Dermal Armor Histology of Saltasaurus loricatus, an Upper Cretaceous Sauropod Dinosaur from Northwest Argentina

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The first unambiguous evidence of the presence of osteoderms in sauropod dinosaurs came from the discovery of *Saltasaurus loricatus*, a titanosaur from the Upper Cretaceous of Argentina. The dermal armor of *Saltasaurus* is composed of bony plates and small dermal ossicles. Here, we analyze the bone microstructure of these elements and provide information regarding its origin and development. The bony plates are composed almost entirely of reconstructed cancellous bone. Remains of primary bone consist of coarse bundles of mineralized collagenous fibers towards the external surface. Also, woven fibered bone tissue appears in the basal and lateral regions. Dermal ossicles lack secondary remodeling, and their matrix is formed by three orthogonal systems of collagenous fiber bundles. Growth lines are present in both bony plates and ossicles. Bone histology reveals that osteoderms mainly originated through direct mineralization (metaplasia) of the dermis, although other mechanisms are also involved (at least in the origin of dermal plates). The common features of development and integumental location of the osteoderms of *Saltasaurus* and other non-related vertebrates (e.g., lepidosaurs, crocodylomorphs) are linked to the intrinsic skeletogenic properties of the dermis.

Key words: Sauropoda, Titanosauria, osteohistology, osteoderms, dermal ossicles, metaplasia, Argentina.

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Introduction

One of the most striking features documented in titanosaur dinosaurs is the possession of osteoderms (Powell 1980; Le Loeuff et al. 1994; Dodson et al. 1998; Salgado 2003; D'Emic et al. 2009). The first record of this kind of structure in titanosaurs came from Depéret (1896), who described and tentatively assigned a thick osteoderm to *Titanosaurus madagascariensis* (a nomen dubium taxon [Upchurch et al. 2004]). The first uncontroversial evidence of osteoderms in titanosaurs was presented by Bonaparte and Powell (1980) for *Saltasaurus loricatus*, a small bodied species from northwestern Argentina (Bonaparte and Powell 1980; Powell 1980, 2003). The *Saltasaurus* dermal armor consists of two distinct elements: bony oval plates with a conical external surface and small sub-spherical ossicles arranged in contact forming an irregular mosaic (Bonaparte and Powell 1980; Powell 1980, 2003). After the discovery in *Saltasaurus*, osteoderms have been found isolated (Sanz and Buscalioni 1987; Le Loeuff et al. 1994; Azevedo and Kellner 1998; Dodson et al. 1998; Powell 2003; Salgado 2003; O'Leary et al. 2004; Marinho and

Candeiro 2005; D'Emic et al. 2009) or in a few instances associated with specimens of titanosaurs (Salgado and Coria 1993; Sanz et al. 1999; González Riga 2003; Gomani 2005; Salgado et al. 2005; Kellner et al. 2006).

Although the external morphology of titanosaurian osteoderms has been well described previously (Huene 1929; Powell 1980, 2003; Dodson et al. 1998; Salgado 2003; D'Emic et al. 2009), knowledge about their bone microstructure is rather poor. In a review of osteoderms referred to titanosaurs, Salgado (2003) describes the histology of an osteoderm from the Allen Formation (Upper Cretaceous of Patagonia), inferring the possible function and mode of histogenesis in osteoderms. The poor knowledge about bone histology of titanosaur osteoderms contrasts with the important number of studies that have described and interpreted the bone histology of other dinosaur osteoderms (Buffrénil et al. 1986; Reid 1996; Ricqlès et al. 2001; Barrett et al. 2002; Scheyer and Sander 2004; Main et al. 2005; Burns 2008; Hayashi et al. 2009).

In the present study we analyze and characterize the bone tissue histology of bony plates and ossicles of *Saltasaurus*

loricatus. The aim of this work is to obtain information about the origin and development of these structures. We also want to know if there is a common pattern in the microstructure and development of the osteoderms of *Saltasaurus* and other dinosaurs (titanosaurs and thyreophorans) described in previous studies.

Institutional abbreviations.—MUCPh, Paleohistology collection of the Museo de la Universidad Nacional del Comahue, Neuquén Province, Neuquén, Argentina; PVL, Paleovertebrate collection of Instituto Miguel Lillo, Tucumán Province, San Miguel de Tucumán, Argentina; PVLPh, Paleohistology collection of Instituto Miguel Lillo, Tucumán Province, San Miguel de Tucumán, Argentina.

Other abbreviation.—LAG, lines of arrested growth.

Materials and methods

Our study focused on osteoderms that were found in direct association with many disarticulated individuals of *Saltasaurus* (Powell 1980). The material was collected from the Upper Cretaceous (?late Campanian–Maastrichtian) sediments of the Lecho Formation at the locality of El Brete (south of Salta Province, Argentina) (Bonaparte and Powell 1980; Powell 2003). The close association between osteoderms and postcranial elements of *Saltasaurus* allows their assignment to this titanosaurid dinosaur (Bonaparte and Powell 1980; Powell 1980, 2003). Furthermore, groups of dermal ossicles have been observed in direct contact with bones of the holotype of *Saltasaurus* (PVL 4017-92) (personal observation). For the histological analysis, an incomplete plate (PVL 4017-113) and several ossicles (PVL 4017-208) were sectioned. Before obtaining the thin sections, the plate was cut along the sagittal plane (Fig. 1). Two transverse sections, perpendicular to the sagittal plane, were obtained from one half plate (PVLPh 011-1, PVLPh 011-2, Fig. 1A). The other half plate was sectioned in a longitudinal plane, including the marginal ring of tuberosities of the plate (PVLPh 011-3, Fig. 1B).

Five dermal ossicles were obtained from a small cluster (PVL 4017-208) and sectioned transversally along the major axis (PVLPh 001-I, PVLPh 001-II and PVLPh 001-III) and longitudinally across the lateral margin (PVLPh 002-I, 002-II). Also, a small block containing several ossicles in situ was sampled, obtaining transverse and oblique thin sections (PVLPh 008, PVLPh 009, PVLPh 010).

Thin sections were prepared according to the methodology of Chinsamy and Raath (1992) and were examined using normal transmitted light and polarized light. Histological terms follow established nomenclature of bone (Francillon-Vieillot et al. 1990). Regarding the relative locations of specific structures within the osteoderm, we avoid the traditional terms "dorsal" and "ventral" to refer to the opposite surfaces. Instead, we adhere to the most accurate convention "external" and "basal" proposed by Scheyer and Sander (2004). These terms are synonyms of "superficial/deep" (Hill 2006),

"distal/proximal" (Main et al. 2005) and "external/internal" (D'Emic et al. 2009).

Results

Dermal plate

External morphology.—The bony plate (Fig. 1) has a more or less oval outline (although it is broken in some areas), with the greater axis longitudinally oriented and with irregular margins. The external surface is conical, and the slightly concave basal face has a longitudinal ridge. Plate width and thickness are 11 and 5.5 cm respectively. Both external and basal surfaces exhibit rugose textures, although this is most prominent on the external face, which is ornamented with numerous irregular rugosities formed by fossae of various sizes. A ring of
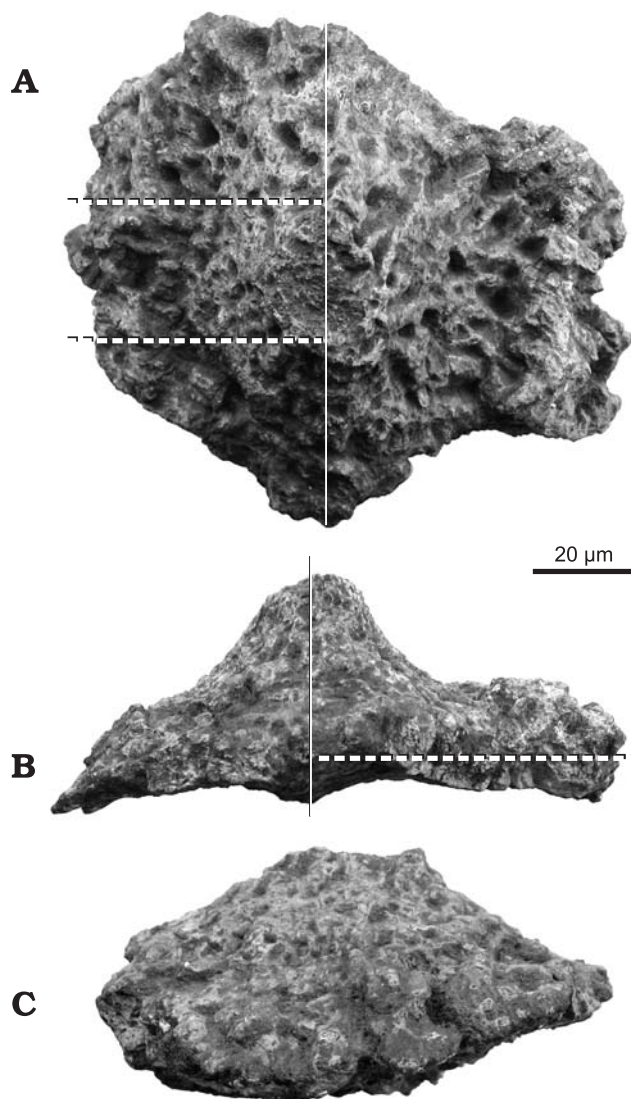

Fig. 1. *Saltasaurus loricatus* Bonaparte and Powell, 1980 bony plate (PVL 4017-113) from El Brete locality (Late Cretaceous, ?late Campanian–Maastrichtian, Salta Province, Argentina) in external (**A**) and lateral (**B**, **C**) views. Dashed lines show the location and orientation of the thin sections.

small tuberosities (cingulum) is located on the margin of the plate. This cingulum is more developed on one of the marginal sides, giving an asymmetrical shape to the plate. Although this morphology coincides with other *Saltasaurus* bony plates (PVL 4017-112), the shape is not the same for all scutes. In other bony plates, the basal crest is absent (PVL 4017-134), the basal surface is rugose (PVL 4669), or the lateral margin is ornamented with small ossicles, which are fused to the larger element (PVL 4017-115).

Histology.—Except for the lateral margins, the plate is composed mainly of reconstructed cancellous bone (Fig. 2A). Besides the cancellous spaces, there are elongated canals that connect the external, basal and lateral surfaces with the inner region, within which endosteal lamellar bone has been centripetally deposited. Also, some sections reveal the presence of very important internal cavities. The strongly remodelled trabecular bone exhibits lamellar bone remnants from previous generations of cancellous tissue (Fig. 2B). Although most of the basal surface has been removed (perhaps during the mechanical preparation of the plate), some regions reveal that this area is composed of numerous secondary osteons, which conform to a dense Haversian bone tissue (Fig. 2C). Despite the extensive Haversian reconstruction, remains of primary bone tissue are preserved in some areas of the osteoderm. In the external cortex of the plate, there are remnants of primary bone tissue, which is entirely formed by closely packed bundles of mineralized collagenous fibers (Fig. 2D). Most of the fibers are oriented perpendicular or slightly oblique to the surface, although parallel fiber bundles can also be seen. Following the terminology outlined by Scheyer and Sander (2004), we differentiate this kind of fibers from Sharpey's fibers and we use the term "structural fibers". This matrix clearly shows lines of arrested growth (LAGs) parallel to each other and to the external surface (Fig. 2E). In the region less affected by secondary reconstruction, at least seven lines are observed. Vascularization of the primary tissue is rather scarce, and there is no evidence for periosteal bone tissue deposition. Other type of bone tissue is located in the basal and the lateral region of the plate, occupying some areas around the largest internal cavities. This bone tissue is rich in osseous cell lacunae and contains loosely packed fibers oriented in different directions (Fig. 2F). The matrix contains enlarged, simple vascular spaces that give a fine cancellous aspect to the bone tissue. Taking into account these histological features, we interpreted this tissue as a woven fibered bone tissue. The absence of well defined, closely packed bundles of fibers and the high density of cell lacunae and vascular spaces allows a clear differentiation of this tissue from the structural fiber bundles previously described in the external cortex of the plate.
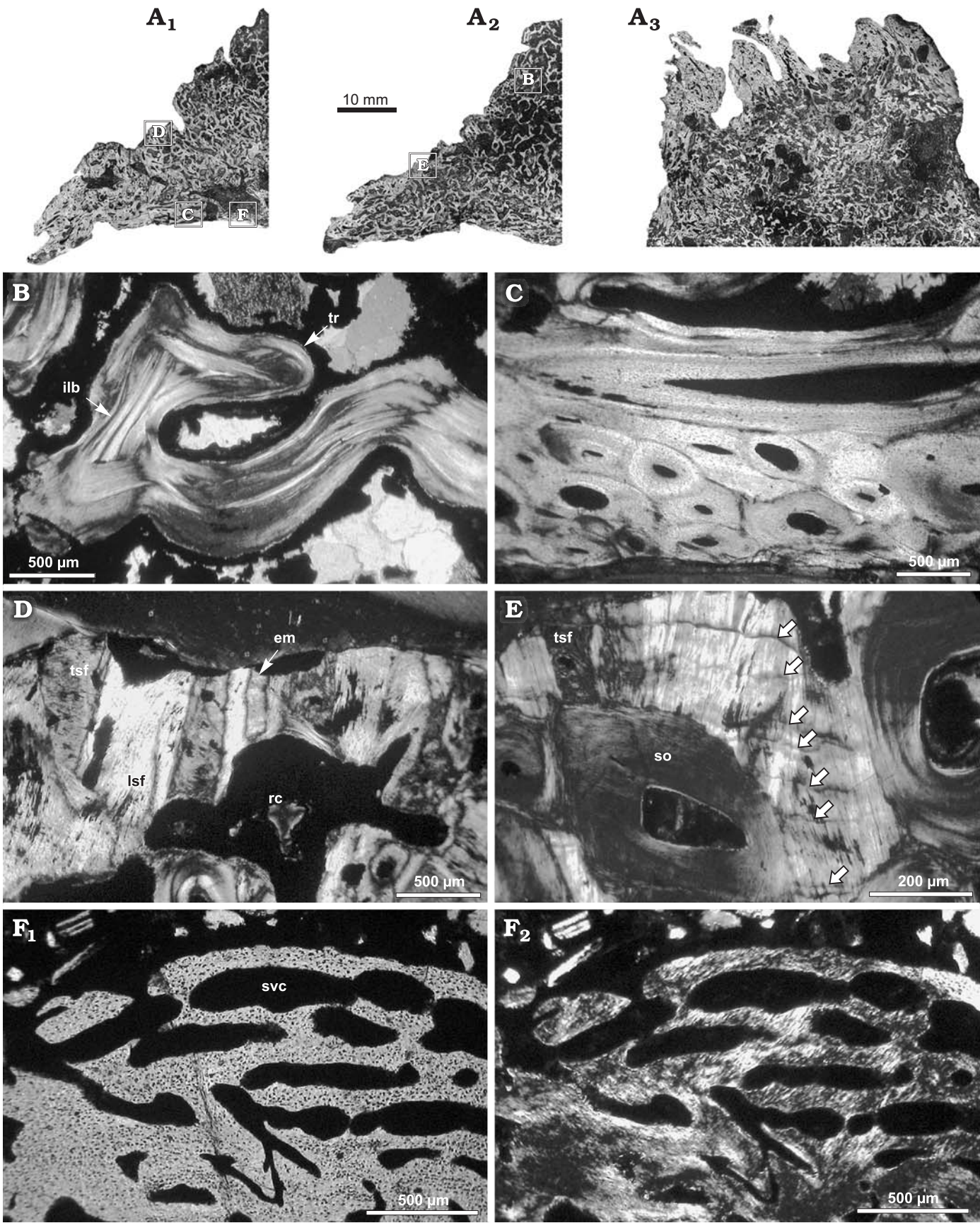
Ossicles

External morphology.—Although the morphology of the dermal ossicles is quite variable, in general terms subspherical and lenticular shapes with well defined external

and basal surfaces predominate (Fig. 3). Since the ossicles were not collected in the original position with regard to other skeletal elements, the external and basal surfaces were determined by comparison with other osteoderms from the literature. Previous works (Dodson et al. 1998; Ricqlès et al. 2001; D'Emic et al. 2009) have identified the basal surface by its interwoven texture. Following such criteria, what we interpret as the external surface of an ossicle is smooth and flat, with a straight border in the latero-external region (Fig. 3A, B). This border does not correspond with the lateral margin of the whole ostederm and give a roughly polygonal shape to the ossicles in external view (Fig. 3B). On the other hand, the basal surface is strongly convex and shows evidence of a system of straight horizontal fibers which cross orthogonally. The longest axis of the elements here studied ranges from 7 to 10 mm. Groups of associated ossicles are arranged in contact forming an irregular mosaic with a density of around 18 to 25 elements per 10 cm^2 (Fig. 3C) that resembles the ground tubercles scale pattern described in titanosaurian embryos from Patagonia (Chiappe et al. 1998; Coria and Chiappe 2007). In previous studies (Powell 1980, 2003), dermal ossicles have been illustrated and shown in basal view, where they appear to be sub-spherical in shape.

Histology.—All studied ossicles are composed of compact primary bone tissue, with few vascular canals in the internal region (Fig. $4A_1$). The matrix is entirely formed by densely packed bundles of mineralized structural fibers, which form different systems of bundles orientated in the same direction (Fig. $4A_2$, B, C). There is a complex and highly ordered spatial organization of the bundle systems in the ossicle. Transverse and horizontal sections allow three orthogonal systems of fiber bundles to be distinguished; one vertical and two horizontal. Horizontal systems are organized in successive layers. In each layer fiber bundles are mutually parallel, but the direction changes from one layer to the next, forming angles of 90°. These layers are crossed perpendicularly by the vertical system of fiber bundles.

The highly fibrous bone matrix contains lacunae wherein the osseous cells were once housed (Fig. 4D). These spaces exhibit irregular shapes and do not present filamentous canaliculi. Vascularization is rather poor and consists of simple vascular spaces organized mainly in the internal area of the ossicles, where anastomoses occur. Vascular orientation typically parallels the spatial arrangement of fiber bundles. As in the dermal plates, the presence of LAGs, which are parallel to the bone surface, is very common in the cortical region (Fig. 4E). The number of LAGs is quite variable, even in associated ossicles. The maximum number of LAGs recorded in a single element is 17 LAGs (PVLPh 009). The distance between LAGs decreases from the center to the periphery of the element. In addition, the space between two successive lines is always greater at the lateral portion of the ossicles. There is no evidence of secondary reconstruction or deposition of periosteal bone tissue.

Discussion

Besides differences in size and shape between the dermal ossicles and plates of *Saltasaurus*, differences in their microstructure also exist. In general terms, bony plates consist of highly reconstructed trabecular bone tissue. Remains of non-remodeled, primary bone tissue consist of well developed bundles of structural fibers in the external cortex. Also, woven fibered bone tissue is observed in the basal and lateral region of the plate. Dermal ossicles are characterized by the presence of non-remodeled bone matrix, which is composed of highly ordered orthogonal systems of structural fibers. The bone histology of the osteoderms of *Saltasaurus* allows us to elucidate the origin and further development of these structures. Also, we can compare and discuss previous histological studies focusing on other dinosaurian taxa in light of our results.

Histogenesis.—Although fossil material does not allow direct observation of the ossification process, the structure of the resulting tissue and the comparison with extant groups can provide hints to how it was produced. Studies on living taxa reveal that osteoderms found in tetrapods may be formed through intramembranous ossification, as in xenarthrans (Vickaryous and Hall 2006), metaplastic ossification, as in most reptiles (Moss 1969; Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986; Hill, 2006; Scheyer 2007, Scheyer and Sánchez-Villagra 2007; Scheyer and Sander 2007; Scheyer et al. 2007; Vickaryous and Hall 2008), or a combination of different processes (Reid 1996; Vickaryous and Sire 2009). Metaplastic ossification is a process in which a pre-existing, fully developed tissue is transformed into bone (Haines and Mohuiddin 1968). Metaplastic tissue has been identified in osteoderms by the presence of interwoven bundles of mineralized collagen fibers and the absence of periosteal bone tissue (Moss 1969; Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986). Since this situation is observed in the histology of dermal ossicles in *Saltasaurus*, where the primary bone tissue is composed of coarse bundles of collagenous structural fibers and there is no evidence of periosteal bone deposition, we interpret these structures to have a metaplastic origin. Regarding the kind of soft tissue mineralized in the formation of the ossicles, the structural fiber pattern is similar to the arrangement of the collagen fibers in the dermis of the vertebrates (Moss 1972). Moreover, the tightly packed, highly ordered systems of orthogonal fiber bundles in the ossicles resemble those described for the stratum compactum of the dermis
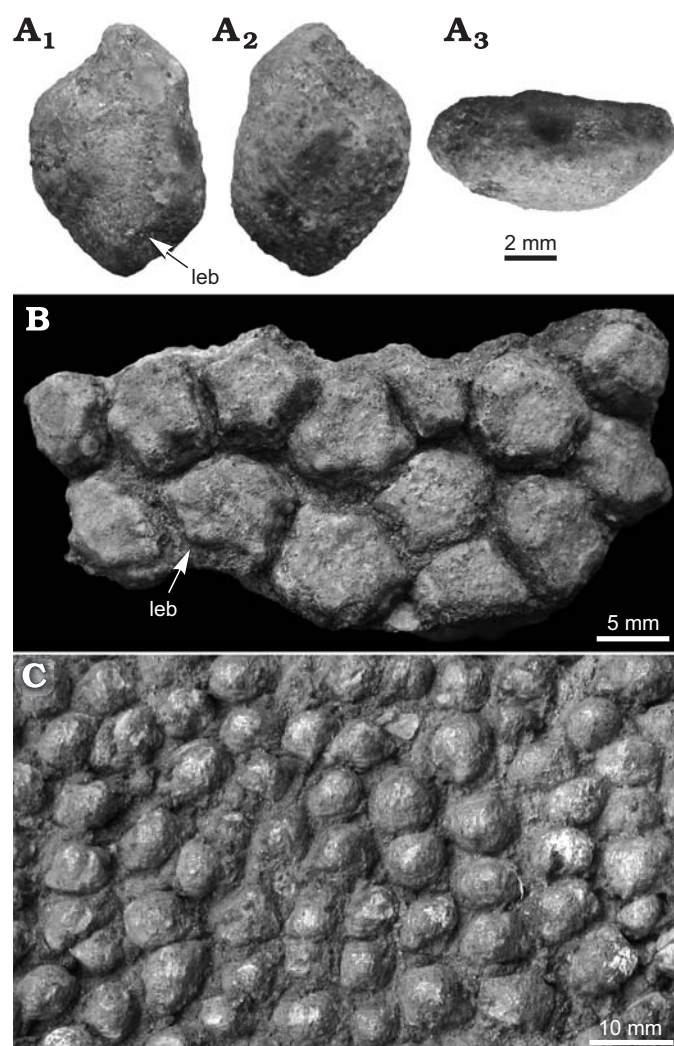

Fig. 3. Dermal ossicles of *Saltasaurus loricatus* Bonaparte and Powell, 1980 from El Brete locality (Late Cretaceous, ?late Campanian–Maastrichtian, Salta Province, Argentina). **A**. Dermal ossicles (PVL 4017-208) in external (A_1), basal (A_2), and lateral (A_3) views. **B**. Group of associated ossicles (PVL 4017-208) in external view preserved in their natural position. Presence of latero-external border (leb) gives a roughly polygonal appearance to the ossicles in this view. **C**. Group of associated dermal ossicles (PVL 4017-119) in basal view.

(Scheyer et al. 2007; Vickaryous and Hall 2008; Sire et al. 2009). Since the ossicles were arranged in contact forming an irregular mosaic, possibly soft fiber bundles of the dermis were continuous with the structural fibers of the ossicles (Fig. 5). This continuity provided a strong union between adjacent ossicles, a high resistance to the integument and also

Fig. 2. Microanatomy and histology of *Saltasaurus loricatus* Bonaparte and Powell, 1980 bony plate (PVL 4017-113) from El Brete locality (Late Cretaceous, ?late Campanian–Maastrichtian, Salta Province, Argentina). **A**. Microanatomical aspect of half the *Saltasaurus* plate in transverse (A_1, A_2) and longitudinal (A_3) sections. Normal light. **B**. Detail of the cancellous bone showing a remodeled endosteal trabecula. Polarized light. **C**. Secondary cancellous bone (top) and Haversian tissue (bottom) in the basal region. Polarized light. **D**. Detail of the structural fiber bundles in the external cortex. Note the presence of erosion cavities near the peripheral margin. Polarized light. **E**. Lines of arrested growth in the external region (arrows). Polarized light. **F**. Woven fibered bone in the basal cortex on normal (F_1) and polarized (F_2) light. Abbreviations: em, external margin; ilb, interstitial lamellar bone; lsf, longitudinally sectioned structural fiber bundle; svc, simple vascular canal; tr, trabecula; tsf, transversely sectioned structural fiber bundle; rc, resorption cavity; so, secondary osteon.
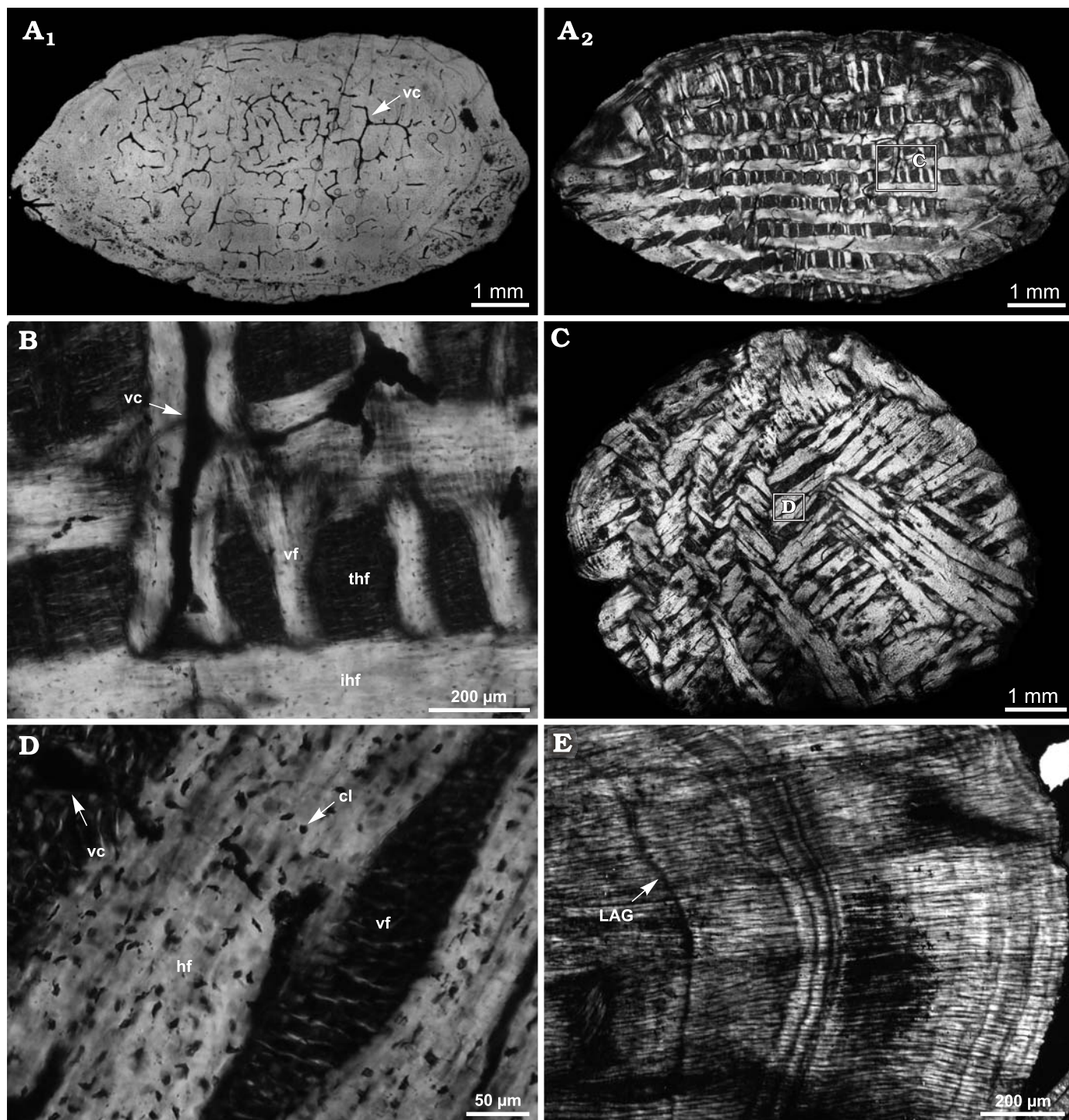
Fig. 4. Microanatomy and histology of *Saltasaurus loricatus* Bonaparte and Powell, 1980 dermal ossicles from El Brete locality (Late Cretaceous, ?late Campanian–Maastrichtian, Salta Province, Argentina). **A**. Transverse section showing the position and arrangement of vascular canals (PVPLh 001-III) in normal (A_1) and polarized (A_2) light. Note the vertical and horizontal system of structural fiber bundles. **B**. Detail of the three orthogonal systems of structural fibers. Horizontal systems of fiber bundles are visible in longitudinal and cross section. **C**. Dermal ossicle in longitudinal section (PVLPh 002-II). Polarized light. **D**. Detail of the fibrous matrix showing the small cell lacunae. **E**. Lines of arrested growth in the lateral region in transversal section (PVLPh 009). Structural fibers give a striate appearance to the sample. Polarized light. Abbreviations: cl, bone cell lacuna; hf, horizontal fiber bundle; LAG, line of arrested growth; lhf, longitudinally sectioned horizontal fiber bundle; thf, transversely sectioned horizontal fiber bundle; vc, vascular canal; vf, vertical fiber bundle.

provided the necessary flexibility to the tissue. This statement has been previously proposed for other reptiles such as trionychid turtles (Scheyer et al. 2007). If the dermal ossicle microstructure directly reflects the spatial arrangement of the fibers in the dermis (Scheyer and Sander 2004; Scheyer et al. 2007; Sire et al. 2009), our results on *Saltasaurus* provide the
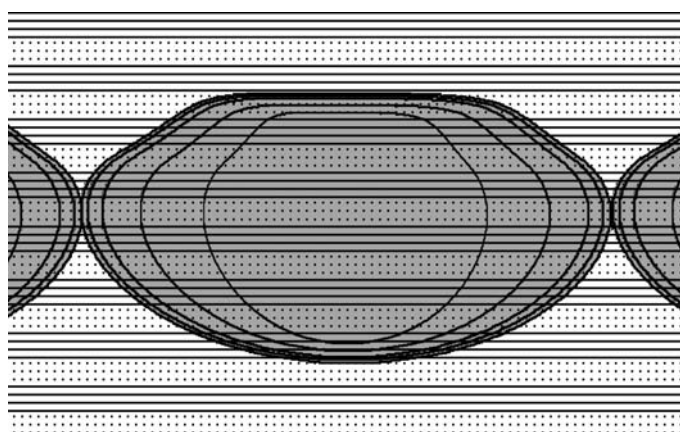
Fig. 5. Schematic sketch of dermal ossicles of *Saltasaurus loricatus* Bonaparte and Powell, 1980 based on the tissue types and growth marks described in the main text. The growing ossicles are embedded in the dermis (for simplification, only horizontal systems of fiber bundles are showed), which contains layers of perpendicularly oriented fiber (lines and points). Horizontal fibers of the ossicle are shown as being continuous with the surrounding dermis. The distance between successive LAGs decreases from the center to the periphery of the element but the space between two successive lines is always greater at the lateral portion of the ossicles.

first information about the structural composition of the dermis in a sauropod dinosaur.

Regarding the origin of the dermal plates of *Saltasaurus*, the presence of structural fibers and woven fibered bone tissue indicates a complex process in which the metaplastic ossification is not the only mechanism involved in the osteoderm formation. As previous authors emphasized, not all vertebrate osteoderms originated exclusively via metaplasia (Main et al. 2005; Vickaryous and Hall 2008; Scheyer and Sander 2009; Vickaryous and Sire 2009). In the dermal plates of *Saltasaurus*, structural fibers present in the external region indicate a metaplastic origin. However, remains of highly vascularized woven bone tissue in the basal and lateral portions of the osteoderm are interpreted as non-metaplastic bone tissue. This woven bone matrix possibly has a periosteal origin. Our results indicate that, besides morphology, size and histology, *Saltasaurus* dermal plates and ossicles are also unique with regard to their histogenesis.

An alternative hypothesis to the origin of the osteoderms has been previously suggested and deserves further discussion. Salgado (2003) proposed that the titanosaur dermal plates could have originated from the epiphyseal tip of the neural spines. This kind of ossification has been reported in the axial skeleton of some reptiles (Haines 1969). Our results indicate that, at least in *Saltasaurus* osteoderms, there is no evidence for such an origin. On the other hand, in their study of the bone histology of dermal ossicles from the Antarctic ankylosaur *Antarctopelta oliveroi*, Ricqlès et al. (2001) have proposed a neoplastic origin for these structures in addition to metaplastic ossification. A neoplastic ossification is defined as avascular, amorphous bone that forms dermally but does not replace pre-existing tissue of any kind (Main et al. 2005). In *Antarctopelta* ossicles, systems of mineralized fiber bundles appear to be arranged according to a radial growth pattern, and the mesh size and diameters of the bundles increase radially for all the systems of bundles. These characteristics have been interpreted by the authors as evidence of a de novo (neoplastic) origin of these elements. Although the microstructure of the *Antarctopelta* ossicles is similar to those described for *Saltasaurus* and could be interpreted as having the same origin, our data do not support a neoplastic origin for these elements in the Argentinean titanosaur. In *Saltasaurus*, the main diameter of the bundles appears to be constant from within the ossicle to its periphery (at least until the first line of arrested growth is reached). Also, to our knowledge, there is no report of a non-pathologic, neoplastic ossification in extant vertebrates. For these reasons, we consider metaplastic ossification as the most plausible explanation for the origin of the dermal ossicles in *Saltasaurus*.

Growth pattern.—Besides the mode of mineralization of the osteoderms, the microstructure gives important information regarding the growth dynamics of the element and changes in its microanatomy and histology. Microstructure of the bony plate reveals a very important secondary reconstruction process through the ontogeny of this element. The reconstruction is evidenced by the Haversian tissue in the basal region and the secondary cancellous bone that composed almost the entire plate. This contrasts sharply with the histology of the dermal ossicle, which lacks secondary tissue. Perhaps the differences can be explained by the distinct functions and metabolic requirements of the osteoderms. In this sense, secondary reconstruction in osteoderms appears to be related to the presence of metaplastic bone and its maintenance. The nutritional supply to metaplastic bone is poor and there is a limit to its possible thickness, because canaliculi are absent and the vascularization is sparse (Haines and Mohuiddin 1968; Main et al 2005). Since the primary bone in the bony plate of *Saltasaurus* (a relatively thick element) appears to be mainly metaplastic in origin, the secondary reconstruction process left an internal cancellous structure which contains vascular channels and allows the maintenance of the osteoderm. Probably, the small size of the ossicles and its internal system of vascular canals allow maintenance of the bone tissue without secondary reconstruction through ontogeny. Another possible explanation is that the bony plate and the ossicles belong to individuals of different ontogenetic stages. If secondary reconstruction is only a time-dependent process in all osteoderms, the plate would likely correspond to an adult and the ossicles to a sub-adult. Of course, this explanation does not imply that ossicles are bony plates in an early stage of formation.

Presence of lines of arrested growth parallel to the osteoderm surface indicates pauses in the process of matrix mineralization. As in extant groups, these marks are probably correlated with annual interruptions of growth in the whole individual (Hutton 1986; Tucker 1997; Erickson and Brochu 1999; Erickson et al. 2003). Whether the LAGs are annual or not, they reflect the growth dynamics of each osteoderm. Regarding the dermal ossicles, the spatial organization of each

element and the distribution of LAGs can provide insights into their development. In an individual ossicle, the distance between successive LAGs decreases to the periphery but it is always greater in the lateral region (Fig. 5). This spatial organization indicates that the amount of mineralized matrix in each growth cycle decreases through the ossicle ontogeny, and there is a differential rate of mineralization of the ossicle, which is higher at the lateral sides (this results in the typical flattened shape of the ossicles).

Comparison with other taxa.—*Saltasaurus* osteoderm microstructure shares some features with other dinosaurs (thyreophorans and other titanosaurs), but also has some peculiarities. Salgado (2003) described the bony plate histology of an undetermined titanosaur from the Upper Cretaceous of Argentina (Salitral Moreno locality, Allen Formation). The plate is composed of reconstructed cancellous bone in the basal region and compact bone in the marginal and external regions (Salgado 2003: 451). The compact bone consists of Haversian tissue and a fiber-bearing primary bone tissue (although well developed, coarse bundles of structural fibers were not described). This pattern contrasts with that described for the bony plate in *Saltasaurus*, where the cancellous bone dominates almost entirely, the primary matrix of the external cortex is composed of structural fiber bundles, and woven fibered bone tissue appears in the basal and lateral regions.

As previously proposed for thyreophoran dinosaurs (Scheyer and Sander 2004), differences in the osteoderm histology of *Saltasaurus* and the undetermined titanosaur described by Salgado (2003) could be used as taxonomic characters in titanosaurs. However, given the small number of osteoderms analyzed up to now, this statement is only tentative.

On the other hand, although osteoderms of thyreophoran dinosaurs share some micro-anatomical and histological features with the dermal plates and ossicles of *Saltasaurus*, the distribution and combination of the different osseous tissues in the plate of *Saltasaurus* are unique. Comparing the amount and distribution of compact and cancellous bone tissue, the dermal plate of *Saltasaurus* exhibits micro-anatomical features similar to those described in *Scelidosaurus* and *Stegosaurus* plates, where the plates are composed of a thin cortex that surrounds an inner cancellous region (Buffrénil et al. 1986; Scheyer and Sander 2004; Main et al. 2005; Hayashi et al. 2009). However, compact bone tissue at the lateral margins as observed in *Saltasaurus* is not present in *Scelidosaurus* and *Stegosaurus*. Taking into account the microstructure of the primary bone tissue, the shape and organization of the structural fiber bundles in the plate of *Saltasaurus* resembles those described for ankylosaurian plates (Reid 1996; Barrett et al. 2002; Scheyer and Sander 2004; Main et al. 2005; Burns 2008). Nevertheless, while the presence of structural fiber bundles is a common feature in ankylosaurs and *Saltasaurus*, ankylosaurs lack well vascularized, woven fibered bone at the basal and lateral region of the osteoderms (Scheyer and Sander 2004; Main et al. 2005). This bone tissue described in the *Saltasaurus* dermal plate also has been reported for *Stegosau-*

rus plates in the basal region (Buffrénil et al. 1986; Hayashi et al. 2009). In the thyreophoran dinosaur, the woven matrix is also a component of the fibro-lamellar complex and comprises the cortical primary bone (Hayashi et al. 2009). As has been proposed for *Stegosaurus* (Buffrénil et al. 1986), the presence of woven fibered bone in the basal region of the plate suggests that this region was where the highest rates of growth took place. Regarding the other types of primary bone tissues, although lamellar and lamellar-zonal has been previously described for thyreophoran osteoderms (Buffrénil et al. 1986; Reid 1996; Scheyer and Sander 2004; Main et al. 2005; Hayashi et al. 2009), *Saltasaurus* entirely lacks these bone tissues. Although *Saltasaurus* plates share some basic histological features with other dinosaurs, the differences discussed above indicate a certain degree of variation in the osteoderm microstructure within the Dinosauria. These microanatomical and histological differences are probably related to differential osteoderm histogenesis, osteoderm function, location in the integument, ontogenetic stage, and forces applied to the osteoderm.

Regarding the dermal ossicles, histology of *Saltasaurus* dermal ossicles is similar to that described by Ricqlès et al. (2001) for dermal ossicles of the Antarctic ankylosaur *Antarctopelta oliveroi*. As in *Saltasaurus*, dermal ossicles of *Antarctopelta* are composed of three orthogonal systems of structural fiber bundles (Ricqlès et al. 2001). This is not exactly the same pattern observed in other ankylosaur osteoderms, where the structural fiber bundles are arranged randomly (ankylosaurids and polacanthids) or forming sets of orthogonal fibers rotated at 45° to each other (nodosaurids) (Scheyer and Sander 2004). The histological features shared between *Saltasaurus* and *Antarctopelta* ossicles are probably related to the osteoderm location and growth pattern. As has been proposed by Hill (2006) for all vertebrates, the common growth pattern in the osteoderms of two non-related dinosaur groups as titanosaurs and ankylosaurs is an example of deep homology in vertebrates. Previous studies have concluded that, although vertebrate osteoderms are not homologous, they share a common origin relating to latent skeletogenic properties of the dermis (Zylberberg and Castanet 1985; Hill 2006; Vickaryous and Hall 2008; Vickaryous and Sire 2009). This can be specially applied to the *Saltasaurus* and *Antarctopelta* dermal ossicles, where the histology reveals a common ossification process that occurs in the same integumental layer of two non-related groups and generates non-homologous structures. These skeletogenic properties are not always related to a particular mechanism of formation in osteoderms. As previously mentioned, although metaplastic ossification appears to be a common process in the osteoderm formation, it is not the only mode of development (Vickaryous and Sire 2009). In turtles, endochondral and intramembranous ossification are involved (in addition to metaplasia) in the development of the carapace (Vickaryous and Sire 2009). Also, histological features of osteoderms in pareiasaurs has been proposed as evidence of an intramembranous ossification of these structures (Scheyer and Sander 2009).

Acknowledgements

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