).
4. Premaxillary scoop wider than long: absent (0); present (1).
5. Premaxillary notch: absent (0); present (1).
6. Edge of premaxilla continuous with lateral edge of maxilla: absent (0); present (1).
7. False palate made up by extension of maxilla: absent (0); small (1); large (2).
8. Palate wide: absent (0); present (1).
9. Hourglass-shaped buccal emargination: absent (0); present (1).
10. Nasal openings placed posteriorly: absent (0); present (1).
11. Nasal openings directed anteriorly: absent (0); present (1).
12. Respiratory passages complex: absent (0); present (1).

13. Lower temporal fenestra not visible in lateral view: absent (0); present (1).
14. Quadrate angled rostroventrally: absent (0); present (1).
15. Occipital condyle at high angle to plane of skull: absent (0); present (1).
16. Occipital condyle with neck: absent (0); present (1).
17. Basioccipital makes up entire spherical occipital condyle: absent (0); present (1).
18. Paraoccipital process rotated into horizontal plane: absent (0); present (1).
19. Basipterygoid process of the basisphenoid: absent (0); shortened (1); secondarily elongate (2).
20. Premaxillary teeth: present (0); absent (1);
21. Cingula on teeth: absent (0); present (1).
22. Fused osteoderm(s) on premaxilla: absent (0); present (1).
23. Wedge-shaped caudolaterally projecting scute on squamosal: absent (0); small (1); large (2);
24. Wedge-shaped caudolaterally projecting scute on jugal or quadratojugal: absent (0); small (1); large (2).
25. Paraoccipital process in dorsal view: visible (0); hidden (1).
26. Medial osteoderm covering nasals: absent (0); present (1).
27. Medial osteoderm on skull roof: absent (0); present (1).

28. Narrow osteoderm along posterior edge of skull: absent (0); present (1).
29. Groove across back of skull: absent (0); present (1).
30. Narial openings ringed by small osteoderms: absent (0); present (1).
31. Thick, raised osteoderms on skull roof: absent (0); present (1).
32. Acrominon: absent (0); present, crest at anterior margin (1); present, bladelike flange perpendicular to long axis (2); present, knoblike process (3).
33. Elongate coracoids: absent (0); present (1); (Kirkland, 1998 #34).
34. Deltopectoral crest large, extending more than halfway down the shaft of the humerus: absent (0); present (1); (Kirkland, 1998 #35).
35. Fused anterior trochanter: absent (0); present (1); (Kirkland, 1998 #36).
36. Ischium ventrally flexed near midlength: absent (0); present (1); (Kirkland, 1998 #37).
37. Ilia directed horizontally: absent (0); present (1); (Kirkland, 1998 #45).
38. Pubis highly reduced: absent (0); present (1); (Kirkland, 1998 #46).
39. Cranial osteoderms: (0) absent; (1) present. Estes et al., 1988 #128; Hill, 2005 #302.
40. Gular osteoderms: (0) absent; (1) present; Hill, 2005 #305.

41. Osteoderms on proximal limb segments: (0) absent; (1) present. deBraga and Rieppel, 1997 #167; Lee, 1997 # 127; Heckert and Lucas, 1999 #60; Hill, 2005 #306.
42. Caudal osteoderms: (0) absent; (1) present on dorsal or dorsolateral surfaces of tail only; (2) completely surrounding tail; Hill, 2005 #307.
43. Osteoderm dimensions: (0) smaller than a dorsal centrum; (1) equal to or larger than a dorsal centrum. Lee, 1997 #125; Hill, 2005 #309.
44. Maximum number of contiguous dorsal osteoderms per transverse row: (0) two; (1) four; (2) six; (3) eight; (4) ten or more. Modified from Brochu, 1997 #37; Hill, 2005 #313.
45. Neurovascular grooves on osteoderms: (0) absent or faint; (1) present and random; (2) present and parallel or radiate; Modified from Hill, 2005 #316.
46. Keel or boss height: (0) shorter than transverse width of osteoderm; (1) taller than transverse width of osteoderm; Hill, 2005 #320.
47. Deep surface of osteoderms: (0) flat or gently concave; (1) deeply excavated; (2) strongly convex; Modified from Carpenter, 2001 #34; Hill, 2005 #331.
48. Lateral thoracic osteodermal spines: (0) absent; (1) present as triangular, flattened elements, (2) present as solid, conical spines; Carpenter, 2001 #36; Hill, 2005 #336.

49. Edge of osteoderms: (0) smoothly tapering or rounded; (1) finely crenulated (“splintery”); (2) vertical with sutural boundary; Hill, 2005 #340.
50. Triangular caudal osteoderms with deep internal concavity: (0) absent; (1) present; Hill, 2005 #342.
51. Peaked caudal keel (heightened relative to dorsal keels): (0) absent (keels equal), (1) present; Hill, 2005 #343.
52. Multiple parasagittal rows of osteoderms on dorsal surface of cervical region: absent (0); present, fused together (1); present, fused to half ring (2); present, unfused (3); Vickaryous et al., 2004 #49.
53. Parasagittal rows of fused osteoderms on dorsal surface of cervical region: absent (0), two present (1), three present (2); Carpenter, 2001 #35.
54. Pelvic osteoderms: (0) not coossified; (1) coossified into a mosaic of small osteoderms surrounding several larger osteoderms; (2) coossified into a solid mosaic of polygonal osteoderms.
55. Superficial cortex in skeletally mature osteoderms: (0)Fibrolamellar bone; (1) Woven bone.
56. Haversian bone: (0) absent in core of skeletally mature osteoderms; (1) may be present in in core of skeletally mature osteoderms.

57. Deep cortex in skeletally mature osteoderms: (0)fibrolamellar bone; (1) woven bone; (2) absent.
58. Superficial rugosity profile of skeletally mature osteoderms: (0) hummocky; (1) pitted; (2) smooth; (3) projecting.
59. Superficial neurovascular grooves on skeletally mature osteoderms: (0) absent; (1) present.
60. Lateral spines on cervical half ring: (0) absent; (1) present, projecting dorsoposteriorly; (2) present, projecting anteriorly; Carpenter, 2001 #83.
61. Osteoderms form posterior cranial “horns”: (0) absent; (1) present; Carpenter, 2001 # 59.
62. Median osteoderms of the cervical half rings: absent (0); present, flat with a low keel (1); present, tall and conical (2).
63. Elongate osteoderm fused to the ventrolateral side of the mandible in adults: absent (0); present (1); Hill et al. 2001 #48.
64. Multiple parasagittal rows of post cervical osteoderms: absent (0); present (1); Vickaryous et al., 2004 #50.
65. Tail club: absent (0); present (1); Vickaryous et al., 2004 #51.
66. Structural fiber arrangement in osteoderms: reaches orthoganoal arrangment near osteoderm surfaces (0); diffuse throughout (1); highly ordered sets of orthoganally arranged fibers in the superficial cortex (2).