Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia), from the Upper Triassic of Argentina and Brazil

IGNACIO A. CERDA AND JULIA B. DESOJO

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One of the most striking features documented in aetosaurs is the presence of an extensive bony armour composed of several osteoderms. Here, we analyse the bone microstructure of these elements in some South American Aetosaurinae aetosaurs, including *Aetosauroides scagliai*. In general terms, Aetosaurinae osteoderms are compact structures characterized by the presence of three tissue types: a basal cortex of poorly vascularized parallel-fibred bone tissue, a core of highly vascularized fibro-lamellar bone, and an external cortex of rather avascular lamellar bone tissue. Sharpey's fibres are more visible at the internal core, toward the lateral margins and aligned parallel to the major axis of the dermal plate. No evidence of metaplastic origin is reported in the osteoderms, and we hypothesize an intramembranous ossification for these elements. The bone tissue distribution reveals that the development of the osteoderm in Aetosaurinae starts in a position located medial to the plate midpoint, and the main sites of active osteogenesis occur towards the lateral and medial edges of the plate. The osteoderm ornamentation is originated and maintained by a process of resorption and redeposition of the external cortex, which also includes preferential bone deposition in some particular sites. Given that no secondary reconstruction occurs in the osteoderms, growth marks are well preserved and they provide very important information regarding the relative age and growth pattern of Aetosaurinae aetosaurs. □ *Aetosauria*, Aetosauroides, *Archosauria, bone microstructure, integumentary skeleton, osteoderm.*

Ignacio Alejandro Cerda [nachocerda6@yahoo.com.ar], CONICET-INIBIOMA, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Buenos Aires 1400 (8300), Neuquén, Argentina; Julia Brenda Desojo [julideso@macn.gov.ar], CONICET, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, C1405DRJ Buenos Aires, Argentina; manuscript received on 03/06/2010; manuscript accepted on 07/09/2010.

Aetosauria is a monophyletic clade of quadrupedal heavily armoured crurotarsan archosaurs. This particular group was a characteristic component of continental ecosystems during much of the Late Triassic of Europe, North Africa, India, North and South America (Heckert & Lucas 1999, 2000). In South America, aetosaurs are represented by *Aetosauroides* Casamiquela 1960 from Argentina and Brazil, *Neoaetosauroides* Bonaparte 1969 from Argentina, and the putative *Chilenosuchus* Casamiquela 1980 from Chile (Desojo 2003; Desojo & Báez 2005, 2007; Parker 2007).

One of the most striking features documented in aetosaurs is the presence of an extensive bony armour (consisting of four columns, two paramedian and two lateral, respectively) of quadrangular interlocking osteoderms that extend from just behind the skull to the tip of the tail (Walker 1961; Heckert & Lucas 2000; Schoch 2007). In addition, ventral and appendicular osteoderms has been reported in some taxa (e.g. *Aetosaurus* Fraas 1877; *Aetosauroides, Coahomasuchus*

Heckert & Lucas 1999; *Stagonolepis robertsoni* Agassiz 1844). The dorsal carapace consists of two paramedian columns of osteoderms on either side of the sagittal plane of the animal, each of which is flanked by an adjacent row of lateral osteoderms (Long & Ballew 1985; Martz & Small 2006; Parker 2007, 2008). Moreover, this bony armour is characterized by an external ornamentation with several patron and types, used in the diagnosis of aetosaurs (Long & Ballew 1985), except Aetosaurinae (Parker 2007).

In recent years, the bone histology of osteoderms in fossil tetrapods has increasingly attracted the interest of the palaeontologists, for example, in temnospondyls amphibians (Scheyer 2007; Witzmann & Soler-Gijón 2008), pareiasaurian parareptiles (Scheyer & Sander 2009), placodonts (Scheyer 2007), turtles (Scheyer & Sánchez-Villagra 2007; Scheyer & Sander 2007; Scheyer *et al.* 2007; Scheyer 2009), squamates (de Buffrénil *et al.* 2010), archosaurs (de Buffrénil *et al.* 1986; Hua & de Buffrénil 1996; de Ricqlès *et al.* 2001; Scheyer &

Sander 2004; Main *et al.* 2005; Hayashi *et al.* 2009), and xenarthran mammals (Hill 2006). In spite of the detailed morphological descriptions of aetosaur osteoderms (Long & Ballew 1985; Heckert & Lucas 2000; Parker 2008), knowledge of their bone microstructure is rather scarce. Heckert & Lucas (2002) described some microscopic features from an osteoderm fragment assigned to *Stagonolepis* Agassiz 1844. However, as the analysis was carried out using a scanning electron microscope (no thin sections), the histological description is not extensive. Recently, Parker *et al.* (2008) described the histology of a paramedian osteoderm of *Sierritasuchus macalpini* Parker, Stocker & Irmis 2008. This analysis was also conducted with the purpose to determine the ontogenetic stage of the type specimen.

The present study is concerned about the microanatomical and histological structure of the osteoderms of some Upper Triassic Aetosaurinae aetosaurs, including *Aetosauroides scagliai*. Aetosaurinae *sensu* Heckert & Lucas (2000) is a stem-based clade containing all taxa more closely related to *Aetosaurus* than to the last common ancestor of *Aetosaurus* and *Desmatosuchus*. This clade is diagnosed by a single synapomorphy: external (=dorsal) eminence of paramedian osteoderms located medial to the plate midpoint (Parker 2007). In South America, Aetosaurinae is represented by *Aetosauroides* and *Neoaetosauroides*. *Aetosauroides* is one of the most characteristic aetosaurs from South America, with *Aetosauroides scagliai* Casamiquela 1960 collected from Argentina and '*Aetosauroides subsulcatus*' from Brazilian outcroups. The latter taxon was described by Zacarias (1982) as a new species of *Aetosauroides* from the Santa Maria Formation. In a revision of the Late Triassic aetosaur record, Heckert & Lucas (2000) interpreted *Aetosauroides* as a subjective junior synonym of *Stagonolepis*. This statement was subsequently followed by Lucas & Heckert (2001) which considered '*A. subsulcatus*', as well as all remaining available aetosaur material from Brazil, as indistinguishable from *A. scagliai* and as a junior synonym of *Stagonolepis robertsoni*. More recently, these authors discuss in more detail the taxonomic status of *A. scagliai* (Heckert & Lucas 2002), and considered the smaller specimens, including the

holotype, as referable to *S. robertsoni* and the larger specimens to *Stagonolepis wellesi* Long & Murry 1995. Nevertheless, the synonymy proposed by Heckert and Lucas was not followed by other subsequent author (Small 2002; Desojo 2003; Desojo & Báez 2007; Parker 2007; Schoch 2007; Parker *et al.* 2008; Desojo & Ezcurra 2009; Sulej 2010), and it was criticized by Desojo (1999) and Desojo & Báez (2005), which claimed that the distinction, based on pelvic characters, between *A. scagliai* and *Stagonolepis* spp. is valid.

The aim of the present contribution is to characterize the dermal armour microanatomy and histology of South American Aetosaurinae aetosaurs, determine the origin and development of these structures, identify the osteogenic mechanisms linked to the development of the osteoderm ornamentation, and establish the relationship of the osteoderms with the associated soft parts in the living animals. We also discuss and compare our results with the osteoderm histology of other tetrapod groups. This is the first study focussing on the osteoderm microstructure of aetosaurs and the first histological study of South American aetosaurs.

Materials and methods

For the present study, post-cranial osteoderms for thin-sectioning have been chosen from different Aetosaurinae specimens collected from Late Triassic outcrops of Argentina and Brazil (Table 1). As the diagnostic characters of *A. scagliai* came from the skeleton, when the sample studied in the present work is only known by osteoderms, we refer to these specimens as Aetosaurinae indet. Sampled elements are mostly paramedian osteoderms, which were transversely and parasagitally sectioned. Specimens were prepared for thin sections based on the methodology outlined in Chinsamy & Raath (1992). The preparation of the histological sections was carried out in Departamento de Geología de la Universidad Nacional de San Luis (Argentina). Osteoderm thin sections were studied under a light microscope in normal and polarized light and they are housed at the Coleccion Nacional de Paleovertebrados from the Museo Argentino de Ciencias Naturales Bernardino Rivadavia of Argentina.

Table 1. Aetosaurinae specimens used in this study and the localities from which the specimens were recovered.

Taxon	Specimen no.	Locality	Age	Sectioned elements
Aetosaurinae indet.	MLP 61-VIII-2-34	Ischigualasto Formation, San Juan province, Argentina	Late Triassic	7 Paramedian osteoderms
Aetosaurinae indet.	MCP 42–80	Cidade dos Meninos, Santa Maria, Rio Grande do Sul, Brazil	Late Triassic	Paramedian osteoderm
Aetosauroides scagliai	MCP 13	Riacho Inhamanda, Santa Maria, Rio Grande do Sul, Brazil	Late Triassic	Paramedian osteoderm
Aetosaurinae indet.	MCP 34–50	Faixa Nova, Santa Maria, Rio Grande do Sul, Brazil	Late Triassic	Lateral osteoderm
Aetosauroides scagliai	UFRGS 11070	Faixa Nova, Santa Maria, Rio Grande do Sul, Brazil	Late Triassic	Paramedian osteoderm

Histological terms follow established nomenclature of bone (Francillon-Vieillot *et al.* 1990; de Ricqlès *et al.* 1991). Morphological terminology of aetosaur dermal plates used here is resumed in Figure 1. 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 & Sander (2004). These terms are synonyms of 'superficial/deep' (Hill 2006) and 'distal/proximal' (Main *et al.* 2005).

Results

External morphology

Paramedian osteoderms have a rectangular shape, being much wider than long (25 × 78 mm in one plate from VIII-61-2-34) and markedly thin (4.6 mm in the thickest specimen, UFRGS 11070). Each plate has an anterior bar, which is a smooth transverse surface that is overlapped by the posterior margin of the plate anterior to it (Fig. 1). Except for this anterior bar, the external surface of the osteoderms are strongly ornamented with a pattern of pits and grooves radiating from a low external eminence. This eminence is located medial to the osteoderm midpoint, near to the posterior margin, without contacting it in the specimen MLP VIII-61-2-34. In specimen MCP 13, the pits and grooves of the external surface are narrow and less marked than the other samples. In all of these dermal bones, the basal surface is flat and smooth (except for
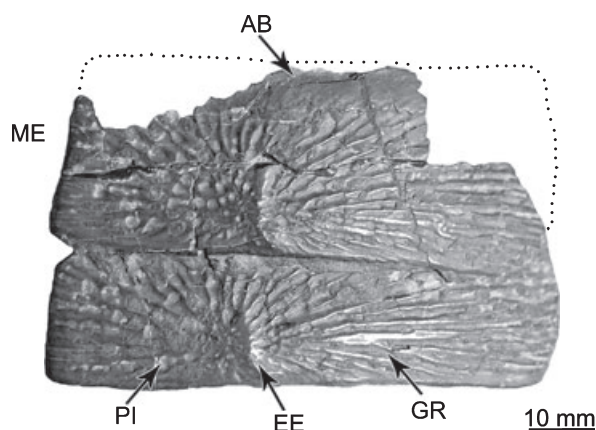
a slight emargination beneath the external eminence), without a ventral keel. The lateral osteoderm studied also exhibits anterior bars and a pattern of pits and grooves from the external eminence, with a slightly ventral flexure.

Bone histology and microanatomy

All osteoderms show similar microstructures, for this reason, they will be described together. Individual variation among the specimens will be mentioned if applicable. All studied plates are composed of compact bone tissue (Fig. 2). No cancellous bone or extensive secondary remodelling was encountered in the plates. Osteoderm microstructure is characterized by the presence of three well defined types of bone tissue distributed in three distinct regions: basal, internal and external (Fig. 3A, B).

The basal cortex is composed of parallel-fibred bone tissue, which exhibits a uniform pattern of extinction under polarized light (Fig. 3C, D). The bone cell lacunae are small and flattened. Vascularization consists of very few primary vascular canals aligned approximately parallel to the basal surface. The maximum thickness of the basal layer is located at the same level of the external eminence (medial to plate midpoint), decreasing toward the lateral and medial margins. In all sections from MLP 61-VIII-2-34, although the basal cortex is well distinct, this layer is more vascularized than in the others specimens. Also, the intrinsic fibres are more disorganized in some areas.

The internal core of the plates is composed by a highly vascularized woven-fibred matrix with a mono-refringent aspect in polarized light. This bone tissue exhibits a high density of rounded osseous cells lacunae and contains loosely packed fibres oriented in different directions. The woven-fibred matrix includes a dense network of primary vascular canals, which are mainly organized as primary osteons. Vascular spaces are generally arranged parallel to the major axis of the plate and dominate the reticular pattern. Taking into account the histological features described at the internal layer of the osteoderms, we interpreted this tissue as a true fibro-lamellar complex (Fig. 3E, F). The thickness of the internal core varies according to the width of the basal cortex, increasing from the level corresponding to the external eminence toward the medial and lateral edges of the plate. At the lateral and medial margins, the internal core is not surrounded by other bone tissues and reaches the outermost surface (Fig. 4A). In the lateral plate MCP30-50, the internal core is less vascularized than in the other osteoderms, although vascular density is still higher than in the external and basal cortex. Another
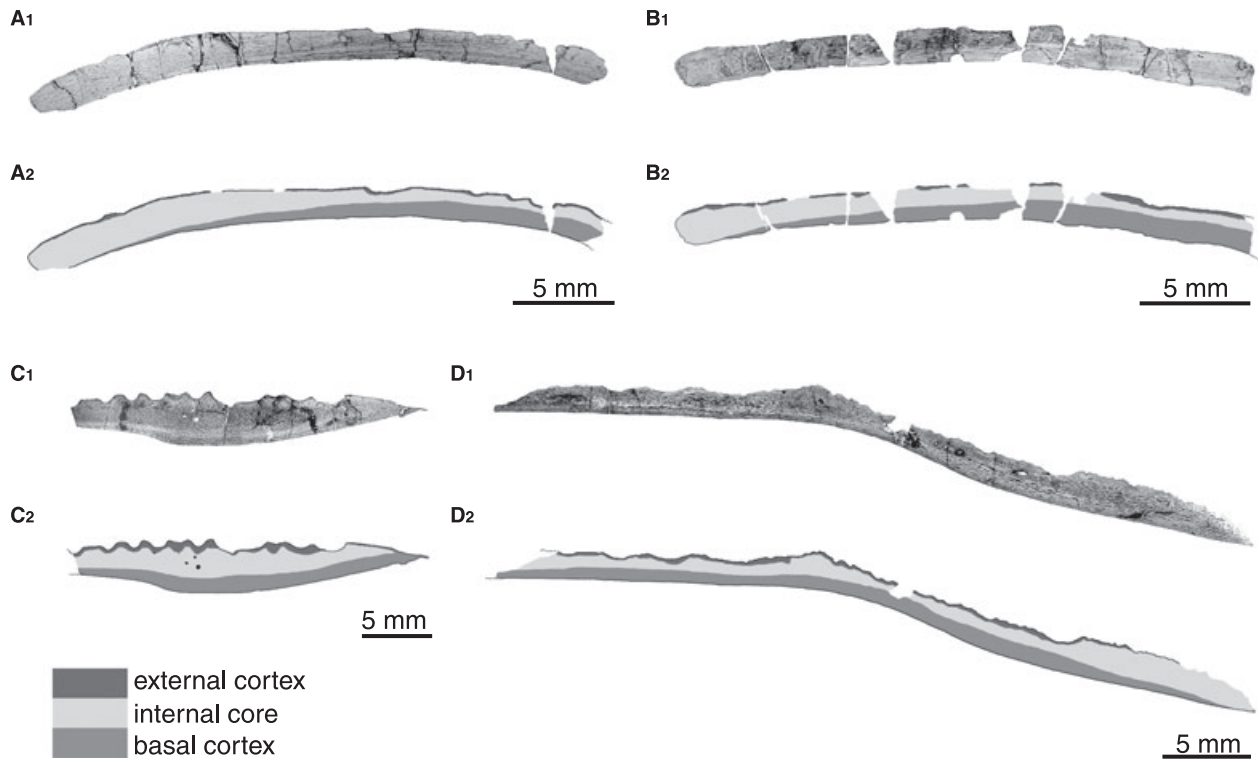

Fig. 1. External morphology of Aetosaurinae paramedian osteoderms (MLP 61-VIII-2-34) from Ischigualasto Formation, San Juan province, Argentina. The figure shows two articulated osteoderms from the right column in external view. Dashed line represents the original outline of the osteoderm. Abbreviations: AB, anterior bar; EE, external eminence; GR, groove; ME, medial side; PI, pit.

Fig. 2. Microanatomy of Aetosaurinae paramedian osteoderms. All sections are accompanied by an interpretative drawing showing the tissue distribution. A, transversal section of MCP 13. B, transversal section of MCP 42–80. C, parasagittal section of MLP 61-VIII-2-34. D, transversal section of MLP 61-VIII-2-34. In transversal sections, the lateral margin is located toward the left of the figure. In parasagittal section, the anterior margin corresponds to the right edge.

difference was observed in the specimen MCP 13, where the internal core entirely lacks primary osteons. In the paramedian osteoderm, Sharpey's fibres are present as thin and long fibrous strands in the bone tissue (Fig. 4B). These extrinsic fibres are more visible in the lateral region of the plate, where they are arranged parallel to the major axis of the element and penetrate the lateral margin at a right angle. In the lateral osteoderm, Sharpey's fibres are more abundant and densely arranged. They are aligned parallel to the basal surface of the plate.

The external surface of the osteoderms exhibits a distinct pattern of valleys and saddles that reflects the pattern of ridges and grooves at the external surface of the plate. As the ridges and groves radiate from a medial positioned knob in the external surface, valleys and saddles are more noticeable in parasagittal sections (Fig. 3B). The external cortex consists mainly of lamellar bone tissue. Parallel bone lamellae from different cycles of erosion and deposition are interrupted by resorption lines. The vascularization of the external region is poor and consists mostly of few primary vascular canals. The bone cell lacunae are less abundant than in the internal core and they are mainly elongated in shape. Under polarized light, the typical banding pattern of the lamellar bone is often obscured by the presence of short and fine Sharpey's fibres that penetrate the external cortex at approximately a right angle to the surface. These extrinsic fibres are regularly but not densely arranged and they only can be observed under polarized light. In some areas, the poorly vascularized, lamellar bone grades outwards into a more vascularized tissue where the intrinsic fibres are more spatially disorganized (Fig. 4C). Regarding the boundaries between the three bone layers (basal, internal and external), the internal and basal layers are continuous, whereas the external and internal layers are commonly separated by a resorption line, which in some regions resembles the external pattern of saddles and valleys.

Cyclic growth marks, in the form of lines of arrested growth (LAGs) are well developed in the basal cortex (Fig. 4D), although its number is quite variable among the different specimens. In the thickest osteoderm (UFRGS 11070), a maximum number of eight LAGs were counted. Only one well defined LAG was observed in the eight sampled osteoderms of the specimen MLP 61-VIII-2-34. In MCP 13, LAGs were not detected. The individual zone between the LAGs decreases in thickness toward the outer surface. In
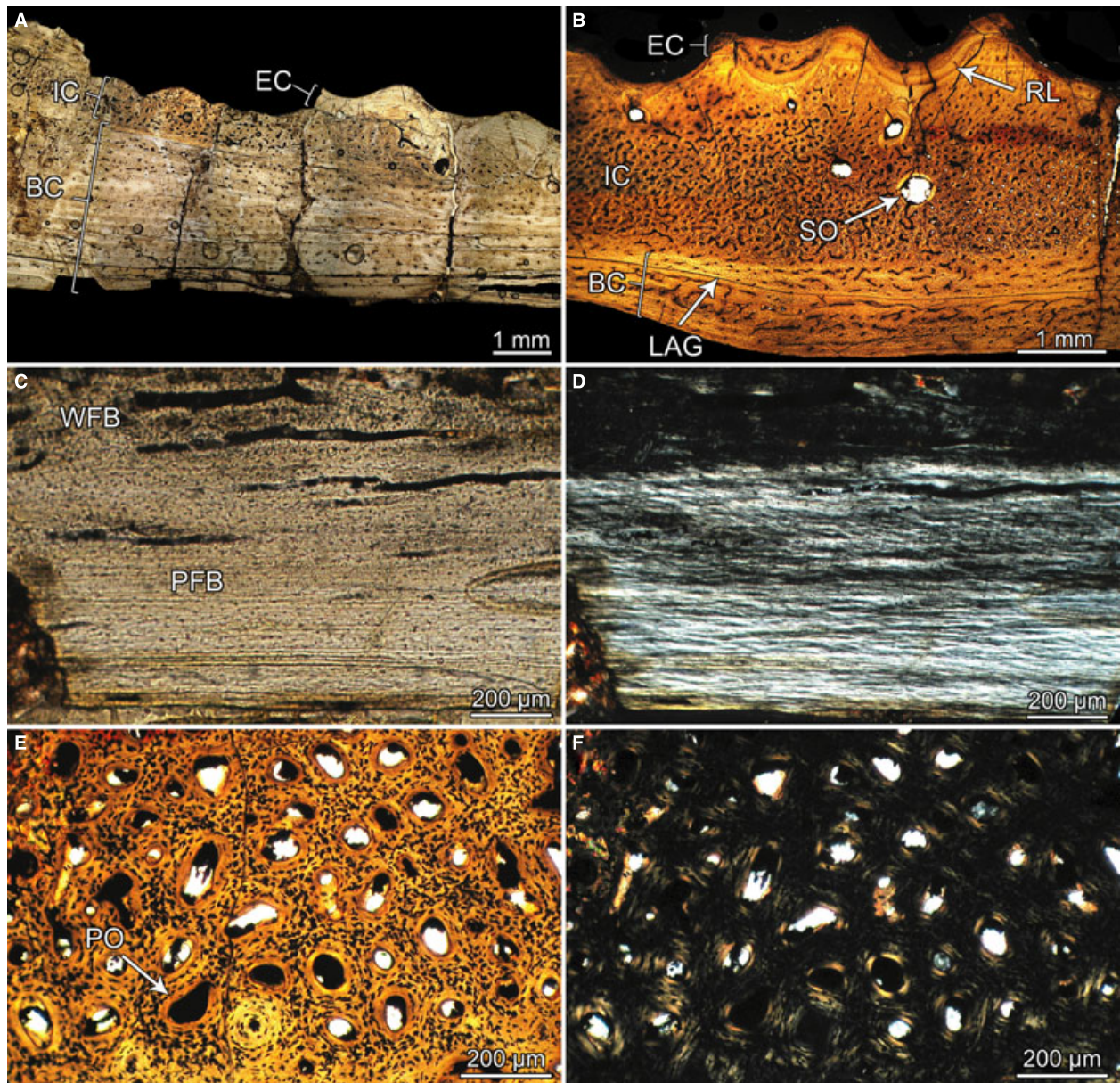
Fig. 3. Bone histology of Aetosaurinae dermal plates. A, transversal section of a paramedian osteoderm (UFRGS 11070) in normal light showing the tri-laminar organization of the bone tissues (the background has been digitally coloured). B, parasagittal section of a paramedian osteoderm (MLP 61-VIII-2-34) in normal light. Note the presence of few secondary osteons in the internal core. C, D, detail of the basal cortex in a paramedian osteoderm (MCP 42–80) in normal (C) and polarized (D) light. Note the mass birefringence in parallel-fibred bone. E, F, detail of the fibro-lamellar in the internal core of MLP 61-VIII-2-34 in normal (C) and polarized (D) light. Note the general isotropy of the woven-fibred matrix and the birefringence of the primary osteons. Abbreviations: BC, basal cortex; EC, external cortex; IC, internal core; LAG, line of arrested growth; PFB, parallel-fibred bone tissue; PO, primary osteon; RL, resorption line; SO, secondary osteon; WFB, woven-fibred bone tissue.

addition, transversal sections reveal that the distance between two successive LAGs is always greater at the lateral portion of the osteoderm.

Internal secondary reconstruction was evident only in osteoderms from individuals MLP 61-VIII-2-34 and UFRGS 11070. In both specimens, very few Haversian systems are scattered in the internal core (Figs 3B, 4C). In the other sampled osteoderms,

evidence of internal resorption or remodelling is completely lacking.

Discussion

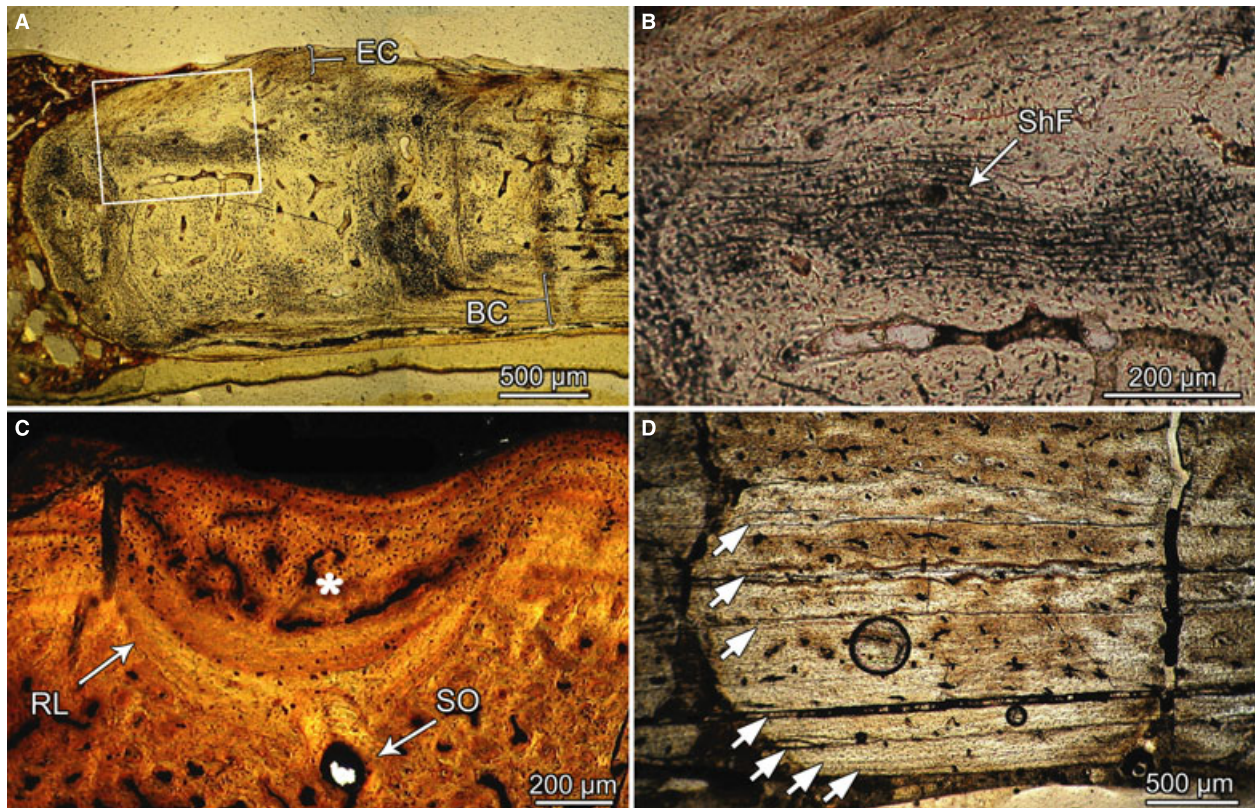The microanatomy and histology of the *A. scagliai* and other undetermined Aetosaurinae is strongly

Fig. 4. Bone histology of Aetosaurinae dermal plates. A, transversal section showing the lateral margin of MCP 42–80 (normal light). The white rectangle indicates portion of the section showed in B. B, detail of the Sharpey's fibres in the internal core of lateral region (normal light). C, detail of saddle in the external cortex in normal light (MLP 61-VIII-2-34). The avascular lamellar bone tissue grades into a more vascularized and disorganized tissue (asterix). D, close up of the basal cortex in UFRGS 11070 showing seven of the eight LAGs recorded (arrows). Abbreviations: BC, basal cortex; EC, external cortex; RL, resorption line; ShF, Sharpey's fibres; SO, secondary osteon.

homogeneous. Dermal plates of the sampled Aetosaurinae aetosaurs reveal a particular combination of microanatomical and histological features in having a basal cortex of poorly vascularized parallel-fibred bone tissue, a core of highly vascularized fibro-lamellar bone but lacking trabeculae and an external cortex of nearly avascular lamellar bone tissue. Growth marks (LAGs) are well developed in the basal cortex only, whereas Sharpey's fibres are more common in the internal core toward the lateral margins and aligned parallel to the major axis of the plate. The bone histology of Aetosaurinae osteoderms allows us to elucidate the origin and further development of these structures. Also, histological data provide information concerning other different biologic issues, such as the relation between osteoderms and soft tissues, the formation of external ornamentations and the possible identification of ontogenetic stages.

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. The most commonly invoked hypothesis for osteoderm development in extant and fossil tetrapods is metaplastic ossification, a process in which a pre-existing, fully developed tissue is transformed into bone (Haines & Mohuiddin 1968). Metaplastic development has been proposed for osteoderm origin in temnospondyl amphibians (Witzmann & Soler-Gijón 2008), extant anurans (Ruibal & Shoemaker 1984), extant squamates (Zylberberg & Castanet 1985; Levrat-Calviac & Zylberberg 1986), fossil and extant archosaurs (Scheyer & Sander 2004; Main *et al.* 2005; Vickaryous & Hall 2008), as well as dermal bones of the turtle shell (Scheyer & Sánchez-Villagra 2007; Scheyer & Sander 2007; Scheyer *et al.* 2007, 2008). In fossil groups, metaplastic tissue has been identified in osteoderms by the presence of interwoven bundles of mineralized collagen fibres (structural fibres *sensu* Scheyer & Sander 2004, 2007; Main *et al.* 2005; Witzmann & Soler-Gijón 2008; Scheyer 2009; Cerda & Powell 2010).

In Aetosaurinae osteoderms, the observed histological features cannot be directly related with a metaplastic ossification, given that interwoven structural fibre

bundles are absent in all sampled osteoderms. As the osteoderms of Aetosaurinae aetosaurs consist of primary bone tissue, a possible obliteration of internal structural fibre bundles by secondary reconstruction can be ruled out.

Another line of evidence comes from the distribution and typologies of the preserved tissues in the osteoderms. The thickness of the internal core (woven-fibred or fibro-lamellar) is the lowest in a region located medial to plate midpoint and increases towards the lateral and medial margins (and *vice versa* for the basal cortex of parallel-fibred bone). This organization of the basal and internal layers is not the expected for a metaplastic ossification, where a fully developed dermal tissue is transformed into bone. The absence of interwoven structural fibres and the distribution of the primary bone tissues indicate that metaplasia was not the main mechanism for the osteoderm formation in the sampled Aetosaurinae. The mode of histogenesis of these elements was very probably related with an intramembranous ossification, in which the newly formed tissues displace the preformed integumentary tissue structures instead of incorporating them. The distribution of basal and internal layers suggests that the centre of ossification was located medial to plate midpoint, at the same level of the external eminence. We propose that both basal and internal layers originated by bone deposition from a peripheral periosteum, which also surrounded the external surface. In contrast to the basal and internal layers, the external cortex is composed of lamellar bone tissue formed in successive erosion and deposition phases that are due to the activity of osteoclasts and periosteal osteoblasts, respectively.

Although intramembranous ossification has been reported in other vertebrates such the xenarthran *Dasypus novemcinctus* (Vickaryous & Hall 2006) and hypothesized for the origin of pareiasaurian osteoderms (Scheyer & Sander 2009), this mode of skeletogenesis has not been reported for archosaurian osteoderms. The development of osteoderms via intramembranous ossification proposed here for *A. scagliai* and undetermined Aetosaurinae indicates variations with regard to the mode of armour skeletogenesis among archosaurs. As has been shown in previous studies (Vickaryous & Hall 2006, 2008; Vickaryous & Sire 2009), our results denote that although metaplastic ossification may certainly contribute to osteoderm ossification and growth in tetrapods, it is not necessarily the only mode of development.

Growth pattern

The spatial distribution of the different bone tissues described in osteoderms can be interpreted in terms of the overall growth of the elements taking into account the properties of each tissue (de Buffrénil *et al.* 1986). Furthermore, the presence and distribution of growth marks can also provide insights into the 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') (de Ricqlès 1980; de 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* (de Ricqlès *et al.* 1991). Presence of lamellar or parallel-fibred bone with highly organized fibrillar matrices and poor vascularization indicate slower rates of osteogenesis. Conversely, woven-fibred bone (fibro-lamellar if their vascular canals are organized as primary osteons) with randomly oriented fibrils and abundant vascular canals is always linked to higher rates of osteogenesis (de Ricqlès 1980; de Ricqlès *et al.* 1991).

As previously mentioned, in Aetosaurinae osteoderms highly vascularized woven-fibred bone tissue (commonly forming a fibro-lamellar complex) occupies the internal region of the plate and is more developed toward the lateral and medial margins. By contrast, parallel-fibred bone is restricted to the basal cortex and its thickness is highest at the level of the external eminence (although important changes in the plate thickness were not observed). This tissue distribution suggests that the main sites of active osteogenesis (and osteoderm growth) were the lateral and medial edges of the plate (Fig. 5). Our assessment is reinforced by the distribution of growth marks. As described above, transversal sections reveal that the distance between two successive LAGs is greater in the lateral region (samples with several LAGs at the medial regions were not obtained). This spatial organization indicates that the amount of mineralized matrix in each growth cycle is higher at the lateral and (very probably) medial sides. This differential growth allows the development of the typical shape of the Aetosaurinae paramedian osteoderms, which are broad and exceptionally thin in comparison to other vertebrate osteoderms. Also, this asymmetrical distribution of the tissues indicates a more active bone growth in the lateral portion of the plate (Fig. 5).

The above explained mechanism for the osteoderm growth is based on transversal sections of paramedian osteoderms. Parasagittal sections do not reveal growth differences between the anterior and posterior regions.

Microanatomy

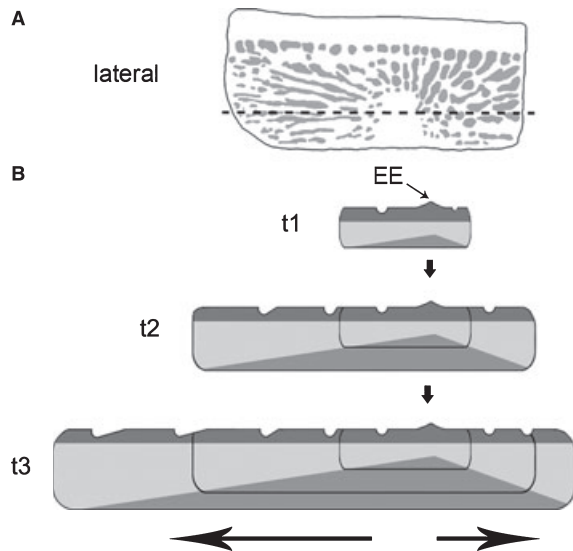One of the most noticeable differences between the sampled Aetosaurinae osteoderms and other tetrapods

Fig. 5. Proposed mode of development in paramedian Aetosaurinae osteoderms. A, drawing of a paramedian osteoderm showing the position of the transversal section (dashed lines) represented in B. B, sketch of the growth mechanism of a paramedian osteoderm in different times (t) as hypothesized from the location of the various tissue types and growth marks in the plate. For simplification, the original proportions have been overstated. The growth starts at level of the external eminence (EE), medial to the plate midpoint. Larger arrow indicates the direction of the main rate of osteogenesis on the plate.

resides in their microanatomy, which is characterized by the total absence of cancellous bone tissue (primary or secondary). Osteoderms consisting of a cortex of compact bone surrounding a inner cancellous core has been commonly reported in temnospondyl amphibians and basal tetrapods (Witzmann & Soler-Gijón 2008), xenarthran mammals (Hill 2006; Vickaryous & Hall 2006), pareiasaurs reptiles (Scheyer & Sander 2009), placodonts (Scheyer 2007), and archosaurs (de Buffrénil *et al.* 1986; Hua & de Buffrénil 1996; Salgado 2003; Scheyer & Sander 2004; Main *et al.* 2005; Hill & Lucas 2006; Hayashi *et al.* 2009; Klein *et al.* 2009). Similarly, the osseous elements of the turtle carapace show a trilaminar organization (diploe) that consist in compact external and internal cortices and a cancellous central core (Scheyer & Sánchez-Villagra 2007; Scheyer & Sander 2007; Scheyer *et al.* 2007). Osteoderms formed entirely by compact bone like those described in *A. scagliai* and other Aetosaurinae are less widespread among tetrapods. This microanatomical organization has been most frequently reported in the small osteoderms of lepidosaurian reptiles (Moss 1969; Zylberberg & Castanet 1985; Levrat-Calviac & Zylberberg 1986; Erickson *et al.* 2003; Scheyer & Sander 2009) and in the dermal ossicles of some armoured dinosaurs (de Ricqlès *et al.* 2001; Cerda & Powell 2010).

Primary cancellous bone tissue can be formed during the early formation of osteoderms, such as described in the neural and costal elements of the carapace of pleurodiran turtles (Scheyer *et al.* 2008). The fact that the compact bone tissue of Aetosaurinae osteoderms is primary in origin reveals the absence of cancellous bone even during the formation of these elements. With regard to the lack of secondary spongy bone (actually the most common type in osteoderms) in all our sample, presence of large cancellous spaces would be limited by mechanical constrains linked to the characteristic broad and thin shape of the sampled plates (78×3.8 mm in MLP 61-VIII-2-34). Although de Buffrénil *et al.* (2010) have reported a cancellous core in the small osteoderms of glyptosaurine squamates, these structures are not so broad as in Aetosaurinae and its body location (cephalic) also differs from the South American taxa. Other possible explanation for the lack of cancellous bone is related to the age of the specimens sampled. If the formation of cancellous bone is a time-dependent process in Aetosaurinae osteoderms, all plates (including the largest ones) would correspond to individuals in an early ontogenetic stage of developed. However, given that our sample includes aged individuals of more than 8 years (see below) we consider this last hypothesis rather improbable. Whatever the exact factor(s) involved in the lack of cancellous bone tissue, we consider that the compact microanatomy of Aetosaurinae osteoderms is a typical feature of the sampled taxa, including *A. scagliai*. Future works on the bone histology of other aetosaurian species allow us to determine if this microanatomical feature is restricted to some Aetosaurinae taxa or widespread in a more inclusive group.

Sharpey's fibres

In osteoderms, the Sharpey's fibres represent extrinsic fibres that became progressively incorporated in bone during the bone histogenesis (Francillon-Vieillot *et al.* 1990). Sharpey's fibres are very common structures in the osteoderm cortical bone tissue of extant and fossil tetrapods (Zylberberg & Castanet 1985; de Buffrénil *et al.* 1986, 2010; Scheyer & Sander 2004, 2009; Hill 2006; Scheyer 2007; Witzmann & Soler-Gijón 2008). In *Aetosauroides* dermal plates, Sharpey's fibres where observed in the external and internal layers (only in the lateral dermal plate they appear at the basal cortex).

In the internal core, the Sharpey's fibres are well developed at the lateral and medial regions, arranged perpendicular to the plate margins (parallel to the osteoderm major axis). These extrinsic fibres are more

abundant and densely packed at the medial region of lateral plate, however, they do not conform to a 'Sharpey-fibred bone' as previous authors have reported in xenarthran mammals (Hill 2006; Vickaryous & Hall 2006; Vickaryous & Sire 2009) and glyptosaurine squamates (de Buffrénil *et al.* 2010). In some extant lepidosaurs and xenarthran, the space between adjacent osteoderms is occupied by a dense connective tissue that contains collagenous fibres that enter the marginal regions of the osteoderms and connect the neighbouring elements (Moss 1969; Levrat-Calviac & Zylberberg 1986; Hill 2006). Our results indicate that the Sharpey's fibres correspond with collagenous fibres anchoring the osteoderm with the dermis and also possibly creating a strong bond between neighbouring plates. As well developed Sharpey's fibres are restricted to the lateral and medial margins of the plates (no Sharpey's fibres where recorded near the anterior and posterior margins in parasagittal sections), adjacent osteoderms in a single row appear to be bonded more strongly than osteoderms in two continuous rows. Hence, while the imbricate rows were capable of moving relative to one another, the individual osteoderms comprising a row were more tightly attached. This pattern resembles the condition described in the 'banded' portion of the extant 'armadillo' armour (Hill 2006).

The Sharpey's fibres located at the external cortex are fine and short, and they only can be observed under polarized light. This pattern strongly differs from the description of the lateral and medial region of the plate and indicates a more loose anchorage of the dermis to the external surface.

Development of ornamentation

Among armoured tetrapods, the superficial ornamentation in osteoderms can be originated mainly 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 crocodilian taxa (de Buffrénil 1982; Hua & de Buffrénil 1996; Scheyer & Sander 2004). The other mechanism, proposed for osteoderms and dermal bones of basal tetrapods (Witzmann & Soler-Gijón 2008; Witzmann 2009), involves preferential growth of the bony areas that correspond with ridges or tubercles, without resorptive processes. In Aetosaurinae osteoderms, the external cortex exhibits layers of lamellar bone delimited by resorption lines, indicating erosion and successive deposition of bone lamellae. Also, in restricted portions of the cortex, the microstructure of few saddles consists of an internal layer of avascular, lamellar bone which grades outwards into a more vascularized tissue

where the intrinsic fibres are more spatially disorganized (similar to the bone tissue described at the internal core). Such variation in the bone matrix is interpreted as an acceleration in the bone tissue growth in these particular portions of the external cortex. The osteohistology of the Aetosaurinae osteoderms investigated here reveals that the ornamentation pattern is originated and maintained by a process of resorption and redeposition of the external cortex, which also includes preferential bone deposition in some particular sites. This pattern of development of bone ornamentation coincides with that proposed by de Buffrénil (1982) for crocodilian dermal skull bones and osteoderms. However, bone sections analysed by de Buffrénil (1982) do not reveal the presence of a well-vascularized bone tissue with a more unorganized matrix in sites of preferential bone histogenesis such as we have described in our sample.

Growth marks and individual age

In dermal plates of extant reptiles, the growth marks (annuli and/or LAGs) are correlated with annual interruptions of the whole individual growth (Hutton 1986; Tucker 1997; Erickson & Brochu 1999; Erickson *et al.* 2003). This correlation has been previously used for the age estimation in fossil archosaurs, including crocodilians (Erickson & Brochu 1999; Hill & Lucas 2006) and aetosaurs (Parker *et al.* 2008). Assuming that the preserved LAGs in Aetosaurinae osteoderms were annually deposited, the age of individuals can be determined by counting the number of LAGs present in the cortical bone. The lacks of intensive secondary remodelling in the plates implies that all counted LAGs in each specimen represent the complete set of growth marks formed in an osteoderm during an individual life-time. However, given that extant crocodilians ossify their osteoderms almost 1 year after hatching (Chiappe *et al.* 1998; Vickaryous & Hall 2008), we hypothesize that one more year may have to be added to the estimated age for a more accurate determination. Hence, the absence of LAGs in MCP 13 indicates that this is the youngest specimen sampled (an estimation that corroborates the obtained data from the size and morphology of the element), whose age of death was possibly minor than 2 years. MCP 42–80 and UFRGS 11070 were the older specimens with estimated ages of 6 and 9 years, respectively. Taking into account the published data for longevity in extant crocodilians (e.g. 50 years in *Alligator mississippiensis* Daudin 1802 (Dodson 1975)), the estimated ages for Aetosaurinae individuals suggest that our sample is mainly composed of subadult specimens.

The lack of post-cranial bones associated with some of the osteoderms studied here precludes the reconstruction of a growth curve from the estimated ages. Nevertheless, given that of the individual MLP 61-VIII-2-34 is comparable in size with the more complete specimen and holotype of *A. scagliai* described by Heckert & Lucas (2002) as *Stagonolepis* and identified as PVL 2073, the approximate size of the MLP 61-VIII-2-34 can be determined. First, we establish the total length of the preserved part of the dorsal armour of the type of *A. scagliai* (PVL 2073), which includes an articulated carapace from the anterior dorsal series through the mid-caudal region (see fig. 4.1 *in* Heckert & Lucas 2002). Then, we compare with the body proportion in reconstructed aetosaurs (Walker 1961; Desojo & Báez 2005; Parker 2007, 2008) from the bibliography and establish which proportion of the whole dorsal armour was included in PVL 2073. Finally, using the obtained measures and proportion, we estimate a total length of around 1.1–1.2 m for PVL 2073 (and MLP 61-VIII-2-34). As all samples from MLP 61-VIII-2-34 reveal the presence of a single LAG, we infer that this individual died before its third year of life. Comparing these results with growth curves of extant and fossil crocodilians (Dodson 1975; Chabreck & Joanen 1979; Tucker 1997; Erickson & Brochu 1999), the growth rate of MLP 61-VIII-2-34 is comparable with the growth rates reported in *Alligator mississippiensis,* which reach one meter length slightly before the third year of life. Although the mentioned interpretations of the growth rate in Aetosaurinae should be treated with some caution (mainly for the limited number of specimens included in the analysis), our results give the first quantitative approach for the determination of growth rates in aetosaurs. Our data should be integrated in future works with information about the morphology and limb bones histology.

Regarding the relative size and age among the studied specimens, an interesting condition was observed in the specimen MCP 42–80. In this sample, the inferred age (6 years) differs from the recorded age for specimen MLP 61-VIII-2-34 (less than 3 years). However, the osteoderm length of these samples only differs in few millimetres (28.5 mm in MCP 42–80 and 25 mm in MLP 61-VIII-2-34). Assuming that the variation of the osteoderm length through the dorsal armour is no significant (Sawin 1947) and this measurement is related with the individual total length, these results implies that MCP 42–80 grew at a slower rate than MLP 61-VIII-2-34. As MCP 42–80 and MLP 61-VIII-2-34 correspond to undetermined Aetosaurinae, the observed differences are possibly related with growth rate variations in different Aetosaurinae taxa.

Conclusions

Aetosaurinae osteoderms studied here have a distinctive combination of microanatomical and histological features clearly different from other previously studied archosaurs. Moreover, our data strongly suggest a mode of skeletogenesis not previously proposed for osteoderms in archosaurs. These differences imply that, besides the morphologic diversity, archosaurian osteoderms demonstrate considerable variation with regard to its microstructure and origin. Future work should increase the sample of archosaur taxa to elucidate if the osteoderm features described for here are shared for a more inclusive group or correspond to specific or generic characters. In this sense, it is very important to investigate if the osteoderm bone histology can be used to address questions regarding the systematics of aetosaurs. In addition, other post-cranial armour elements, such as ventral and appendicular osteoderms, should also be studied to see if the histological trend recognized in the dorsal post-cranial osteoderms can also be observed.

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