# Osteoderm Histology of Proterochampsia and Doswelliidae (Reptilia: Archosauriformes) and Their Evolutionary and Paleobiological Implications

Ignacio A. Cerda,[1,2]* Julia B. Desojo,[1,3] María J. Trotteyn,[1,4] and Torsten M. Scheyer[5]

[1]Conicet: Rivadavia 1917, Buenos Aires 1000–1499, Argentina
[2]Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo Carlos Ameghino, Belgrano 1700, Paraje Pichi Ruca (predio Marabunta), 8300 Cipolletti, Río Negro, Argentina
[3]Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ángel Gallardo 470 C1405DJR, Buenos Aires, Argentina
[4]INGEO. Instituto de Geología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan. Ignacio de la Rosa 590 (oeste), Complejo Universitario Islas Malvinas, San Juan, Argentina, CP 5400
[5]Paläontologisches Institut und Museum der Universität Zürich, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland

ABSTRACT Postcranial osteoderms are commonly developed in the major lineages of Archosauriformes, including forms such as proterochampsids and doswelliids. Here, we survey the histology of osteoderms of the doswelliids *Archeopelta arborensis* and *Tarjadia ruthae*, and the proterochampsids *Chanaresuchus bonapartei* and *Pseudochampsa ischigualastensis* to understand better the morphogenesis of these skeletal elements. Whereas, the Doswelliid osteoderms possess a trilaminar organization, in which two cortices (external and basal) can be differentiated from an internal core of cancellous bone, these elements are compact structures in proterochampsids. The osteoderms of *P. ischigualastensis* are avascular and they consist entirely of parallel-fibered bone. Conversely, the osteoderms of *C. bonapartei* are well vascularized structures composed of zones of woven-fibered bone and annuli of parallel-fibered bone. The rather simple microstructure observed in *P. ischigualastensis* osteoderms suggests that these elements grew at a constant, low rate. Compared with proterochampsids, doswelliid osteoderms possess a more complex histology, which appears to be linked to variations in the growth rate during the osteoderm formation and also to the development of the external ornamentation. A comparison of our findings with the results of earlier studies on other archosauriforms (phytosaurs and pseudosuchians) reveals that the general osteoderm histology of doswelliids bears a closer resemblance to that of phytosaurs and pseudosuchians than the proterochampsid osteoderm microstructure. If all archosauriform osteoderms are homologous structures, the closer resemblance of doswellid osteoderm microstructures to that of phytosaurs and pseudosuchians is in agreement with the hypothesis that doswellids are more closely related to archosaurs than proterochampsids. J. Morphol. 276:385–402, 2015. © 2015 Wiley Periodicals, Inc.

KEY WORDS: doswelliids; proterochampsids; microanatomy; bone microstructure; integument; dermal armor

## INTRODUCTION

Osteoderms represent the most commonly identified and documented element of the tetrapod integumentary skeleton (Vickaryous and Sire, 2009). These skeletal elements have been defined as mineralized organs entrenched within the dermis (Francillon-Vieillot et al., 1990; Vickaryous and Hall, 2008). Osteoderms vary greatly in size, shape, ornamentation, arrangement, and number both among and within taxa (Vickaryous and Sire, 2009 and references therein). These structures are common to most major tetrapod lineages, including "amphibians," lepidosaurs, archosauriforms, turtles, parareptiles (pareiasaurs and procolophonids), placodonts (sauropterygians), and some synapsids (xenarthrans; Vickaryous and Sire, 2009 and references therein). Especially within Archosauriformes, osteoderms are a prominent part of the skeleton of several groups, including pseudosuchian and avemetatarsalian representatives.

In recent years, the bone histology of osteoderms in pseudosuchian and avemetatarsalian archosauriforms has increasingly attracted the interest of paleontologists and several contributions has been published on this topic (e.g., Buffrénil et al., 1986; Scheyer and Sander, 2004; Main et al., 2005;

*Correspondence to: Ignacio A. Cerda, CONICET, Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo Carlos Ameghino, Belgrano 1700, Paraje Pichi Ruca (predio Marabunta), 8300 Cipolletti, Río Negro, Argentina. E-mail: nachocerda6@yahoo.com.ar

Hill 2006, 2010; Vickaryous and Hall, 2008; Cerda and Powell, 2010; Cerda and Desojo, 2011; Scheyer and Desojo, 2011; Burns et al, 2013; Filippi et al., 2013; Scheyer et al., 2014; Cerda et al., in press). With the exception of phytosaurs (Scheyer et al., 2014), the histology of the dermal ossifications of nonarchosaurian archosauriforms, has received less attention. In a recent contribution, Scheyer et al. (2014) described the osteoderm microstructure of the doswelliid *Jaxtasuchus salomoni* from the Ladinian of Germany (Schoch and Sues, 2013), in which the presence of woven-fibered bone tissue was interpreted as evidence of a rapid early growth of the osteoderm.

In this study, we increase the sampling base of nonarchosaurian archosauriforms by focusing on the detailed description of the osteoderm bone tissues occurring in selected taxa of proterochampsids and doswelliids. The proterochampsids are a monophyletic group of archosauriforms from the Middle to Late Triassic of South America (Trotteyn et al., 2013). They usually have been considered as one of the potential successive sister taxa of the crown group Archosauria (Sereno and Arcucci, 1990; Sereno, 1991; Dilkes and Sues, 2009; Ezcurra et al., 2010). This clade includes the genera *Chanaresuchus, Gualosuchus, Tropidosuchus, Proterochampsa, Rhadinosuchus, Cerritosaurus*, and *Pseudochampsa* (Price, 1946; Reig, 1959; Sill, 1967; Romer, 1971, 1972a, 1972b; Barberena, 1982; Arcucci, 1990; Trotteyn et al., 2013; Trotteyn and Ezcurra, in press). With regard to their body "armor," proterochampsids possess a single row of osteoderms dorsal to the vertebral column. The Doswelliidae includes four known genera: *Tarjadia, Archeopelta, Doswellia*, and *Jaxtasuchus* (Arcucci and Marsicano, 1998; Desojo et al., 2011; Schoch and Sues, 2013; Sues et al., 2013). They were a group widely distributed geographically and temporally, present in the Middle and Late Triassic of Europe and America (Desojo et al., 2011; Schoch and Sues, 2013; Sues et al., 2013). Unlike proterochampsids, doswelliids possess paramedian, lateral and, in some taxa (e.g., *Jaxtasuchus*), appendicular osteoderms.

The major aims of the present contribution are: characterize the osteoderm microanatomy and histology of some nonarchosaurian archosauriforms, establish the mode of skeletogenesis of these bones, infer the processes of osteoderm development, and compare the histology of doswellids and proterochampsid osteoderms to other armored archosauriformes. Since armored avemetatarsalian taxa (i.e., certain dinosaur groups) are phylogenetically well separated from those of pseudosuchians and stem-group archosaurs, we focus our comparison on nonavemetatarsalian taxa (Pseudosuchia and Phytosauria).

On the basis of morphological, sedimentary and taphonomic evidence, doswelliids and protero-champsids have been traditionally considered as semiaquatic forms (Sues et al., 2013; Trotteyn et al., 2013). Given that the microanatomy of dermal bones has been previously employed to determine ecological traits in some vertebrates (Scheyer and Sander, 2007, 2009), we discuss whether the semiaquatic hypothesis is supported by the osteoderm microanatomy of doswelliids and proterochampsids.

Finally, given that doswelliids have been in part characterized by the strong degree of ornamentation in their osteoderms (Desojo et al., 2011; Schoch and Sues, 2013; Sues et al., 2013), we aim to identify the osteogenic mechanisms linked to the development of the osteoderm ornamentation.

## Institutional Abbreviations

**CPEZ**–Coleção Municipal, São Pedro do Sul; Brazil; **PULR**–Museo de Ciencias Naturales de la Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**–Instituto Miguel Lillo, Tucumán, Argentina; **PVSJ**–División Paleontología de Vertebrados, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina.

## MATERIALS AND METHODS

Osteoderms of the species *Pseudochampsa ischigualastensis, Chanaresuchus bonapartei, Tarjadia ruthae*, and *Archeopelta arborensis* were used in this study (Fig. 1, Table 1). Specimens were prepared for thin sections based on the methodology outlined in Chinsamy and Raath (1992). Given that the preparation of petrographic thin sections is a destructive method, all specimens were photographed and standard measurements were taken before sectioning. Transverse sections were obtained from each osteoderm. Parasagittal and longitudinal sections were also obtained from *T. ruthae* and *P. ischigualastensis*. The histological sectioning was carried out in the Departamento de Geología de la Universidad Nacional de San Luis (Argentina). Osteoderm thin sections were analyzed under a light microscope in normal and cross-polarized light and they are housed at the Colección Nacional de Paleovertebrados from the Museo Argentino de Ciencias Naturales Bernardino Rivadavia of Argentina.

The terminology used in this study for describing the various types of osseous tissues refers to Francillon-Vieillot et al. (1990). Regarding the relative locations of specific structures within the osteoderm, we use the term "external" to refer the portion of the osteoderm oriented toward the body surface and "basal" for the portion that is oriented toward the interior of the organism (Scheyer and Sander, 2004). These terms are synonyms of "distal/proximal" (Main et al., 2005), "superficial/deep" (Hill, 2006, 2010). Also, we use the term "marginal" cortex to refer the lateral and medial regions of the osteoderms.

## RESULTS
### Doswelliidae

***Archeopelta arborensis.*** The sample consists of two incomplete osteoderms for which the position along the axial column is undetermined. The best preserved osteoderm is thick and roughly quadrangular in external view. The external surface is partially eroded; however, ornamentation is observable. As previously described by Desojo
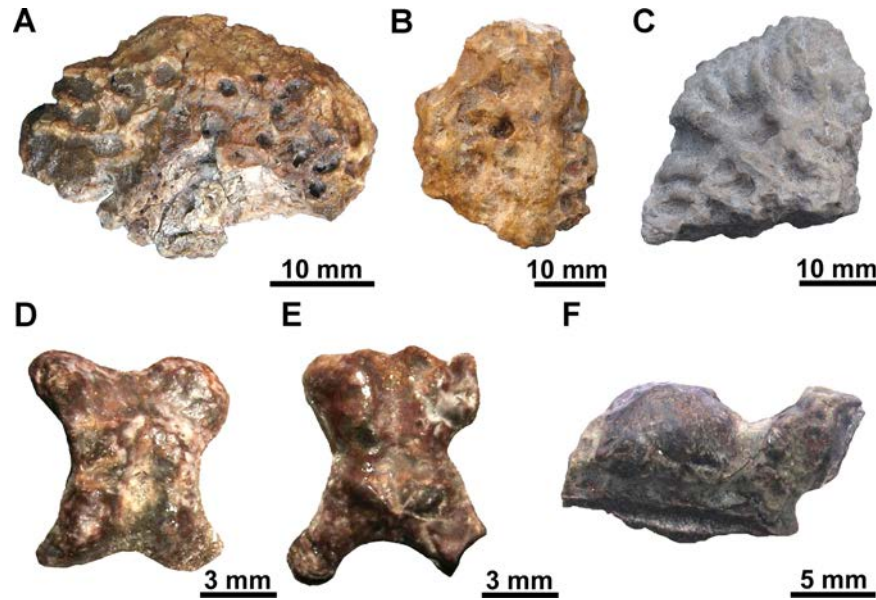
Fig. 1. Sampled osteoderms. **A,B**: *Acheopelta arborensis* CPEZ 239a. **C**: *Tarjadia ruthae* PULR 063. **D,E**: *Pseudochampsa ischigualastensis* PVSJ 567. F: *Chanaresuchus bonapartei* PVL 6244. Except *C. bonapartei*, all elements are in external view with the anterior margin oriented toward the upper portion of the figure. *C. bonapartei* in lateral view.

et al. (2011), the external ornamentation of the osteoderm consists of rounded and deep pits of different sizes. The basal surface texture is smooth. The element bears an unornamented anterior lamina for an overlapping articulation with the preceding osteoderm. The osteoderm exhibits some degree of flexion in anterior view, with the medial and lateral portions of the osteoderm enclosing an angle of 145°.

The osteoderm is a rather compact structure with a trilaminar organization, in which two distinct cortices (external and basal) can be differentiated from an internal core (Fig. 2A). Although the external cortex is partially altered (probably due to the acidic preparation of the material, Desojo et al., 2011), details of its microstructure can be discerned in some regions. The external cortex exhibits a distinct pattern of valleys (concave surface in section) and ridges (convex surface in section) that reflects the pattern of pits at the external surface of the osteoderm. In some areas, the valleys reach the innermost portion of the osteoderm, almost contacting the basal cortex. The external cortex consists mostly of lamellar and woven-fibered bone tissue (but parallel-fibered bone is also locally present). The lamellar tissue is organized in parallel bone lamellae from different cycles of erosion and deposition which are interrupted by resorption lines (Fig. 2B–E). The lamellar matrix is avascular and its bone cell lacunae are mainly elongated in shape. The woven-fibered bone possesses abundant and densely grouped bone cell lacunae and is vascularized by simple canals. The extinction pattern of woven-fibered matrix is not entirely monorefringent and diminutive patches of interwoven fiber bundles can be observed under high magnifications in several areas (Fig. 2F–H).

*TABLE 1. Archosauriformes osteoderms sectioned in the present study*

| Taxon | Collection number | Locality | Horizon and age | Position |
|---|---|---|---|---|
| *Pseudochampsa ischigualastensis* | PVSJ 567 | Cancha de Bochas, San Juan Province, Argentine. | Ischigualasto Formation (late Carnian-earliest Norian) | Presacral? |
| *Chanaresuchus bonapartei* | PVL 6244 | Chañares Formation, La Rioja, Argentina. | Chañares Formation (Ladinian-Carnian) | Dorsal |
| *Tarjadia ruthae* | PULR 063 | Agua Escondida, La Rioja Province, Argentina. | Chañares Formation (Ladinian-Carnian) | Presacral |
| *Acheopelta arborensis* | CPEZ 239a | Sanga da Árvore (Baum Sanga), Xiniquá region, São Pedro do Sul, Rio Grande do Sul State, Brazil. | Santa Maria 1 Sequence (late Ladinian–early Carnian) | Dorsal |
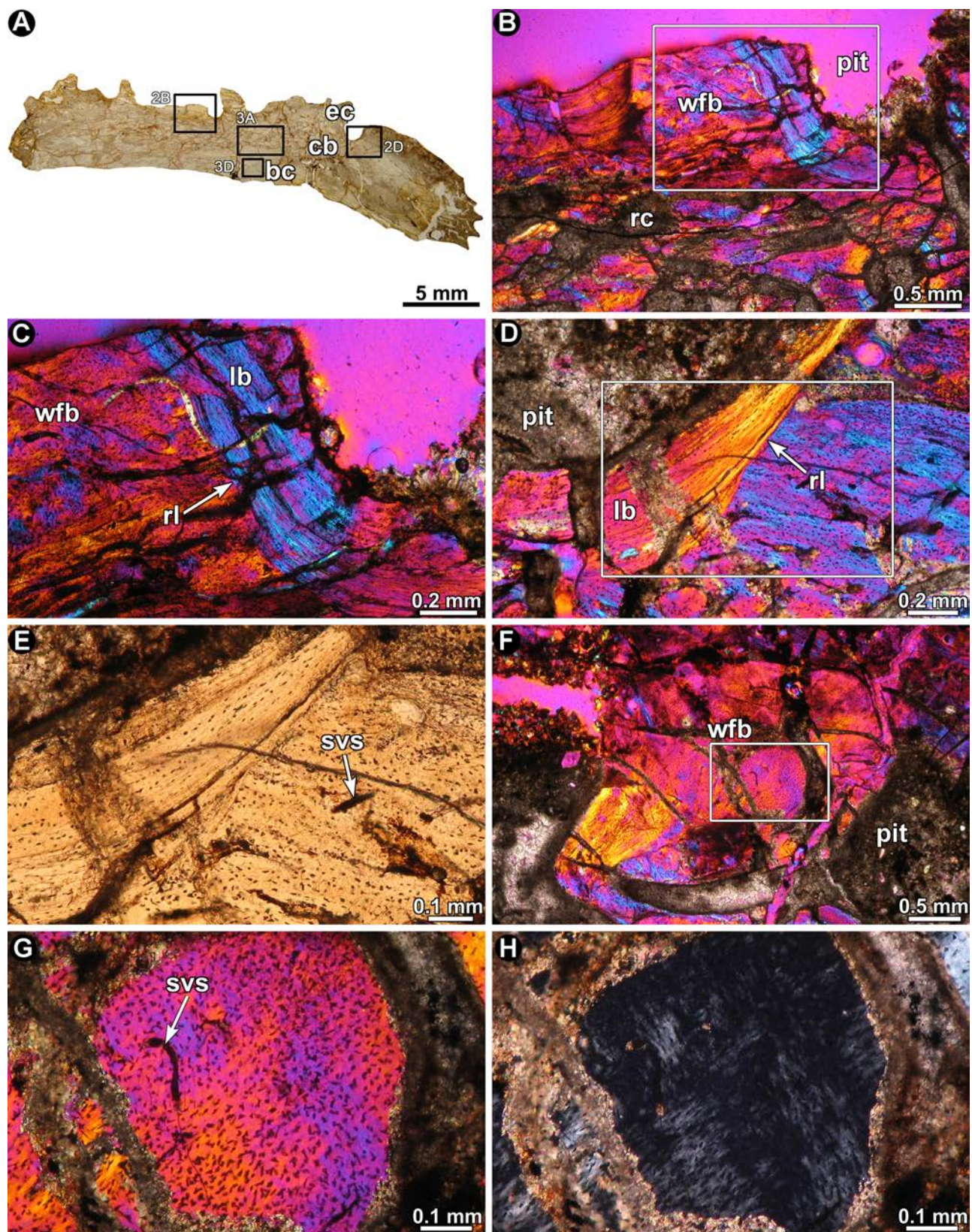
Fig. 2. *Archeopelta arborensis* CPEZ 239a osteoderm histology. **A**: Complete transversal section of the osteoderm. The inset boxes indicate the position of the detailed pictures in Figures 2 and 3. **B**: External cortex composed of lamellar and woven-fibered bone. **C**: Close-up of the same specimen (box inset in B). **D**: Detail of the external cortex. Note resorption and redeposition of cortical bone tissue. **E**: Enlarged view of the same specimen (box inset in D). The bone tissue formed at the deep region of the pit is formed entirely by lamellar bone tissue. **F**: General view of a ridge in the external cortex. **G,H**: Enlarged view of the same specimen (box inset in F). Note the patchy birefringence of the woven-fibered bone and the presence of few simple vascular spaces. A and E: Normal light, B–D,F,G: cross-polarized light with lambda compensator, H: cross-polarized light. Abbreviations: cb: cancellous bone; bc: basal cortex; ec: external cortex; lb: lamellar bone; rc: resorption cavity; rl: resorption line; svs: simple vascular space; wfb: woven-fibered bone.
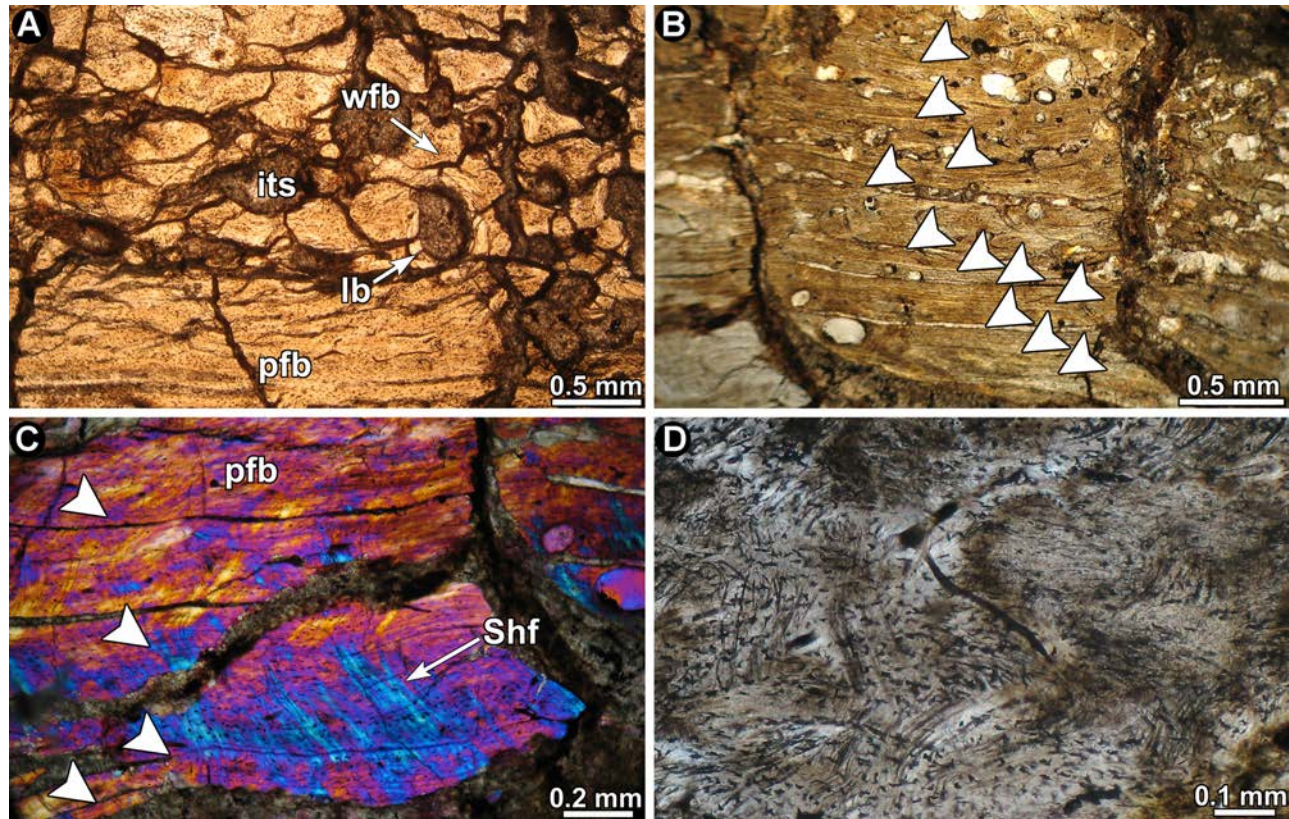
Fig. 3. *Archeopelta arborensis* CPEZ 239a osteoderm histology. **A**: Cancellous bone of the internal core. The bony trabeculae are composed of secondary lamellar bone tissue and remains of woven-fibered bone. **B**: Growth marks (arrowheads) in the basal cortex. **C**: Growth marks (arrowheads) and Sharpey's fibers in the basal cortex. **D**: Detail of the basal cortex in the middle region. Note the variable orientation of the Sharpey's fiber bundles. A,B,D: Normal light, C: cross-polarized light with lambda compensator. Abbreviations: its: intertrabecular space; lb: lamellar bone; pfb: parallel-fibered bone; Shf: Sharpey's fibers; wfb: woven-fibered bone.

The external cortex grades into a well differentiated internal core. The internal core has cancellous bone with short thick trabeculae and small intertrabecular spaces only at the innermost portions of the osteoderm (Fig. 3A). The other portions of the internal core exhibit a more compact aspect. Intertrabecular spaces are commonly coated by endosteally deposited secondary bone tissue, which is clearly delimited by cementing lines (Fig. 3B). The inner portion of the bony trabeculae and the compact bone tissue of the inner core are composed of primary tissue, which consists of woven-fibered bone and coarse parallel-fibered bone. Bone cell lacunae are abundant and they exhibits irregular shapes. The core of the osteoderm is more vascularized than the basal and external cortices and contains several primary osteons, erosion cavities and some secondary osteons. Vascular orientation is variable, although longitudinal canals predominate.

In the basal cortex, parallel-fibered bone tissue constitutes the matrix and the bone cell lacunae are elongated in shape. The pattern of birefringence of the parallel-fibered boned is obscured in some areas by the abundant Sharpey's fibers. The basal cortex is poorly vascularized in comparison with the internal core. Vascularization consists of simple vascular canals and primary osteons. Vascular spaces are arranged in different orientations and they commonly anastomose. In some areas, several primary vascular spaces open up to the basal surface, penetrating the cortex at acute angles (20–35°).

Growth marks in the form of lines of arrested growth (LAGs) are well developed mostly in the basal cortex (Fig. 3B). A maximum of 11 of them can be discerned in the smaller fragment sectioned. Sharpey's fibers, that is, mineralized ingrowing fibrillary processes from adjacent soft tissues (Francillon-Vieillot et al., 1990), are present in both external and internal cortices. In the unremodeled portions of the external cortex, fine Sharpey's fibers penetrate the compacta at an approximately right angle to the surface. These extrinsic fibers are regularly but not densely arranged and they only can be observed under cross-polarized light. Sharpey's fibers are quite abundant at the basal cortex (Fig. 3C). At the

lateral and marginal portions, they are organized as long bundles and penetrate the cortex at acute angles (14° or less). When these fibers approximate to the osteoderm midline (near the curvature point), they become more perpendicularly oriented. This variation in the orientation of the Sharpey's fibers results in a radial pattern of these fibers in the basal cortex. Near the osteoderm midline (the "transition" zone), the Sharpey's fibers are organized as short bundles arranged in different orientations (Fig. 3D). Sharpey's fibers also occur in the internal core, particularly at the medial portion of the osteoderm. In this region they are present as thin and long fibrous strands in the bone tissue. These extrinsic fibers are arranged perpendicularly to the sagittal plane axis of the element.

*Tarjadia ruthae.* Although fragmentary, the sampled osteoderm is well preserved. The osteoderm is a thick element with identifiable external and basal surfaces. The external face is strongly ornamented by deep pits. The pits at the periphery of the osteoderm are often more elongate and open to the side. The basal surface is smooth and has a large nutrient foramen. The osteoderm preserves portions of two borders, but is not possible to identify if they correspond to the anterior, posterior, medial or lateral edges. One of these borders possesses a rather acute margin. The other preserved border displays an irregular texture and possibly represents a sutural surface.

The osteoderm exhibits a diploe structure with a central cancellous core bordered by two compact cortices (Fig. 4A). The external cortex is thicker than the basal one, occupying almost 1/2 of the complete osteoderm thickness. As described for *Archeopelta*, the external cortex shows an external ornamentation of ridges and valleys in various stages of remodeling. Lines of resorption mark separate areas of bone deposition, which consist locally of parallel-fibered or woven-fibered bone tissue (Fig. 4B–D). In some areas, the parallel-fibered bone grades into a more ordered lamellar matrix. Whereas bone cell lacunae display an elongated shape in the lamellar matrix, they possess more plump and rounded shapes in the parallel-fibered and woven-fibered tissue. Branching canaliculi are well preserved mostly in the parallel-fibered bone. The particular preservation of the sample allows a three dimensional view of the vascular lattice in the compact bone. Vascular spaces consist of thin (the internal diameter never surpasses 0.035 mm), branching canals scattered throughout the cortex. Although scarce in number, they are developed in the whole compacta and they are more abundant in the woven-fibered bone than in the parallel-fibered and lamellar matrices. Vascular spaces are commonly simple and they are mostly oriented toward the external surface. An unusual (pathological?) structure of secondary origin is developed in the external cortex. This struc-

ture consists of a cavity filled with few bony trabeculae and it is enclosed by a distinct cementing line (Fig. 4E,F). The trabeculae are composed of woven-fibered and lamellar bone.

The inner core consists of heavily remodeled bone with numerous, irregularly shaped resorption cavities and intervening trabeculae (Fig. 5A). Some primary bone persists between the cavities, but much of the structure has been reconstituted as concentric bony lamellae that line the cavities. The lamellar bone tissue that surrounds the intertrabecular spaces exhibits a distinct pattern of alternated extinction under cross-polarized light. Interstitial primary bone consists of parallel-fibered and woven-fibered bone (Fig. 5B–D). Bone cell lacunae are more abundant and more densely arranged than in the external cortex.

The basal cortex is composed of parallel-fibered bone tissue, which exhibits a uniform pattern of extinction under cross-polarized light. The bone cell lacunae are small and they display round or slightly elongated shapes. Vascularization mainly consists of small, simple vascular canals similar to those developed in the external cortex. These vascular spaces are more abundant at the inner portion of the basal cortex and they are mostly longitudinally and radially organized. Few resorption cavities and secondary osteons are also visible in the basal cortex. Growth marks are best preserved at the basal cortex. At least 20 LAGs were counted in this portion of the osteoderm.

Sharpey's fibers are developed in the osteoderm, although their density and arrangement is variable (Fig. 5E–H). The external cortex exhibits abundant fine Sharpey's fibers, which are mostly embedded in the parallel-fibered matrix. They are projected perpendicularly to the external surface. At the cortical portion of the osteoderm that corresponds with the suture region, Sharpey's fibers are abundant and they are oriented perpendicularly to the osteoderm margin (Fig. 5E). These extrinsic fibers are coarse and densely packed and as such this organization resembles the Sharpey's fiber bone described for *Dasypus novemcinctus* (Vickaryous and Hall, 2006). Such arrangement is possibly related to a sutural attachment with the adjacent osteoderm. Sharpey's fibers located at the basal cortex are long and they are organized in a radiating pattern (from the midline to the lateral margins), similar to those described for *Archeopelta*. Contrary to those observed in other portions of the osteoderm (e.g., external cortex), the Sharpey's fibers embedded in the basal cortex are arranged in long coarse bundles (Fig. 5H).

## Proterochampsia

*Pseudochampsa ischigualastensis.* The sectioned osteoderms are small bones, with lengths of around 10 mm. The osteoderms are longer than high, and waisted at midlength in external view
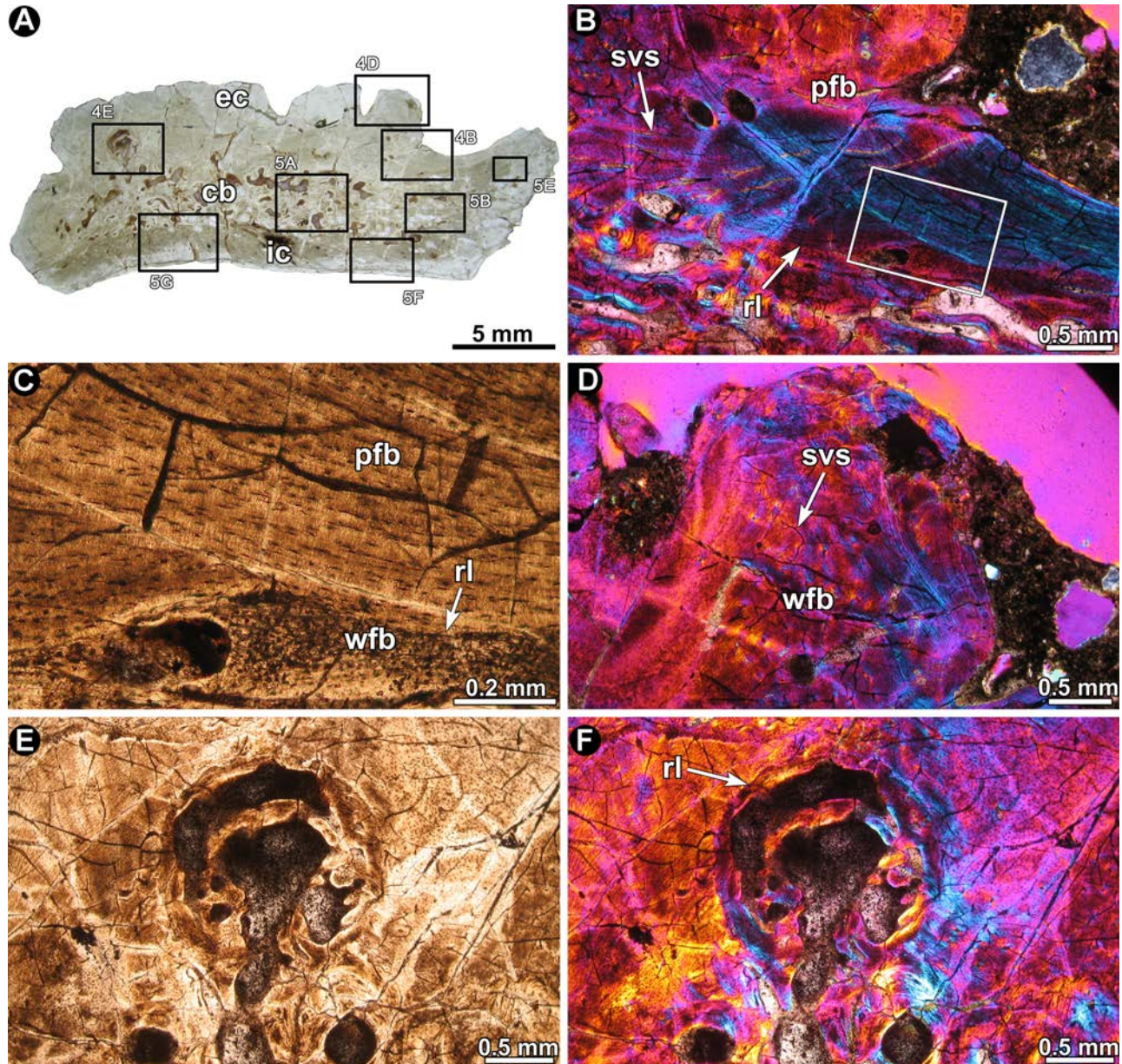
Fig. 4. *Tarjadia ruthae* PULR 063 osteoderm histology. **A**: General view of the osteoderm in cross section. The inset boxes indicate the position of the detailed pictures in Figures 4 and 5. **B**: External cortex composed of parallel-fibered and woven-fibered bone. **C**: Close-up of the same specimen (box inset in B). Note the variation in the woven-fibered and parallel-fibered tissues with regard to the bone cell lacunae shape, orientation and density. **D**: General view of a ridge in the external cortex. **E,F**: Abnormal resorption cavity in the external cortex partially filled with bony trabeculae. A, C, E: Normal light, B, D, F: cross-polarized light with lambda compensator. Abbreviations: cb: cancellous bone; bc: basal cortex; ec: external cortex; pfb: parallel-fibered bone; lb: lamellar bone; rl: resorption line; svs: simple vascular space; wfb: woven-fibered bone.

(Fig. 1D,E). Both anterior and posterior edges exhibit excavated margins. Trotteyn et al., (2012) described a deep longitudinal sulcus in the external face of the osteoderm. However, based on histology and compared with the articulated osteoderms of *C. bonapartei*, we interpret that such a sulcus is actually located at the basal face of the element.

The osteoderm is kidney-shaped in transverse section, with a flat, slightly concave external surface and a strongly concave basal surface, the latter of which result from the development of a longitudinal sulcus in this face (Fig. 6A,B). The osteoderm possesses a compact internal structure. Surprisingly, the whole element is completely avascular. The primary bone consists entirely of
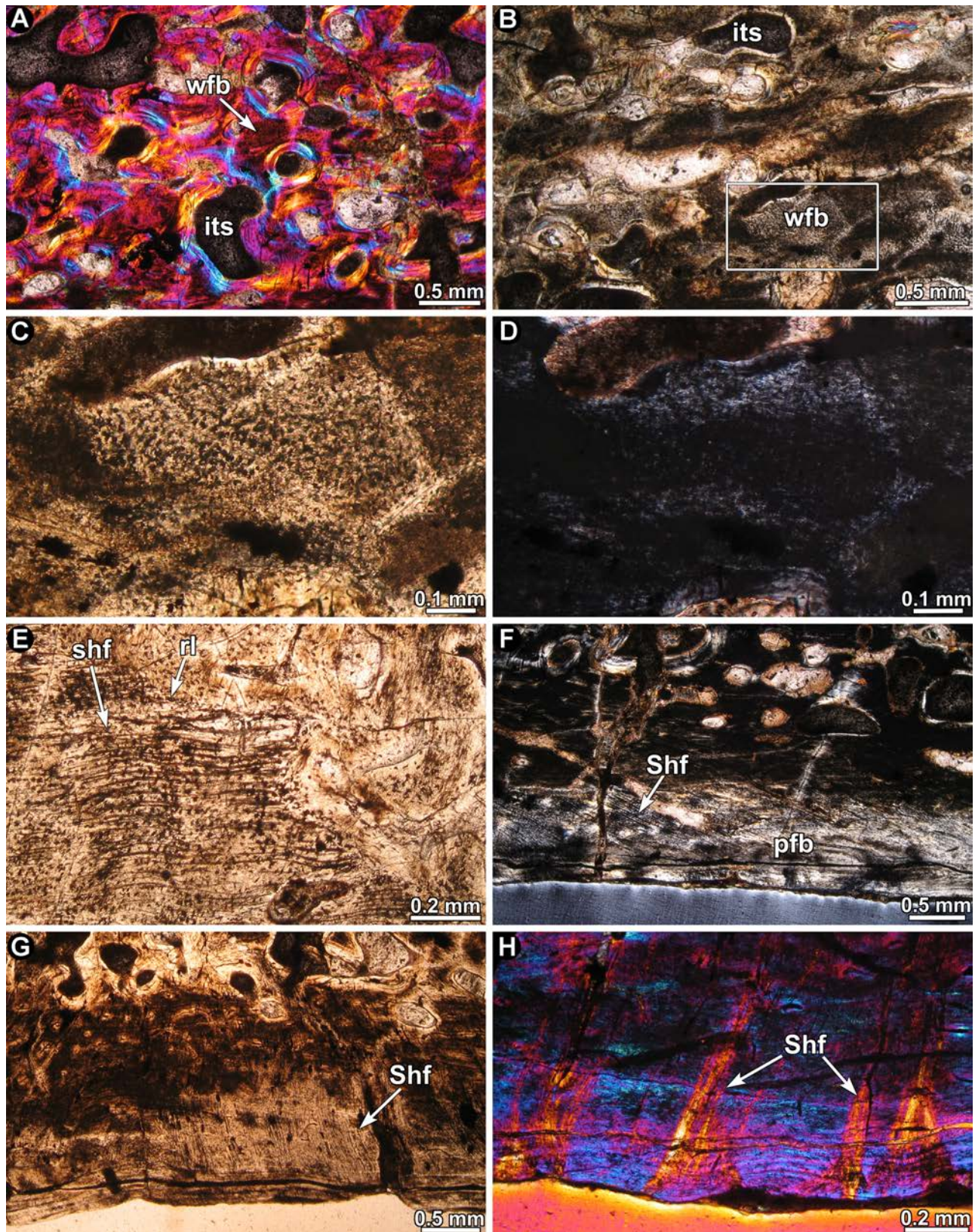
Fig. 5. *Tarjadia ruthae* PULR 063 osteoderm histology. **A,B**: Cancellous bone of the internal core. The bony trabeculae are composed of secondary lamellar bone tissue and remains of woven and parallel-fibered bone. **C,D**: Close-up of the woven-fibered bone in the inner core of the osteoderm (box inset in B). Note the general monorefringence of the matrix and the abundance bone cell lacunae. **E**: Detailed view of dense packed Sharpey's fibers oriented toward the marginal surface of the osteoderm. **F**: Basal cortex composed of parallel-fibered bone. Sharpey's fibers are arranged forming acute angles with the basal surface. **G**: General view of the basal cortex. The Sharpey's fibers in this area are oriented almost perpendicularly to the basal surface. **H**: bundles of Sharpey's fibers in the basal cortex. A and H: Cross-polarized light with lambda compensator; B,C,E,G: normal light. D, F: cross-polarized light. Abbreviations: its: intertrabecular space; pfb: parallel-fibered bone; rl: resorption line; Shf: Sharpey's fibers; wfb: woven-fibered bone.
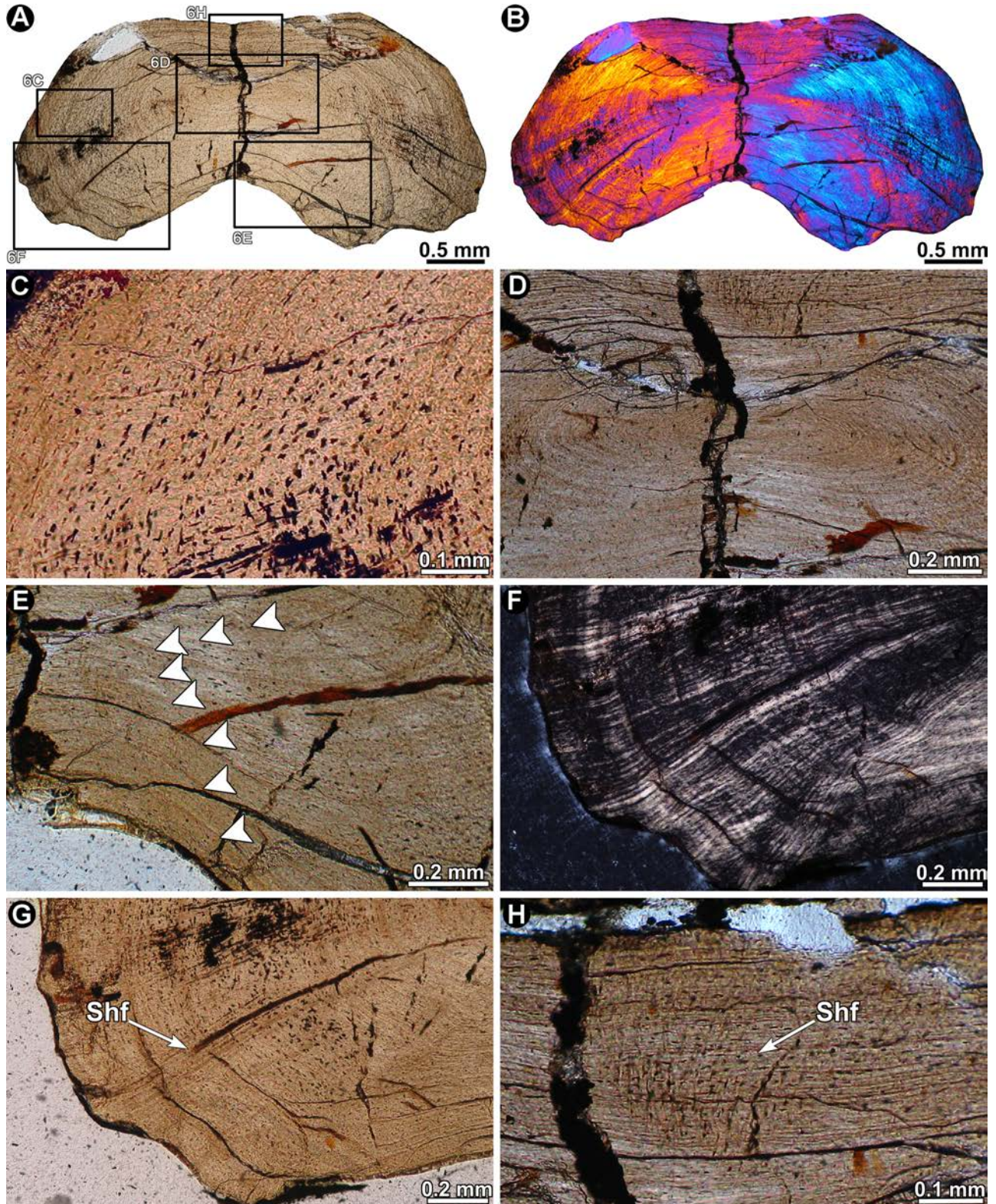
Fig. 6. *Pseudochampsa ischigualastensis* PVSJ 567 osteoderm histology. **A,B**: General view of the osteoderm in cross section. The inset boxes in A indicate the position of the detailed pictures in the figure. **C**: Close-up of the cortical bone. Note the organized arrangement and the elongated shape of the bone cell lacunae. **D**: Detail of the inner core showing several concentric growth marks. **E**: Growth marks (arrowheads) in the basal cortex. **F,G**: Abundant Sharpey's fibers in the marginal region of the cortex. **H**: Sharpey's fibers in the mid area of the external cortex. A,C–E,G,H: Normal light; B: cross-polarized light with lambda compensator; F: cross-polarized light. Abbreviations: Shf: Sharpey's fibers.

parallel-fibered bone tissue (Fig. 6B,C). The intrinsic fibers of the matrix are concentrically arranged to the inner core of the element. Bone cell lacunae are elongated and they do not present filamentous canaliculi. The organization of the bone cell lacunae network mirrors the extracellular matrix orientation in bone (Fig. 6C). There is no evidence of secondary remodeling. Otherwise, there are no particular histological differences that allow differentiation between the external, basal and internal regions of the osteoderm.

Cyclic growth marks (LAGs) are clearly observed in the osteoderm (Fig. 6D,E). Given that there is not secondary remodeling, each LAG can be traced around the whole osteoderm. A total of 20 LAGs can be observed. The LAGs are arranged concentrically to the inner core and they encircle areas that resemble to the osteoderm shape, including the deep basal sulcus. The inner LAG encircles a small area of 0.39 × 0.05 mm of diameter.

Abundant Sharpey's fibers are present in the osteoderm. These extrinsic fibers are long and they extend from the inner core region toward the latero-basal surface (Fig. 6F,G). In the inner region of the osteoderm, Sharpey's fibers are arranged forming angles that ranging from 84 to 53 degrees to the sagittal plane. At the level of approximately the 11th LAG, the Sharpey's fibers are more basally oriented, forming angles that vary between 66° and 25°. Few fine and short Sharpey's fibers are also developed in the mid portion of the external cortex. They are oriented perpendicularly to the outer surface (Fig. 6H).

***Chanaresuchus bonapartei.*** Osteoderms of *C. bonapartei* are small elements (their lengths are less than 10 mm) of rather globose shape (Fig. 1F). These elements are narrow along the anterior edge and wider toward the posterior edge. The anterior end of each osteoderm underlies the posterior edge of the one anterior to it. Contrary to those of *P. ischigualastensis*, the osteoderms of *C. bonapartei* are taller than wide. The basal surface possesses a prominent groove, in which the neural spine contacts the osteoderm. No particular ornamentation was observed in the sampled osteoderms.

The studied osteoderms are composed of compact bone tissue (Fig. 7A,B). No cancellous bone or extensive secondary remodeling was encountered in these elements. The compact bone is however highly vascularized with radial and circumferential vascular spaces, which anastomose and lend the tissue a plexiform organization (Fig. 7C–F). Radially oriented canals predominate over the circumferential ones. Several vascular spaces are opened to the surface. Vascular canals are mostly organized as simple vascular spaces. Few secondary osteons and resorption spaces are developed in the inner core (Fig. 8A–D). Some large resorption cavities are radially arranged and they are partially lined by lamellar bone tissue.

The compact bone is composed of zones of woven-fibered bone and annuli of parallel-fibered bone tissue (Fig. 7C–E). Bone cell lacunae of irregular shape are abundant in the woven-fibered matrix and randomly distributed. Conversely, the cell lacunae in the parallel-fibered matrix are less dense, possess elongated shapes and they are oriented parallel to one other (Fig. 7F). Branching canaliculi are often observed in the bone cell lacunae. At least eight growth marks (LAGs and annuli) can be observed in the osteoderm. The LAGs are more closely spaced in the basal cortex. The innermost LAG cannot be entirely traced because of the presence of secondary osteons and resorption cavities in the inner core.

Sharpey's fibers are abundant and they are most conspicuous at the basal cortex, where they are observed in two main regions. The first corresponds to the latero-basal region, in which Sharpey's fibers are densely arranged forming angles that range from 44° to 80° with the sagittal plane. The second one is the basal cortex in the mid region of the osteoderm. Here, the extrinsic fibers are fine and they insert perpendicularly to the osteoderm surface.

## DISCUSSION
### Microanatomical and Histological Characterization of Nonarchosaurian Archosauriforms Osteoderms

Correlating with their differences in size and shape, the osteoderms of doswelliids and proterochampsids examined here reveal distinctive microstructural variations. The osteoderms of *Archeopelta* and *Tarjadia* are relatively compact structures, in which the inner core possesses short and thick trabeculae and small intertrabecular spaces. The bone tissues in these osteoderms are distributed in three distinct regions: a thick external cortex of lamellar, parallel-fibered and woven-fibered bone with distinct reversal lines; an internal core of parallel-fibered and woven-fibered bone; and a basal cortex of parallel-fibered bone. These microstructural features are mostly similar with those described for *Jaxtasuchus* (Scheyer et al., 2014) and suggest a common histological pattern in doswelliid osteoderms.

Conversely, the osteoderms of proterochampsids *Chanaresuchus bonapartei* and *Pseudochampsa ischigualastensis* exhibit important histological differences and preclude establishing a common microstructural pattern in proterochampsids. Whereas, the osteoderms of *P. ischigualastensis* are avascular structures composed entirely of parallel-fibered bone, the osteoderm of *C. bonapartei* are highly vascularized and they are composed of zones of woven-fibered bone and annuli of parallel-fibered bone. The only histological
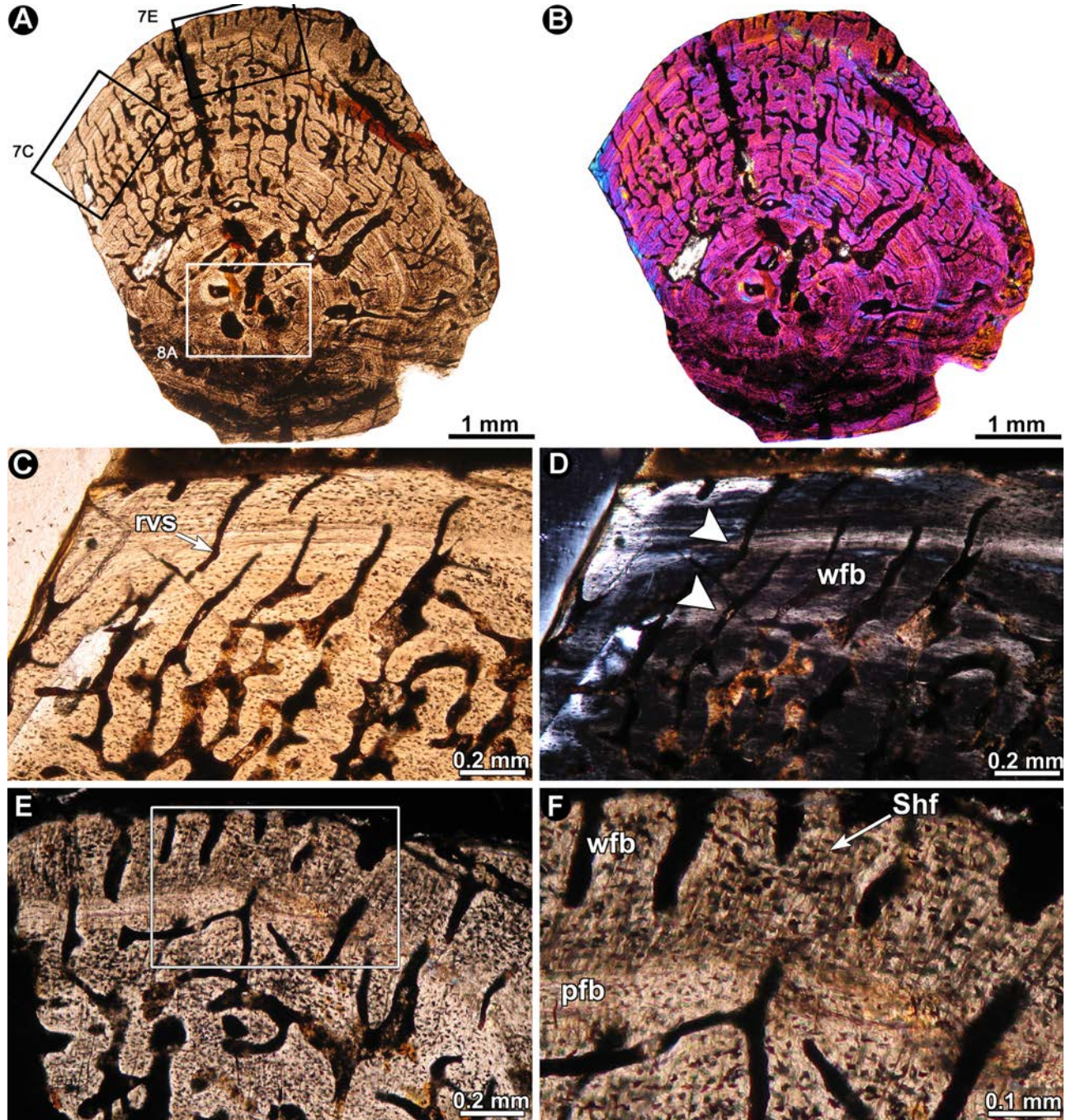
Fig. 7. *Chanaresuchus bonapartei* PVL 6244 osteoderm histology. **A,B**: General view of the osteoderm in cross section. The inset boxes in A indicate the position of the detailed pictures in Figures 7 and 8. **C,D**: Detailed view of the external cortical bone tissue showing alternating zones and annuli (arrowheads). Note the high birefringence of the annuli and the isotropic nature of the zones of woven-fibered bone under cross-polarized light (D). **E**: Highly vascularized external cortex. Several vascular spaces are opened to the outer surface. **F**: Close-up of the external cortex (box inset in B) showing abundant Sharpey's fibers. A,C,E,F: Normal light; B: cross-polarized light with lambda compensator; D: cross-polarized light. Abbreviations: pfb: parallel-fibered bone; rvs: radial vascular space; Shf: Sharpey's fibers; wfb: woven-fibered bone.

features shared between *P. ischigualastensis* and *C. bonapartei* osteoderms are the absence of a trilaminar organization of the element and the absence of trabecular bone in the inner core.

Our data indicate that, while the osteoderm microstructure of doswelliids appears to be conservative, there is an important variation within proterochampsids (at least within *Chanaresuchus*
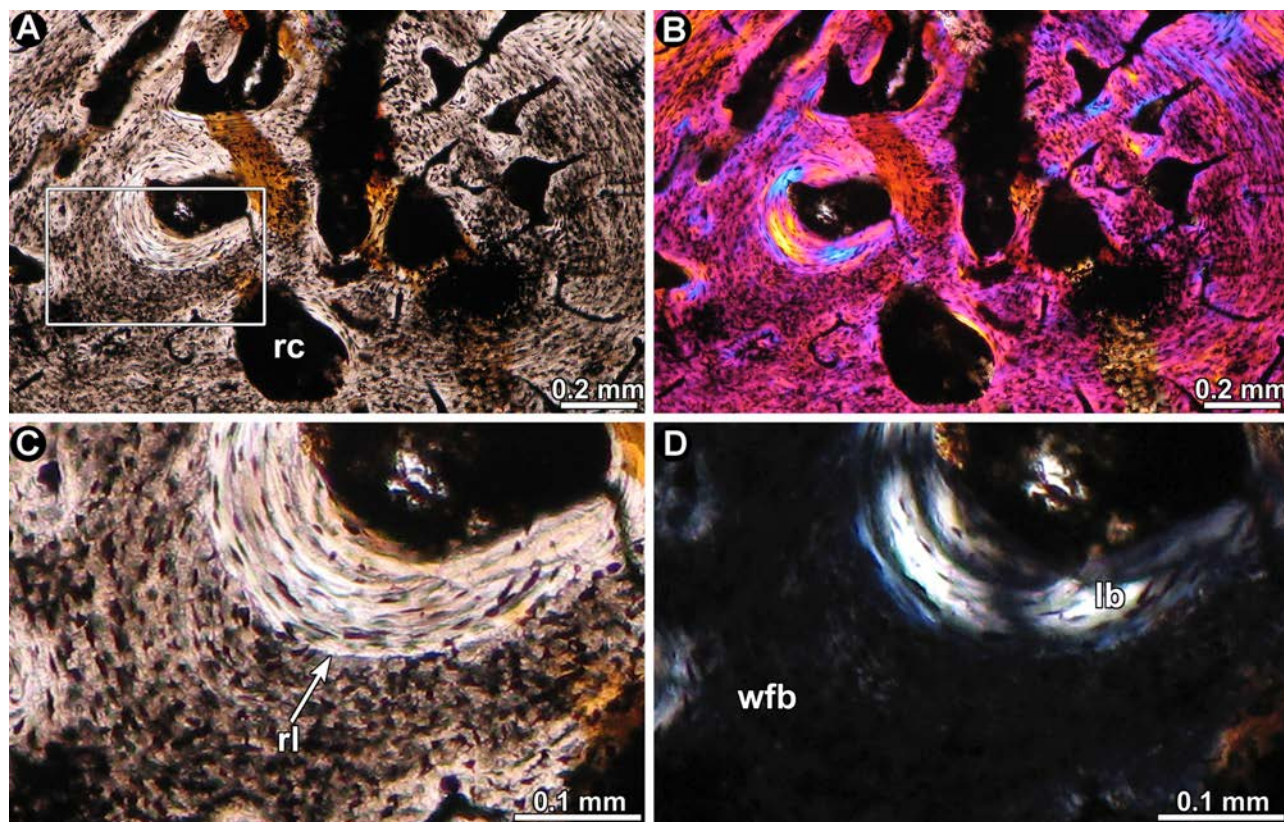
Fig. 8. *Chanaresuchus bonapartei* PVL 6244 osteoderm histology. **A,B**: Inner core of the element composed of lamellar and woven-fibered tissue. **C,D**: Close up of the inner core (box inset in A). Note the strong variation in the woven-fibered and lamellar tissues with regard to shape, orientation and density of the bone cell lacunae and also regarding the optical tissue properties. A,C: Normal light; B: cross-polarized light with lambda compensator; D: cross-polarized light. Abbreviations: lb: lamellar bone; rc: resorption cavity; rl: resorption line; wfb: woven-fibered bone.

and *Pseudochampsa*). The reported variation in *Chanaresuchus* and *Pseudochampsa* could be related to several, nonmutually exclusive causes (e.g., osteoderm size and shape, osteoderm function, gender, biomechanics, and environment).

### Avascular Bone Tissue in *P. ischigualastensis*

The total absence of vascular spaces in the osteoderms of *P. ischigualastensis is* a rather unexpected finding. Although avascular osteoderms have been reported in other tetrapods (Zylberberg and Castanet, 1985; Levrat-Calviac and Zylberberg, 1986; Bauer and Russell, 1989; Erickson et al., 2003; Vickaryous and Sire, 2009), they have so far never been described in Archosauriformes. Although vascular spaces are commonly absent in diminutive osteoderms (e.g., the Gila monster *Heloderma horridum*, Vickaryous and Sire, 2009), such feature cannot explain the pattern described for *P. ischigualastensis*. In this sense, similar sized osteoderms of other taxa (e.g., *C. bonapartei* and the ankylosaurid dinosaur

*Antarctopelta oliveroi*) possess well developed vascular spaces (Ricqlès et al., 2001). Although the avascular pattern in *P. ischigualastensis* osteoderms is perhaps related to a very low rate of bone deposition in the element, other possible (e.g., functional) causes cannot be ruled out.

Whereas, the small size of the *P. ischigualastensis* osteoderms cannot explain the cause for the absence of vascular spaces, it actually can explain why such pattern can be maintained. The short distance from the osteoderm surface to the osseous cell lacunae (even those located at the innermost region) could be enough for the metabolic maintenance of these cells through branching canaliculi. Given that bone cells (e.g., osteocytes) may have a half-life of decades if the particular bone they reside in has a slow turnover rate (Nijweide et al., 2002), even the early deposited osseous cells could survive through the time using solely canalicular nutrition. Nevertheless, we would like to note again that no branching canaliculi could be recognized in *P. ischigualastensis* osteoderms (although this can be a preservation artifact).

## External Ornamentation in Doswelliidae

The external surface of the osteoderm in tetrapods is commonly ornamented by ridges, tubercles, and/or pits. This superficial ornamentation in osteoderms can develop by two different mechanisms. First, local resorption and partial redeposition of the cortical bone has been reported in sculptured dermal skull bones and osteoderms from several archosaurian taxa (Buffrénil, 1982; Hua and Buffrénil, 1996; Scheyer and Sander, 2004; Cerda and Desojo, 2011; Scheyer et al., 2014). The second mechanism, proposed for osteoderms and dermal bones of basal tetrapods (Witzmann and Soler-Gijón, 2008; Witzmann, 2009), involves preferential deposition of the bony areas that correspond with ridges or tubercles, without resorptive processes.

In doswelliids, the external surface shows a pattern of rounded and irregular pits. The external cortex exhibits lamellar, parallel-fibered and woven-fibered bone tissue delimited by resorption lines, indicating erosion and successive deposition of bone. Hence, the osteoderm ornamentation appears to be mainly maintained by a process of resorption and redeposition of the external cortex. Given that lamellar, parallel-fibered and woven-fibered matrices are deposited at different rates (Chinsamy-Turan, 2005), the local variations between these types of matrices are interpreted as changes in the rate of bone deposition in the external cortex. The areas composed of woven-fibered bone are formed faster than those formed by lamellar bone tissue. Summarizing, the current evidence indicates that, during the osteoderm development, the ornamentation pattern is maintained by both osteoclastic and osteoblastic activity, which produce preferential bone resorption and deposition, respectively, and allows the "migration" of particular structures (e.g., pits) without further modification of the whole original pattern.

This pattern of development of bone ornamentation proposed here for doswelliids was first recognized by Buffrénil (1982) for dermal skull bones and osteoderms of several crocodilian taxa, including: *Crocodylus niloticus*; *Crocodylus moreletii*; *Crocodylus siamensis*; *Crocodylus affinis*, and *Diplocynodon* sp. However, based on the absence of multinucleated osteoclasts along the superficial surfaces of the ornamented bones of *Alligator mississippiensis*, Vickaryous and Hall (2008) argued that ornamentation in crocodylians develops as a result of localized concentrations of bone deposited by osteoblasts. This claim was followed by Burns et al. (2013), who considered that the pitted sculpturing in *Alligator mississippiensis* and *Caiman crocodilus* is the result of localized bone deposition, and not the action of osteoclastic resorption (they nevertheless describe "scalloped resorption lines, often associated with the cortex-core interface" in both taxa). We consider that the presence of distinct resorption lines cutting abruptly through several generations of newly deposited bone in the external cortex indicates that resorptive process actually occur in the ornamented bones of several Archosauriformes, including doswelliids, several aetosaurs, and various crocodylian taxa. The absence of multinucleated osteoclasts in the bones of *A. mississippiensis* sampled by Vickaryous and Hall (2008) does not refute the hypothesis of Buffrénil (1982) for other crocodilian taxa. Instead, such absence suggests that variation might occur in the patterns of formation and maintenance of ornamentation of sculptured bones. Whereas in some taxa (e.g., *Simosuchus clarki, Alligator mississippiensis*) the ornamentation is mainly the result of localized bone deposition (Vickaryous and Hall, 2008; Klein et al., 2009; Hill, 2010), in others (e.g., *Crocodylus niloticus*, some aetosaurs) the ornamentation is maintained by both resorption and new bone deposition (Buffrénil, 1982; Cerda and Desojo, 2011). Moreover, the reported presence of resorption lines in the external cortex of some osteoderms of *Alligator mississippiensis* (Burns et al., 2013) suggest that intraspecific or intraelemental variation can also occur on this regard. The variation in the formation and maintenance of the external ornamentation of osteoderms and other bones among different taxa appears to be more complex than expected and it is possibly related to different, nonmutually exclusive causes, including degree and pattern of ornamentation, ontogenetic stage and osteoderm location within the armor, among others.

## Osteoderm Formation

Different ossification mechanisms have been proposed for the origin of osteoderms in extant and fossil tetrapods. The most commonly invoked mechanism is metaplastic ossification, a process in which a pre-existing, fully developed tissue is transformed into bone (Haines and Mohuiddin, 1968). Metaplastic development has been proposed for osteoderm origin in temnospondyl amphibians (Witzmann and Soler-Gijón, 2008), extant anurans (Ruibal and Shoemaker, 1984), extant squamates (Zylberberg and Castanet, 1985; Levrat-Calviac and Zylberberg, 1986), fossil and extant archosaurs (Reid, 1996; Scheyer and Sander, 2004; Main et al., 2005; Vickaryous and Hall, 2008; Cerda et al., in press), as well as osteoderms and dermal bones of the turtle shell (Barrett et al., 2002; Scheyer and Sánchez-Villagra, 2007; Scheyer and Sander, 2007; Scheyer et al., 2007, 2008; Sterli et al., 2013). In fossil groups, metaplastic tissue has been identified in osteoderms by the presence of interwoven bundles of mineralized collagen fibers (structural fibers; Scheyer and Sander,

2004, 2007; Main et al., 2005; Witzmann and Soler-Gijón, 2008; Cerda and Powell, 2010). Another common possible mode of osteoderm formation is intramembranous ossification, in which the newly-formed osseous tissue displaces the preformed soft-tissue structures instead of incorporating them. Based on the absence of mineralized structural fibers, this kind of ossification has been proposed for different extant but also extinct taxa, including some basal tetrapods (Buchwitz et al., 2012), pareiasaurs (Scheyer and Sander, 2009), aetosaurs (Cerda and Desojo, 2011; Scheyer et al., 2014), *Revueltosaurus* (the sister group of Aetosauria, Scheyer et al., 2014) and in *Jaxtasuchus* (Scheyer et al., 2014). A third mode of osteoderm formation has been proposed by Scheyer (2007) for placodonts and comprises a calcification process derived from a fibro-cartilage precursor. Finally, several authors have considered that the osteoderm formation could involve an interaction of different mechanisms (Reid, 1996; Vickaryous and Hall, 2008; Buffrénil et al., 2011; Scheyer and Desojo, 2011; Cerda et al., 2013).

In proterochampsid osteoderms, the observed histological features cannot be directly related with a metaplastic ossification, given that interwoven structural fiber bundles are absent in all sampled osteoderms. Given that the osteoderms of proterochampsids include primary bone tissue (especially in *P. ischigualastensis*), a possible obliteration of internal structural fiber bundles by secondary reconstruction can be ruled out. In the same way, the primary bone tissue preserved at the internal core of doswelliid osteoderms lacks structural fiber bundles. Nevertheless, given that some degree of osseous reconstruction is evident at the internal core, resorption of early formed structural fibers is not impossible. The predominant mode of osteoderm formation in proterochampsids and doswelliids appears to be compatible with intramembraneous ossification, although a clear diagnosis of one mode or the other remains tentative in fossils, because of the lack of soft-tissue preservation (Vickaryous and Sire, 2009).

## Aspects of Osteoderm Development

The spatial distribution of the different bone tissues in the osteoderms can be interpreted in terms of the overall growth of the elements taking into account the properties of each tissue (Buffrénil et al., 1986). In addition, the presence and distribution of growth marks can also provide insights into osteoderm development. Regarding the typology of the osseous tissue, there is a direct relationship between the tissue structure of the primary bone and its rate of deposition (the so-called "Amprino's rule"; Ricqlès, 1980; Ricqlès et al., 1991). Amprino's rule predicts that the rate of osteogenesis is higher when the degree of the fibrillar matrix spatial organization is

lower, and vice versa (Ricqlès et al., 1991). Presence of lamellar or parallel-fibered bone with highly organized fibrillar matrices and poor vascularization indicate slower rates of osteogenesis. Conversely, woven-fibered bone (fibro-lamellar if their vascular canals are organized as primary osteons) with randomly oriented fibrils and abundant vascular canals is linked to higher rates of osteogenesis (de Ricqlès, 1980; de Ricqlès et al., 1991).

In doswelliid osteoderms, the presence of woven-fibered bone tissue, together with increased vascularization in the core region, is an indication of higher deposition rates during earlier stages of development. The presence of lamellar, parallel-fibered and woven-fibered bone tissue in the external cortex suggest variable rates of bone deposition, possibly related to the development and maintenance of the external ornamentation (see "External ornamentation in doswelliids").

The microstructure of proterochampsid osteoderms indicates important differences with regard to their development. In *P. ischigualastensis* osteoderms, the entire elements consist of avascular parallel-fibered bone, which indicates slow deposition rates of formation, even in the early stages of development. The interpretation that the formation of the *P. ischigualastensis* osteoderms was actually slow is in agreement with the number and distribution of LAGs in the element. The LAGs are numerous (20) and there is no important variation in the distances between these growth marks (widespaced LAGs are expected at the inner core if the deposition rate was faster in the early stages of the osteoderm development). Conversely, the osteoderms of *C. bonapartei* are composed of zones of well vascularized woven-fibered bone, which suggests an overall rapid deposition rate. The presence of annuli of parallel-fibered bone indicates that the osteoderm (and possibly the whole individual) experienced periodic interruptions in its rapid growth. The abundance of radial vascular spaces opened to the osteoderm surface reveals that the osteoderm was actively growing at the moment of the death of the individual.

## Skeletochronology

In osteoderms of extant reptiles, the growth marks (annuli and/or LAGs) are correlated with annual interruptions or phases of reduced bone deposition during the overall growth of the individual (Hutton, 1986; Tucker, 1997; Erickson and Brochu, 1999; Erickson et al., 2003). This correlation has been previously used for age estimation (minimum or absolute) in fossil pseudosuchians (Erickson and Brochu, 1999; Hill and Lucas, 2006; Parker et al., 2008; Hill, 2010; Cerda and Desojo, 2011; Scheyer and Desojo, 2011; Taborda et al., 2013).

Assuming that the preserved growth marks in proterochampsid and doswelliid osteoderms were

annually deposited, we infer ages of 11 for *A. arborensis* CPEZ 239a, 20 to *T. ruthae* PULR 063, 8 to *C. bonapartei* PVL 6244 and 20 years to *P. ischigualastensis* PVSJ 567. Given that the ages obtained from growth mark counting could be underestimated for different reasons, the ages inferred here must be considered as minimum ages. Resorption of growth marks deposited during early ontogeny is possibly one of the main factors for inaccuracy in age estimation (Hutton, 1986; Tucker, 1997). Another possible source for age underestimation is related to the plane in which the osteoderms were sectioned. In this sense, if the section plane does not include exactly the center of ossification of the element (which is enclosed by the first deposited growth mark), the number of growth marks is always underestimated (Taborda et al., 2013). Finally, given that we actually ignore if the osteoderms in fossil taxa are formed during the first year of life or later, it is not possible to infer if the total count of growth marks equals exactly to the age of the individual. For example, extant crocodilians ossify their osteoderms almost 1 year after hatching (Chiappe et al., 1998; Vickaryous and Hall, 2008). The age deduced from the growth mark counting in proterochampsids (especially in *P. ischigualastensis*) is probably not affected by the two first listed factors, given that the degree of secondary remodeling is low or absent and the area enclosed by the first growth mark is diminutive. For this reason, we consider that the inferred relative ages of *P. ischigualastensis* and *C. bonapartei* are very close to the absolute age of the individuals. Comparing the maximum age estimations among nonarchosaurian archosauriforms and pseudosuchians, this parameter in proterochampsids and doswelliids (20 years) is similar to the maximum ages reported for aetosaurs (Taborda et al., 2013; Scheyer et al., 2014) and poposaurs (Ricqlès et al., 2003), higher to those reported for "rauisuchians" (Scheyer and Desojo, 2011; Cerda et al., 2013) and phytosaurs (Scheyer et al., 2014), and lower than those of extant and fossil crocodylians (Hutton, 1986; Erickson and Brochu, 1999). Our data reveal that the lifespan of doswelliids and proterochampsids surpasses two decades in at least some taxa.

### Lifestyle Inferences

Several studies have demonstrated that some modifications in the bone microanatomy in tetrapods are correlated with lifestyle (Ricqlès and Buffrénil, 2001; Houssaye, 2009). Such relation between the bone microanatomy and the lifestyle has been extensively studied in axial and appendicular bones of several taxa of fossil and extant tetrapods (Ricqlès and Buffrénil, 2001; Houssaye, 2009). Apart from the axial and appendicular bones, some studies have also applied this approach to osteo-derm microanatomy of different tetrapod groups (Hua and Buffrénil, 1996; Scheyer, 2007; Scheyer and Sander, 2009; Witzmann, 2009; Buchwitz et al., 2012). In this sense, osteoderms of aquatic or semiaquatic organism are commonly more dense and massive (pachyostotic *sensu lato*, Houssaye, 2009) than those of the taxa strictly adapted to a terrestrial habit (Hua and Buffrénil, 1996; Scheyer, 2007; Scheyer and Sander, 2009; Witzmann, 2009; Buchwitz et al., 2012). The increase of the skeletal mass in pachyostotic (*sensu lato*) bones is usually interpreted as an adaptation to reduce buoyancy (Taylor, 2000). In aquatic or semiaquatic taxa, the resulting increase in skeletal mass is considered to play the functional role of ballast for buoyancy control and hydrostatic regulation of body trim (Ricqlès and Buffrénil, 2001; Houssaye, 2013).

Doswelliid osteoderms are thick and rather compact structures, in which the inner core possesses short and thick trabeculae and small intertrabecular spaces. The cortical thickness is also important in these osteoderms, occupying 1/2 of the total osteoderm thickness in *Tarjadia*. These microanatomical features correspond with a bone mass increase pattern (sensu Houssaye, 2013) and agree with an aquatic or semiaquatic lifestyle in doswelliids. The lifestyle inferred here from the osteoderm microanatomy is in accordance with a previous hypothesis based on morphological, sedimentary and taphonomic evidence, which considered doswelliids as semiaquatic forms (Sues et al., 2013).

In the case of proterochampsids, the compact nature of their osteoderms also fits with a bone mass increase condition (*sensu* Houssaye, 2013) and supports an aquatic or semiaquatic lifestyle for this group. Such a lifestyle was actually previously suggested by other authors (see Trotteyn et al., 2013 for review). However, given the diminutive size and the low number of osteoderms in each individual (just a single row of osteoderms dorsal to the vertebral column), it appears to be rather improbable that the variation in relative osteoderm compactness actually modify significantly the whole skeletal mass.

### Comparison with Other Archosauriformes

Archosauriform osteoderm histology has been studied extensively recently and an abundant amount of comparative information is available (Scheyer and Sander, 2004; Hill and Lucas, 2006; Parker et al., 2008; Vickaryous and Hall, 2008; Hill, 2010, Klein et al., 2009, Vickaryous and Sire, 2009; Cerda and Desojo, 2011; Scheyer and Desojo, 2011; Cerda et al., 2013; Filippi et al., 2013; Scheyer et al., 2014). Previous studies on phytosaurs and pseudosuchians reveal that their general osteoderm structure resembles more that of to doswelliids than that of proterochampsids. In these groups the osteoderms are formed by a

trilaminar structure, which cannot be discerned in proterochampsids. Similar to those reported in doswelliid osteoderms, the basal cortices of phytosaur and pseudosuchian osteoderms are commonly composed of parallel-fibered bone tissue. Conversely, important variation occurs in the internal core and the external cortex. In osteoderms of phytosaur and pseudosuchian archosauriforms the internal cortex (when not remodelled) can be composed of different types of primary bone, including parallel-fibered, woven-fibered, fibro-lamellar bone and, in some taxa, mineralized structural fiber bundles (Scheyer and Sander, 2004; Hill and Lucas, 2006; Vickaryous and Hall, 2008; Klein et al., 2009; Vickaryous and Sire, 2009; Scheyer and Desojo, 2011; Cerda et al., 2013; Scheyer et al., 2014). As in *Revueltosaurus*, aetosaurs, and several crocodylomorphs, the external cortex of doswelliid osteoderms reveals a continuous process of resorption and redeposition of the bone tissue, which also includes differential bone deposition in some particular sites. This observation contrasts with that reported for "rauisuchians" and phytosaurs and is possibly related to the degree of ornamentation of the superficial surface.

The observed microstructural variation between proterochampsids and the other nonavemetatarsalian archosauriforms raises interesting questions about the value of the histological structure of osteoderms as a phylogenetically meaningful character. In this sense, the relative similarity of the osteoderm microstructure between doswelliids and pseudosuchians and phytosaurs support the phylogenetic hypothesis of Ezcurra et al. (2010) and Desojo et al. (2011). In both studies, doswelliids are more closely related to Archosauria than to proterochampsids. Given the still limited information related to osteoderm microstructure in basal archosauriforms and closely related groups, the inferences with regard to the state and distribution of histological characters (e.g., identification of ancestral characters in Archosauriformes) and their influence for phylogenetic studies must be treated with prudence.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Arcucci A. 1990. Un nuevo Proterochampsidae (Reptilia- Archosauriformes) de La Fauna Local de Los Chanares (Triásico Medio), La Rioja, Argentina. Ameginiana 27:365–378.

Arcucci A, Marsicano CA. 1998. A distinctive new archosaur from the Middle Triassic (Los Chañares Formation) of Argentina. J Vertebr Paleontol 18:228–232.

Barberena MC. 1982. Uma nova espécie de *Proterochampsa* (*P. nodosa* sp. nov.) do Triássico do Brasil. An Acad Bras Cienc 54:127–141.

Barrett PM, Clarke JB, Brinkman DB, Champman SD, Ensom PC. 2002. Morphology, histology and identification of the "granicones" from the Purbeck Limestone Formation (Lower Cretaceous: Berriasian) of Dorset, southern England. Cret Res 23:279–295.

Bauer AM, Russell AP. 1989. Supraorbital ossifications in geckos (Reptilia: Gekkonidae). Can J Zool 67:678–684.

Buchwitz M, Witzmann F, Voigt S, Golubev V. 2012. Osteoderm microstructure indicates the presence of a crocodylian-like trunk brancing system in a group of armoured basal tetrapods. Acta Zool (Stockh) 93:260–280.

Buffrénil V de. 1982. Morphogenesis of bone ornamentation in extant and extinct crocodilians. Zoomorphology 99:155–166.

Buffrénil V de, Farlow JO. Ricqlès A de. 1986. Growth and function of *Stegosaurus* plates: Evidence from bone histology. Paleobiology 12:459–473.

Buffrénil V de, Dauphin Y, Rage JC, Sire JY. 2011. An enamel-like tissue, osteodermine, on the osteoderms of a fossil anguid (Glyptosaurinae) lizard. C R Palevol 10:427–437.

Burns M, Vickaryous MK, Currie PJ. 2013. Histological variability in fossil and recent alligatoroid osteoderms: Systematic and functional implications. J Morphol 274:676–686.

Cerda IA, Desojo JB. 2011. Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia), from the Upper Triassic of Argentina and Brazil. Lethaia 44:417–428.

Cerda IA, Powell JE. 2010. Dermal armor histology of *Saltasaurus loricatus*, an Upper Cretaceous sauropod dinosaur from Northwest Argentina. Acta Palaeontol Pol 55:389–398.

Cerda IA, Desojo JB, Scheyer TM, Schultz CL. 2013. Osteoderm microstructure of "rauisuchian" archosaurs from South America. Geobios 46:273–283.

Cerda IA, García RA, Powell JE, López O. Morphology, microanatomy and histology of titanosaur (Dinosauria, Sauropoda) osteoderms from the Upper Cretaceous of Patagonia. J Vertebr Paleontol (in press).

Chiappe LM, Coria RA, Dingus L, Jackson F, Chinsamy A, Fox M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. Nature 396:258–261.

Chinsamy-Turan A. 2005. The Microstructure of Dinosaur Bone–Deciphering Biology with Fine-scale Techniques. Baltimore/London: Johns Hopkins University Press.

Chinsamy A, Raath MA. 1992. Preparation of fossil bone for histological examination. Palaeontol Afr 29:39–44.

Desojo JB, Ezcurra MD, Schultz CL. 2011. An unusual new archosauriform from the Middle-Late Triassic of southern Brazil and the monophyly of Doswelliidae. Zool J Linn Soc 161:839–871.

Dilkes DW, Sues H-D. 2009. Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. J Vertebr Paleontol 29:58–79.

Erickson GM, Brochu CM. 1999. How the 'terror crocodile' grew so big. Nature 398:205–206.

Erickson GM, Ricqlès A de, Buffrénil V de, Molnar RE, Bayless MK. 2003. Vermiform bones and the evolution of gigantism in Megalania—How a reptilian fox became a lion. J Vertebr Paleontol 23:966–970.

Ezcurra MD, Lecuona A, Martinelli A. 2010. A new basal archosauriform diapsid from the Lower Triassic of Argentina. J Vertebr Paleontol 30:1433–1450.

Filippi LS, Cerda IA, Garrido A. 2013. Morfología e histología de osteodermos de un Peirosauridae de la Cuenca Neuquina. Ameghiniana 50:3–13.

Francillon-Vieillot H, Buffrénil V de, Castanet J, Géraudie J, Meunier FJ, Sire JY, Zylberberg L, Ricqlès A de. 1990. Microstructures and mineralization of vertebrate skeletal tissues. In: Carter J, editor. Skeletal Biomineralizations: Patterns,

Processes and Evolutionary Trends, Vol. 1. New York: Van Nostrand Reinhold. pp 471–530.

Haines RW, Mohuiddin A. 1968. Metaplastic bone. J Anat 103: 527–538.

Hill RV. 2006. Comparative anatomy and histology of xenarthran osteoderms. J Morphol 267:1441–1460.

Hill RV. 2010. Osteoderms of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. J Vertebr Paleontol Mem 10:154–176.

Hill RV, Lucas SG. 2006. New data on the anatomy and relationships of the Paleocene crocodylian *Akanthosuchus langstoni*. Acta Palaeontol Pol 51:455–464.

Houssaye A. 2009. "Pachyostosis" in aquatic amniotes: A review. Integr Zool 4:325–340.

Houssaye A. 2013. Palaeoecological and morphofunctional interpretation of bone mass increase: An example in Late Cretaceous shallow marine squamates. Biol Rev Camb Philos Soc 88:117–139.

Hua S. Buffrénil V de. 1996. Bone histology as a clue in the interpretation of functional adaptations in the thalattosuchia (Reptilia, Crocodylia). J Vertebr Paleontol 16:703–717.

Hutton JM. 1986. Age determination of living Nile crocodiles from the cortical stratification of bone. Copeia 1986:332–341.

Klein N, Scheyer TM, Tütken T. 2009. Skeletochronology and isotopic analysis of a captive individual of *Alligator mississippiensis* Daudin, 1802. Fossil Rec 12:121–131.

Levrat−Calviac V, Zylberberg L. 1986. The structure of the osteoderms in the gekko: *Tarentola mauritanica*. Am J Anat 176:437–466.

Main RP, Ricqlès A de, Horner J, Padian K. 2005. The evolution and function of thyreophoran dinosaur scutes: Implications for plate function in stegosaurs. Paleobiology 31:291–314.

Nijweide PJ, Burger EH, Klein-Nulend J. 2002. The osteocyte. In: Belezikian JP, Raisz G, Rodan GA, editors. Principle of Bone Biology. Amsterdam: Academic Press. pp 93–107.

Parker WG, Stocker MR, Irmis RB. 2008. A new desmatosuchine aetosaur (Archosauria: Suchia) from the Upper Triassic Tecovas Formation (Dockum Group) of Texas. J Vertebr Paleontol 28:692–701.

Price LI. 1946. Sobre um novo pseudossuquio do Triassico Supeiror do Rio Grande do Sul. Bol Div Geol Mineral 120:1–38.

Reid REH. 1996. Bone histology of the Cleveland−Lloyd dinosaurs and of dinosaurs in general. Part I: Introduction to bone tissues. Brigham Young Univ Geol Stud 41:25–72.

Reig OA. 1959. Primeros datos descriptivos sobre nuevos reptiles Arcosaurios del Triásico del Ischigualasto (San Juan, Argentina). Rev Asoc Geol Argent 8:257–270.

Ricqlès A de. 1980. Tissue structure of the dinosaur bone: Functional significance and possible relation to dinosaur physiology.In: Thomas RDK, Olson EC, editors. A Cold Look of the Warm-Blooded Dinosaurs. Boulder: Westview Press. pp 103–139.

Ricqlès A de, Buffrénil V de. 2001. Bone histology, heterochronies and the return of the tetrapods to life in water: Where are we? In: Mazin J, Buffrénil V de, editors. Secondary Adaptation of Tetrapods to Life in Water. Germany: Verlag Dr. Friedrich Pfeil, München. pp 289–310.

Ricqlès A.de, Padian K, Horner JR. 2003. On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. Ann Paléontol 89:67–101.

Ricqlès A de, Meunier FJ, Castanet J, Francillon-Vieillot H. 1991. Comparative microstructure of bone. In: Hall BBK, editor. Bone, Vol. 3. Bone Matrix and Bone Specific Products. Boca Raton, Florida: CRC press. pp 1–78.

Ricqlès A de, Pereda Suberbiola X, Gasparini Z, Olivero E. 2001. Histology of the dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antartica. Asoc Paleontol Argent, Pub Esp 7:171–174.

Romer AS. 1971. The Chañares (Argentina) Triassic reptile fauna. XI. Two new long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus*. Breviora 379:1–22.

Romer AS. 1972a. The Chañares (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipanicicorum*, gen. et sp. nov. Breviora 389:1–24.

Romer AS. 1972b. The Chañares (Argentina) Triassic reptile fauna. XII. The postcranial skeleton of the thecodont *Chanaresuchus*. Breviora 385:1–21.

Ruibal R, Shoemaker V. 1984. Osteoderms in anurans. J Herpetol 18:313–328.

Scheyer TM. 2007. Skeletal histology of the dermal armor of Placodontia: the occurrence of "postcranial fibro-cartilaginous bone' and its developmental implications. J Anat 211:737–753.

Scheyer TM, Desojo JB. 2011. Palaeohistology and microanatomy of rauisuchian osteoderms (Archosauria: Pseudosuchia). Palaeontology 54:1289–1302.

Scheyer TM, Sánchez−Villagra MR. 2007. Carapace bone histology in the giant pleurodiran turtle *Stupendemys geographicus*: Phylogeny and function. Acta Palaeontol Pol 52:137–154.

Scheyer TM, Sander PM. 2004. Histology of ankylosaur osteoderms: Implications for systematics and function. J Vertebr Paleontol 24:874–893.

Scheyer TM, Sander PM. 2007. Shell bone histology indicates terrestrial palaeoecology of basal turtles. Proc R Soc B 274: 1885–1893.

Scheyer TM, Sander PM. 2009. Bone microstructures and mode of skeletogenesis in osteoderms of three pareiasaurs taxa from the Permian of South Africa. J Evol Biol 22:1153–1162.

Scheyer TM, Sander PM, Joyce WG, Böhme W, Witzel U. 2007. Unique plywood structure in the shell of fossil and recent soft shelled turtles (Trionychidae) revealed by soft tissue and bone histology: A key adaptation? Org Divers Evol 7:136–144.

Scheyer TM, Brüllmann B, Sánchez−Villagra MR. 2008. The ontogeny of the shell in side-necked turtles, with emphasis on the homologies of costal and neural bones. J Morphol 269: 1008–1021.

Scheyer TM, Desojo JB, Cerda IA. 2014. Bone histology of phytosaur, aetosaur, and other archosauriform osteoderms (Eureptilia, Archosauromorpha). Anat Rec 297:240–260.

Schoch RR, Sues H-D. 2013. A new doswelliid archosauriform from the Middle Triassic of Germany. J Syst Palaeontol 12: 113–131.

Sereno PC. 1991. Basal archosaurs: Phylogenetic relationships and functional implications. Soc Vertebr Paleontol Mem 2:1–53.

Sereno PC, Arcucci AB. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. Neues Jahrbuch Geol Paläontol Abhandlungen 180:21–52.

Sill WD. 1967. *Proterochampsa barrionuevoi* and the early evolution of the Crocodilia. Bull Mus Comp Zool Harvard Univ 135:415–446.

Sterli J, de la Fuente MS. Cerda IA. 2013. A new species of meiolaniform turtle and a revision on the Upper Cretaceous meiolaniforms of southern South America. Ameghiniana 50: 240–256.

Sues HD, Desojo JB, Ezcurra MD. 2013. Doswelliidae: A clade of unusual armoured archosauriforms from the Middle and Late Triassic. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin. Geological Society London Special Publications. London 379. pp 49–58.

Taborda JRA, Cerda IA, Desojo JB. 2013. Growth curve of *Aetosauroides scagliai* (Pseudosuchia: Aetosauria) inferred from osteoderm histology. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin. Geological Society London Special Publications. London 379. pp 413–423.

Taylor MA. 2000. Functional significance of bone ballast in the evolution of buoyancy control strategies by aquatic tetrapods. Hist Biol 14:15–31.

Trotteyn MJ, Ezcurra MD. Osteology of *Pseudochampsa ischigualastensis nov. comb.* (Archosauriformes: Proterochampsidae) from the early Late Triassic Ischigualasto Formation of NW Argentina. Plos One (in press).

Trotteyn MJ, Martínez RN, Alcober OA. 2012. A new proterochampsid *Chanaresuchus ischigualastensis* (Diapsida, Archosauriformes) in the early Late Triassic Ischigualasto Formation, Argentina. J Vertebr Paleontol 32:485–489.

Trotteyn MJ, Arcucci AB, Raugust T. 2013. Proterochampsia: an endemic archosauriform clade from South America. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin. Geological Society London Special Publications. London 379. pp 59–90.

Tucker AD. 1997. Validation of skeletochronology to determine age of freshwater crocodiles (*Crocodylus johnstoni*). Mar Freshwater Res 48:343–351.

Vickaryous MK, Hall BK. 2006. Osteoderm morphology and development in the nine-banded armadillo, *Dasypus novemcinctus* (Mammalia, Xenartha, Cingulata). J Morphol 267: 1273–1283.

Vickaryous MK, Hall BK. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. J Morphol 269:398–422.

Vickaryous MK, Sire J-Y. 2009. The integumentary skeleton of tetrapods: origin, evolution, and development. J Anat 214: 441–464.

Witzmann F. 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis. Palaeodiversity 2:233–270.

Witzmann F, Soler-Gijón R. 2008. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. Acta Zool (Stock) 89:1–19.

Zylberberg L, Castanet J. 1985. New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). J Morphol 186:327–342.