

INTRASPECIFIC VARIATION IN *AETOSAUROIDES SCAGLIAI* CASAMIQUELA (ARCHOSAURIA: AETOSAURIA) FROM THE UPPER TRIASSIC OF ARGENTINA AND BRAZIL: AN EXAMPLE OF SEXUAL DIMORPHISM?

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Abstract. Aetosaurs are a group of quadrupedal, armoured pseudosuchian archosaurs from the Upper Triassic. They are characterized by dorsal and ventral carapaces, and appendicular osteoderms, all of them ornamented. Aetosaurs have been proposed as index fossils largely based on the distinctiveness of some osteoderms. Therefore, it is important to understand the intraspecific variation of these elements in the clade. In the present contribution, we describe three types of ornamentation on the medial area of paramedian osteoderms in the dorsal armour of *Aetosauroides scagliai* Casamiquela: the "radial pattern" the "anastomosing pattern"; and an "intermediate" or "transitional pattern", that is an intermediate between "radial" and "anastomosing" patterns. The articulated dorsal armour preserved in specimens PVL 2059 and PVL 2073 possesses osteoderms carrying all three patterns of ornamentation, but they differ by the position of each type of osteoderm on the carapace. Recent studies on histological thin-sections of osteoderms of *A. scagliai* reveal the absence of osteoderm tissue remodeling, allowing the estimation of age by counting LAGs (lines of arrested growth). PVL 2073 is slightly shorter (~10% longer centra) but also ontogenetically younger (5 LAGs) than PVL 2059 (10 LAGs; slightly wider osteoderms). Combining this information and comparing it with that of living crocodiles (where male specimens typically are relatively larger than females of the same age), we conclude that the intraspecific variation observed in *A. scagliai* is compatible with the hypothesis of sexual dimorphism. These results suggest the need to explore the sources of intraspecific variation in aetosaurs.

Key words. Pseudosuchia, osteoderms, aetosaurs, Suchia, South America.

Resumen. VARIACIÓN INTRAESPECÍFICA EN *AETOSAUROIDES SCAGLIAI* CASAMIQUELA (ARCHOSAURIA: AETOSAURIA) DEL TRIÁSICO SUPERIOR DE ARGENTINA Y BRASIL: UN EJEMPLO DE DIMORFISMO SEXUAL?. Los aetosaurios son un grupo de arcosaurios pseudosuquios cuadrúpedos y acorazados del Triásico superior. Se caracterizan por tener una coraza dorsal, una ventral, y osteoderms apendiculares, todos ornamentados. Los aetosaurios fueron propuestos como fósiles guía con base en características distintivas en algunos osteoderms. Por lo tanto, es importante comprender las variaciones intraespecíficas de estos elementos dentro del clado. En la presente contribución, se describen tres tipos de ornamentación en el área medial de los osteoderms paramediales de la coraza dorsal de *Aetosauroides scagliai* Casamiquela 1960: un "patrón radial"; un "patrón anastomosado"; y uno "intermedio" o "patrón transicional" entre el radial y el anastomosado. Las corazas articuladas de los especímenes PVL 2059 y PVL 2073 muestran los tres tipos de ornamentación, pero con una variación en la posición dentro de la coraza de los osteoderms con estas ornamentaciones. Recientes estudios paleohistológicos en osteoderms de *A. scagliai* muestran la ausencia de remodelación en los tejidos de los mismos permitiendo la estimación de edad mediante el conteo de LACs (líneas anuales de crecimiento). El PVL 2073 es ligeramente más corto (~10% en los centros) pero también más joven ontogenéticamente (5 LACs) que el PVL 2059 (10 LACs; y osteoderms ligeramente más anchos). Combinando esta información y comparándola con los cocodrilos actuales (donde los machos son generalmente más grandes que las hembras para una misma edad), concluimos que la variación intraespecífica observada en *A. scagliai* es compatible con la hipótesis de un dimorfismo sexual. Estos resultados evidencian la necesidad de estudiar las variaciones intraespecíficas en aetosaurios.

Palabras clave. Pseudosuchia, osteoderms, aetosaurios, Suchia, América del Sur.

AETOSAURS are quadrupedal, armoured pseudosuchian archosaurs recovered from Upper Triassic continental sediments of Europe, India, Africa and the Americas (Heckert and Lucas 2000; Desojo *et al.*, 2013) (Fig. 1.1). They are

characterized by a large ornamented carapace covering most of the body. The relationship of aetosaurs within Pseudosuchia is the focus of some debate, although they are generally considered to be a monophyletic group close

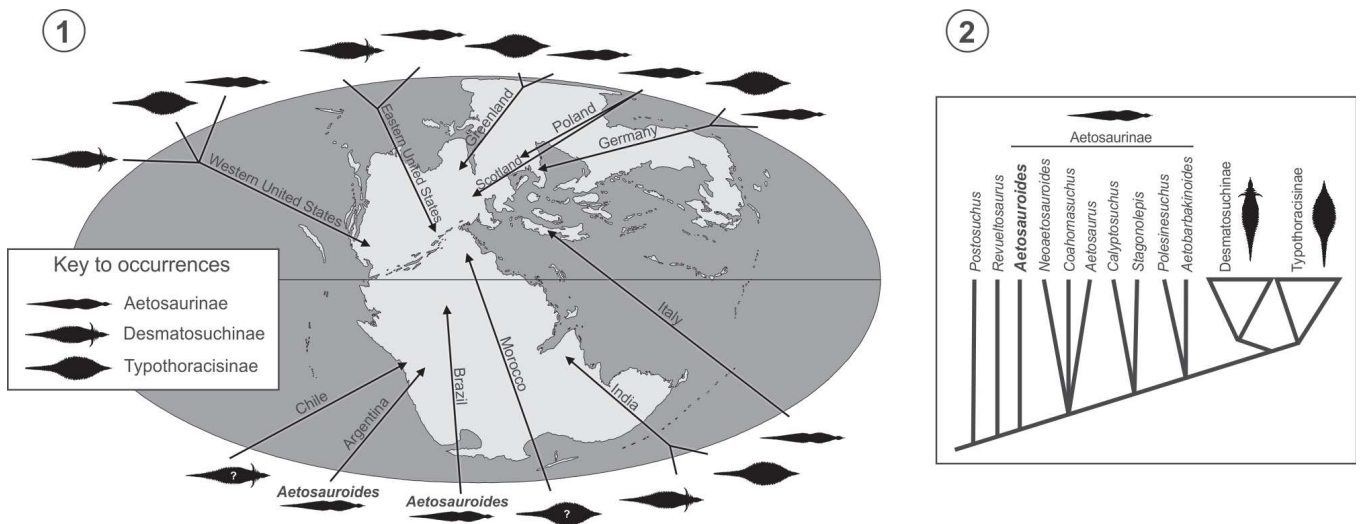


Figure 1. Generalized distribution and phylogeny of aetosaurs, especially *Aetosauroides*. **1,** Geographic distribution of aetosaur occurrences during the Late Triassic (modified from Desojo *et al.*, 2013). **2,** simplified cladogram of the Aetosauria based on Da Silva *et al.* (2014).

to the base of the crocodile line (Gower and Wilkinson, 1996; Gower and Walker, 2002; Brusatte *et al.*, 2010; Nesbitt, 2007, 2011; Desojo *et al.*, 2012, 2013; Butler *et al.*, 2014). Based on the most recent phylogenetic analyses of the clade (Parker, 2007; Desojo *et al.*, 2012; Heckert *et al.*, 2015), three groups can be recognized within Aetosauria (Fig. 1.2): the relatively derived Desmatosuchinae, with lateral and, sometimes, dorsal osteoderms with pronounced horns; their sister taxon, the Typothoracisinae, which are less spinose and generally have wide bodies with a sub-oval outline in dorsal view; and the paraphyletic “aetosaurines”, or basal aetosaurs, which have narrower bodies and lack horns on the dorsal armour (Desojo *et al.*, 2013).

Aetosaurs have been proposed as index fossils by some authors (*e.g.*, Lucas and Hunt, 1993; Heckert and Lucas, 1998, 2000; Lucas, 1998a, b; Small, 1998; Parker and Martz, 2011), largely based on the distinctiveness of osteoderm morphology. However, there is some disagreement on the extent to which osteoderms are taxonomically reliable (*e.g.*, Martz and Small, 2006; Parker, 2007; Rayfield *et al.*, 2009; Desojo and Ezcurra, 2011; Parker and Martz, 2011; Small and Martz, 2013). Osteoderm and carapace characters have been used in most phylogenetic analyses (*e.g.*, Parrish, 1994; Heckert *et al.*, 1996; Heckert and Lucas, 1999; Parker, 2007; Desojo *et al.*, 2012), but problems related to primary homology and character construction remain ambiguous

(see Harris *et al.*, 2003; Heckert and Lucas, 2003). Therefore, detailed studies on osteoderm morphology accounting for multiple sources of variation (*e.g.*, positional, ontogenetic, dimorphic) are essential to determine the extent to which osteoderm characters are taxonomically and phylogenetically informative. Understanding the taxonomic significance of osteoderm morphology is especially crucial to understand the diversity of the group in South America, because all the Argentine and Brazilian aetosaurs are “aetosaurines”, which have a generalized basal *bauplan* (Desojo and Ezcurra, 2011; Desojo *et al.*, 2012, 2013).

South American aetosaurs are presently represented by five species, *Aetosauroides scagliai* Casamiquela, 1960, from Argentina and Brazil; *Neoaetosauroides engaeus* Bonaparte, 1967, from Argentina; *Chilenosuchus forttae* Casamiquela, 1980, from Chile; and *Aetobarbakinoides brasiliensis* Desojo *et al.*, 2012, and *Polesinesuchus aurelioi* Da Silva *et al.*, 2014 from Brazil (Fig. 1). With the possible exception of *Chilenosuchus* Casamiquela 1980, which is too incomplete to assign it to an aetosaur subfamily (Desojo, 2003), all the others are “aetosaurines”, which are widely distributed throughout Pangea and overall have a similar osteoderm morphology (Desojo *et al.*, 2013).

Aetosaurs are characterized by an extensive carapace, composed of a dorsal armour covering the postcranial region, a ventral armour located between the limbs (thorax) and in the caudal region, and appendicular armour covering the

limbs (Fig. 2.1–5). The size and shape of osteoderms is generally related to the position in the armour (Casamiquela, 1961; Walker, 1961; Bonaparte, 1971; Long and Ballew, 1985; Heckert and Lucas, 2000; Desojo, 2005; Schoch, 2007; Heckert *et al.*, 2010). The dorsal armour is composed of two columns of paramedian osteoderms contacting one another along the median (sagittal) line of the body, and flanked by lateral osteoderms on both sides (Long and Ballew, 1985; Heckert and Lucas, 1999, 2000) (Fig. 2.4–5). Additionally, the dorsal armour is divided antero-posteriorly in rows (or rigid transverse bands) composed of one osteoderm in each of the four longitudinal columns (Long and Ballew, 1985; Heckert and Lucas, 1999, 2000). Depending on the position of the rows along the vertebral column, there are four primary regions: cervical, dorsal, sacral and caudal (Parker, 2007: Fig 2A). The paramedian osteoderms are rectangular in shape and typically wider than long, especially in “aetosaurines”. The anterior margin of the osteoderm carries an unornamented, thin articular projection termed the anterior bar (AB) or anterior lamina depending on the thickness of the projection (Long and Ballew, 1985; Long and Murry, 1995; Parker, 2007). This structure under-

lies the posterior margin of the next more anterior osteoderm of the column, allowing a relative displacement (movement) between consecutive rows. Lateral osteoderms are usually flexed to form distinct medial and lateral flanges and have a dorsal eminence at the vertex of the angle; in some cases, including all desmatosuchines and most typtothoracisines, the eminence projects laterally outward from the angle to form a spine or horn (Long and Ballew, 1985).

The ventral armour has received less attention in previous studies than the dorsal armour because of its poor preservation potential and/or generally brief descriptions (Casamiquela, 1961; Walker, 1961; Long and Ballew, 1985; Heckert and Lucas, 1999, 2000; Schoch, 2007; Heckert *et al.*, 2010; Desojo and Ezcurra, 2011). The thoracic portion of the ventral armour is almost complete in one of the specimens (PVL 2052) of *Aetosauroides scagliai*, consisting of six columns and ten rows of osteoderms (Casamiquela, 1967: fig. 3 and lám.14). These osteoderms are flat, quadrangular, carry an anterior articular structure (usually an anterior bar), and have a smooth, slightly elevated center (Fig 2.2).

The appendicular armour covering the limbs is com-

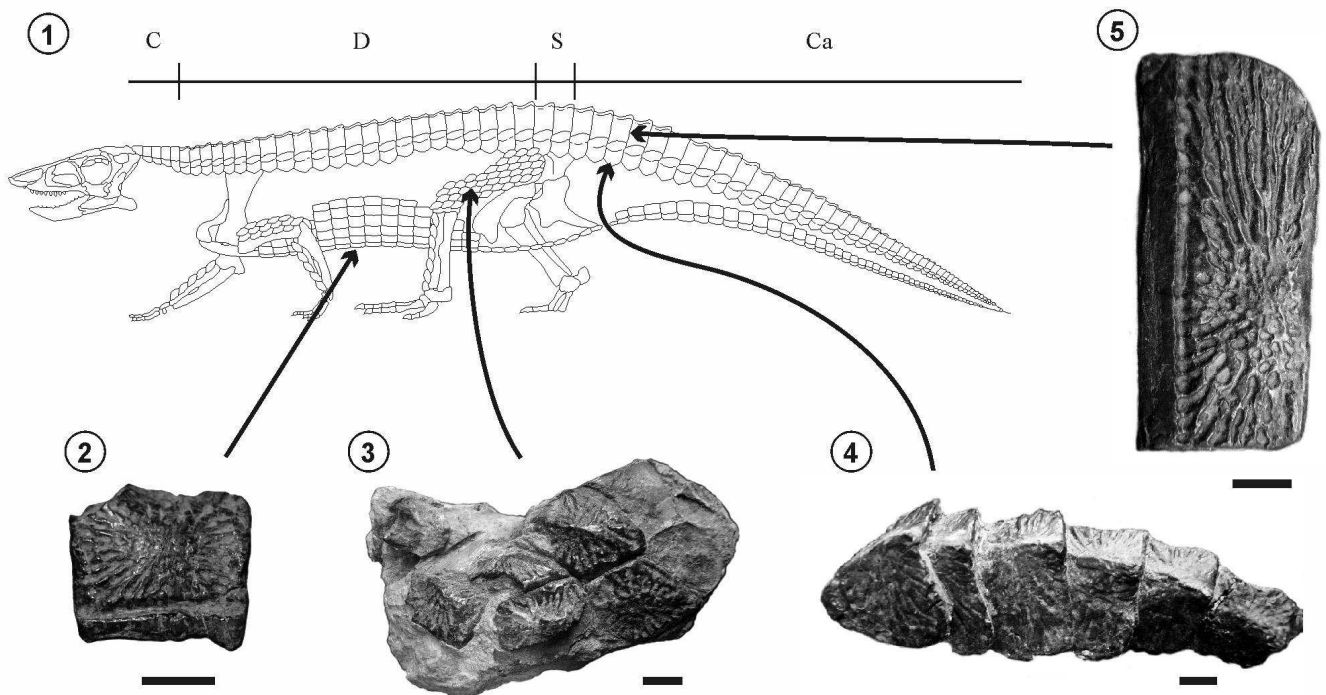


Figure 2. Description of the armour organization. 1, Generalized body for Aetosaurinae showing the position of different osteoderms in the armour, and the regions of the dorsal armour (modified from Schoch, 2007); 2, Ventral osteoderms; 3, Appendicular osteoderms; 4, Lateral osteoderms; 5, Paramedian osteoderms. Abbreviations: C, cervical region; D, dorsal region; S, sacral region; Ca, caudal region. Scale bar= 1cm.

posed of rhomboid osteoderms. It is known from several taxa, such as *Aetosauroides scagliai*, *Aetosaurus ferratus*, *Stagonolepis robertsoni*, *Coahomasuchus kahleorum*, *Typhothorax coccinarum*, and *Stenomyti huangae* (Cope, 1875; Fraas, 1877; Casamiquela, 1960, 1961; Walker, 1961; Heckert and Lucas, 1999; Heckert *et al.*, 2010; Small and Martz, 2013) and may have been present in all aetosaurs. In contrast to those in the dorsal and ventral armours, the appendicular osteoderms are not organized in columns and rows, nor do they have any articular structures. However, appendicular osteoderms contact one another on their sides, allowing flexibility of the limbs. These osteoderms often have a low dorsal eminence from which grooves and ridges radiate (Fig. 2.3).

Recent studies based on histological thin-sections have provided new information on the growth and ornamentation of aetosaur osteoderms (Cerdeja and Desojo, 2011; Scheyer *et al.*, 2014). Cerdeja and Desojo (2011) discussed the composition of the dorsal armour and type of growth pattern of the paramedian osteoderms of *A. scagliai*. Importantly, they noted the absence of remodeling of osteoderm tissues, thereby allowing estimations of the age of the individuals based on LAGs (lines of arrested growth). Taborda *et al.* (2013) combined this data with body mass and size estimations to generate growth curves for *A. scagliai*. Scheyer *et al.* (2014) noted that LAG counts were not always reliable because they found remodeling of base of the basal cortex and diploe structure in the internal core, independent of the ontogenetic state (such as the presumably juvenile *Aetosaurus ferratus* specimen SMNS 12670), in most aetosaur taxa sampled. The histological variation observed by Scheyer *et al.* (2014) in osteoderms of three different sizes in *Typhothorax* (including the extent of interior cancellous core

area) was considered to represent different ontogenetic stages of the individuals sampled. They did, however, confirm that the compact microanatomy of *A. scagliai* described by Cerdeja and Desojo (2011) was a unique feature of this taxon (or restricted to some aetosaurs) and appeared to be a reliable archive of LAG information.

In this contribution we describe and analyze in detail the dorsal armour of three specimens assigned to *Aetosauroides scagliai* (Desojo and Ezcurra, 2011) that preserve homologous regions of their carapaces. We discuss the intraspecific variation of the osteoderm ornamentation and the possible reasons behind their different morphologies, such as variation due to sexual dimorphism, ontogeny and individual variation, or other causes.

MATERIALS AND METHODS

Institutional abbreviations. PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; MPC, Museu de Ciências e Tecnologia, PUC/RS, Porto Alegre, Brazil.

Specimens analysed. Three incomplete carapaces of *Aetosauroides scagliai* are analysed first hand, including the holotype (PVL 2073) and two referred specimens (PVL 2059 and MCP13a-b-PV) (Tab. 1, Fig. 3). The provenance and stratigraphic data for the Argentine specimens are not precisely known. Casamiquela (1960, 1961, 1967) only mentioned that PVL 2073, PVL 2059, and PVL 2052 came from the lower ("Inferior"), middle ("Medio"), and upper ("Superior") sections ("tercios"), respectively, of the Ischigualasto Formation, in the Hoyada de Ischigualasto area, but no further detail is provided. Martinez *et al.* (2013) mentioned that 90% of unpublished *Aetosauroides* Casamiquela 1960 occurrences are in the lowest (B1) biozone, which corresponds to the Cancha de Bochas Member, with only two

TABLE 1 - Paramedian osteoderms conserved in each region of dorsal armour, and numbers of LAGs and age estimation (in year) of each specimen.

	# Paramedial osteoderms				N° LAGs	Age
	Cervical	Dorsal	Sacral	Caudal		
PVL 2073	1-7	1-13	1-2	1-6	5	6
PVL 2059	1-7	1-9	x	x	10	11
MPC 13 a-b-PV	4	1-13	1-2	1-3	1	2

specimens known from the second biozone (the Valle de Luna Member of Currie *et al.* 2009). Unfortunately, the lack of detailed lithological and stratigraphic information in Casamiquela (1967) hampers the assignment of the aetosaur-bearing stratigraphic levels to any of the members recognized by Currie *et al.* (2009) for the Ischigualasto Formation.

The two specimens referred to *Aetosauroides scagliai* by Desojo and Ezcurra (2011) preserving parts of the carapace that overlap with those of the holotype (PVL 2073; Fig. 3.1) are PVL 2059 and MCP 13a-b-PV. In particular, PVL 2059 preserves most of the osteoderms in the first 16 rows behind the nuchal osteoderm (which articulates with the skull and lacks a lateral osteoderm) (Fig. 3.2) and MCP 13a-b-PV preserves the first 22 rows (Fig. 3.3). Desojo and Ezcurra (2011) referred all three of these specimens to the same species, *Aetosauroides scagliai*, based on postcranial characters, such as the shared presence of oval fossae ventral to the neurocentral suture on the lateral sides of the centra, the presence of a posterior infra-diapophyseal, and the postero-laterally divergent post-zygapophyses in PVL 2073 and MCP 13a-b-PV (Desojo and Ezcurra, 2011).

We also provide comparisons with the referred specimen of *Aetosauroides scagliai* PVL 2052 (*sensu* Desojo and Ezcurra, 2011). This is a larger individual first described by Casamiquela (1967), but it is not articulated and too incomplete to positively assign its osteoderms to specific regions of the dorsal carapace.

DESCRIPTION OF THE ORNAMENTATION PATTERNS IN PARAMEDIAN OSTEODERMS OF "AETOSAURINAE"

The most complete carapace of *Aetosauroides scagliai* belongs to the holotype (PVL 2073; Fig. 3.1). Therefore, a detailed study of variation in osteoderm morphology of this specimen is essential in order to evaluate sources of individual variation, especially those related to position, size, sexual dimorphism, and ontogenetic stage.

Aetosaur osteoderms have two primary surfaces; the basal surface (BS) oriented toward the inner part of the animal, and the external surface (ES) oriented toward the external surface (Scheyer and Sander, 2004; Cerda and Desojo, 2011). The ornamentation of the ES is generally composed of grooves, pits, and ridges arranged in different patterns, some of which have taxonomic significance (Long and Ballew, 1985; Heckert and Lucas, 2000; Desojo *et al.*, 2013). We divide the ES of the paramedian osteoderms into two areas, the medial area (mA) that contacts the opposite paramedian osteoderm along the medial margin, and the lateral area (IA), the lateral margin of which articulates with the lateral osteoderm. These areas are separated by a dorsal eminence (DE; "boss" of some authors, *e.g.*, Parker, 2007 and Parker *et al.*, 2010). In the specimens described here, the ornamentation in the mA and IA of the paramedian osteoderms is composed of pits, grooves, and ridges, with a generally radial disposition from the DE. The pits consist of sub-circular small depressions with a deeply concave bottom, and are isolated or located inside the grooves. The

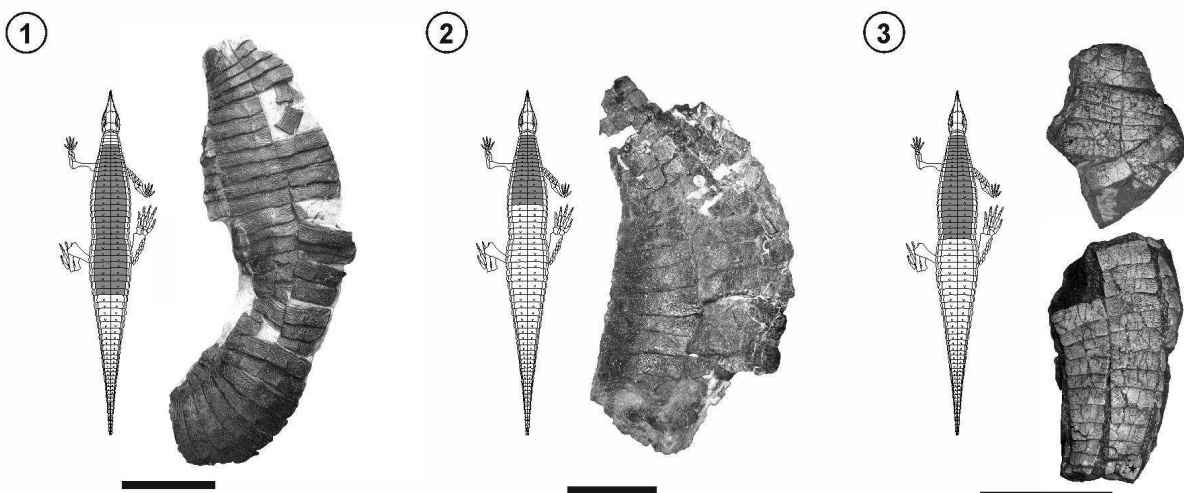


Figure 3. Carapaces of the aetosaurs studied here. 1, PVL 2073; 2, PVL 2059; 3, MCP13-a-b-PV, with sketches (modified from Schoch, 2007) to show the approximate position of the preserved regions (grey). Scale bar= 10cm.

ridges are narrow and elongate projections, whereas the grooves are elongated depressions limited on each side by the ridges. There are small, isolated pits distributed around the base of the DE. We recognize different ornamentation patterns based on the position of the elements in the MA of each paramedian osteoderm.

Comparison of medial areas in paramedian osteoderms

Typically aetosaurs have been identified as having either a “radial” pattern of pits and/or grooves and ridges, or a “random” pattern of pits, with most taxa having a “radial” pattern but some (e.g., *Typhothorax coccinarum*) exhibiting a randomly distributed array of pits (e.g., Long and Ballew, 1985; Heckert and Lucas, 2000; Parker, 2007). However, there is a great deal of variation within the radial pattern that has been mentioned previously (Desojo, 2005; Desojo and Báez, 2005, 2007), albeit not examined in detail, both between different taxa and within an individual carapace. In the case of individual variation, this is hard to evaluate due to the rarity of preserved articulated carapaces.

The paramedian osteoderms of PVL 2073 present two end-members of ornamentation in their medial area: a “radial pattern” (R) and an “anastomosing pattern” (A). There is also an intermediate or transitional pattern between them.

Radial Pattern. This is mainly composed of straight grooves and crests that are arranged radially from the DE. The crests and grooves have similar width. Inside the grooves there may be small pits with diameters that do not exceed the width of the groove, so that the ridges are straight and of constant width. The crests may bifurcate near the medial margin of the osteoderms (Fig. 4.1).

Anastomosing Pattern. This pattern is characterized by large and irregular pits without a particular arrangement on the bone surface (Fig. 4.3). The random arrangement of the pits causes the crests of the ridges to appear anastomosing in dorsal view. Some pits may be connected, but the resulting ridges are not straight.

Intermediate or Transitional Pattern. We adopted here an extremely strict approach in assigning osteoderms to the “radial” or “anastomosing” patterns. Accordingly, only those that match exactly the definitions are assigned to such osteoderm patterns. Thus, there is an intermediate condition between the R and A patterns, and this is actually the most common condition in the carapace of PVL 2073. It consists

of radial grooves that contain pits with a diameter greater than the width of the groove, resulting in sinuous crests along the ridges, which may otherwise have a generally radial pattern (Fig. 4.2). The average diameter of the pits gradually increases posteriorly from the dorsal to the sacral osteoderms before decreasing again in the caudal elements of PVL 2073. We can differentiate two additional types of intermediate osteoderms, which are respectively closer to, but not perfectly matching, either R or A patterns.

Intermediate-radial type (IR). This is a particular situation between the intermediate (I) and radial (R) patterns. In this pattern, the pits are not much larger than the grooves and the ridges are slightly sinuous, but with a clear radial arrangement. In some cases the ridges may bifurcate, but they do not anastomose. Many osteoderms appear superficially radial, but still have sinuous ridges because the pits are slightly wider than the grooves; this category is employed for those osteoderms.

Intermediate-anastomosing type (IA). This is a particular situation between the intermediate (I) and anastomosing (A) pattern. This pattern is characterized by sinuous ridges, slightly anastomosed and larger pits arranged somewhat radially and connected by small radial grooves. The diameter of the pits is approximately twice the width of the grooves. This category is employed for osteoderms that are very close to those with the A pattern, but with some indication of a radial pattern that prevents them from being strictly assigned to it.

Patterns of ornamentation in *Aetosauroides scagliai*

Desojo and Ezcurra (2011) assigned the three carapaces studied here to *Aetosauroides scagliai* based on the vertebral characteristics listed previously. Here we compare and contrast details of the armour of these specimens, especially the size and ornamentation of the paramedian osteoderms (Fig. 3). The holotype of *Aetosauroides scagliai* (PVL 2073) preserves articulated osteoderms from the posterior cervical, dorsal, sacral, and anterior caudal regions (Fig. 3.1). The ESs of the osteoderms are well preserved, allowing observation of the ornamentation patterns, especially in the MA. Table 2 summarizes our observations of the ornamentation pattern preserved in this specimen.

The type of ornamentation preserved in the articulated dorsal armour of PVL 2059 includes all three patterns ob-

served in PVL 2073, but they differ by their position throughout the carapace (Tab. 2). Because PVL 2059 is not as well preserved as PVL 2073, we were not able to assess the pattern in all of the osteoderms with certainty.

SIZE AND COMPLETENESS

Of the three specimens, PVL 2073 is the most complete, with parts of 29 rows of dorsal armour osteoderms pre-

served, although all are embedded in a plaster block, and thus are only visible in dorsal view. All or most parts of the first 16 rows of armour osteoderms are preserved in PVL 2059. Specimen MCP 13a-b PV preserves a more complete carapace than PVL 2059, with parts of at least 20 rows of dorsal paramedian osteoderms, but they are mostly disarticulated. Specimen PVL 2059 is slightly wider than PVL 2073, as the widest paramedian osteoderms (forming rows

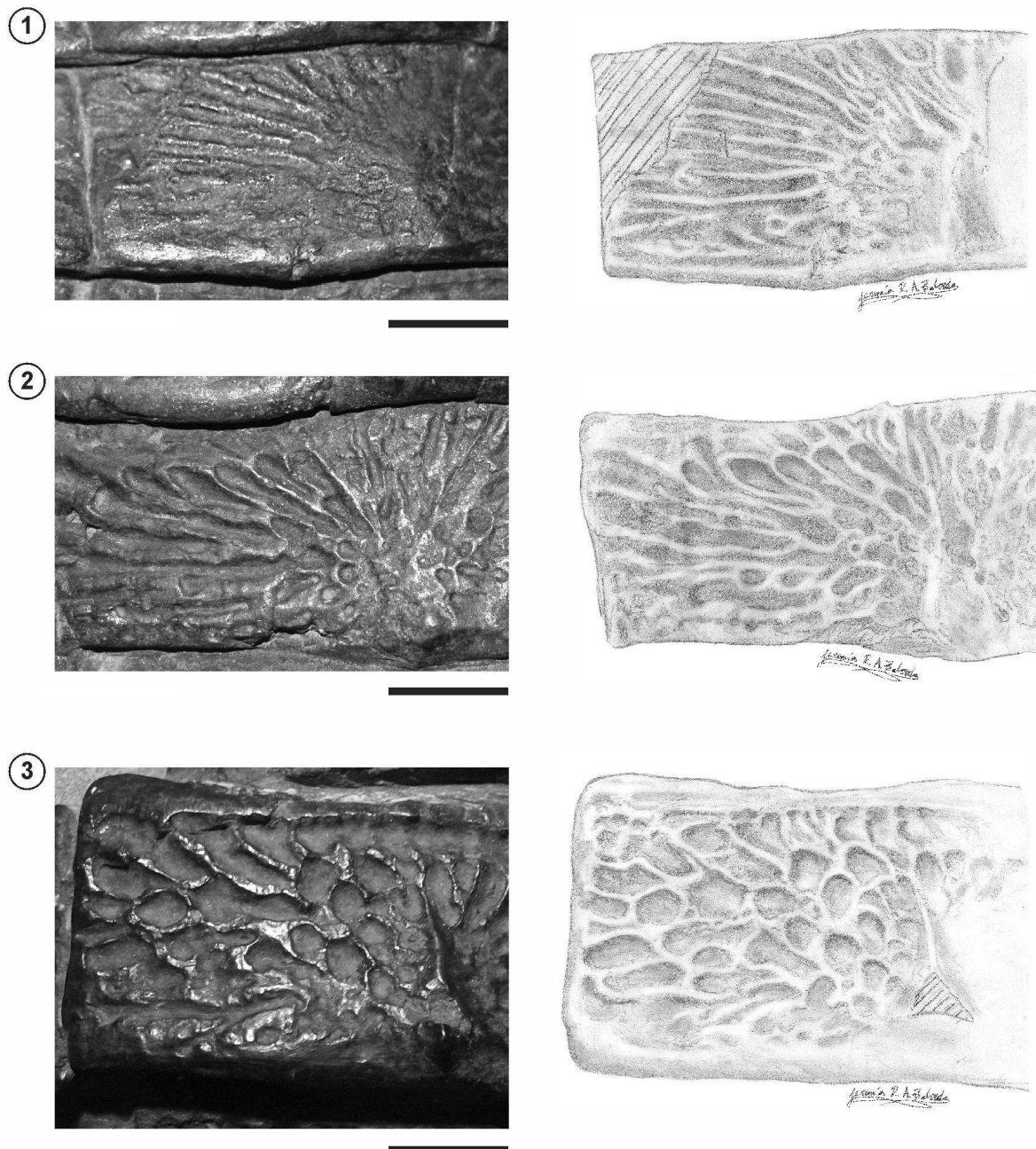


Figure 4. Variation in the ornamentation patterns of right paramedian osteoderms of PVL 2073. 1, Radial pattern; 2, Intermediate or transitional pattern; 3, Anastomosing pattern. Left column, photograph of the osteoderm medial area; right column, drawing of ornamentation for each osteoderm, anterior bar at top, striped lines indicate plaster reconstruction. Scale bar= 1cm.

TABLE 2 - Ornamentation patterns in medial area of paramedian osteoderms.

<i>Osteoderms</i>	<i>PVL 2059</i>	<i>PVL 2073</i>
<i>Cervical 1</i>	x	x
<i>Cervical 2</i>	x	x
<i>Cervical 3</i>	x	x
<i>Cervical 4</i>	x	x
<i>Cervical 5</i>	<i>IR</i>	<i>IR</i>
<i>Cervical 6</i>	<i>IR</i>	<i>R</i>
<i>Cervical 7</i>	x	x
<i>Dorsal 1</i>	<i>IA</i>	<i>IR</i>
<i>Dorsal 2</i>	<i>A</i>	<i>IR</i>
<i>Dorsal 3</i>	<i>A</i>	<i>IR</i>
<i>Dorsal 4</i>	<i>I</i>	<i>IR</i>
<i>Dorsal 5</i>	<i>I</i>	<i>I</i>
<i>Dorsal 6</i>	<i>IA</i>	<i>X</i>
<i>Dorsal 7</i>	<i>IA</i>	<i>I</i>
<i>Dorsal 8</i>	<i>IR</i>	<i>I</i>
<i>Dorsal 9</i>	x	<i>I</i>
<i>Dorsal 10</i>	x	<i>I</i>
<i>Dorsal 11</i>	x	<i>I</i>
<i>Dorsal 12</i>	x	<i>IA</i>
<i>Dorsal 13</i>	x	<i>IA</i>
<i>Sacral 1</i>	x	<i>IA</i>
<i>Sacral 2</i>	x	<i>IA</i>
<i>Caudal 1</i>	x	x
<i>Caudal 2</i>	x	<i>A</i>
<i>Caudal 3</i>	x	<i>A</i>
<i>Caudal 4</i>	x	<i>IA</i>
<i>Caudal 5</i>	x	<i>IA</i>
<i>Caudal 6</i>	x	<i>I</i>
<i>Caudal 7</i>	x	<i>I</i>
<i>Caudal 8</i>	x	<i>IR</i>
<i>Caudal 9</i>	x	<i>IR</i>

A, anastomosing patterns; *I*, intermediate pattern; *IA*, intermediate-anastomosing pattern; *IR*, intermediate-radial pattern; *R*, radial pattern; *x*: missing, poorly preserved, or not identified.

10–14 of both specimens) are approximately 101 mm across in PVL 2059, but only ~92 mm wide in PVL 2073 (Tab. 3). On the other hand, MCP 13-ab PV is by far the smallest specimen, with no paramedian osteoderms wider than ~50 mm (Zacarias, 1980: tabs. 1–2). Interestingly, the vertebrae of PVL 2073 are slightly shorter antero-posteriorly than are those of PVL 2059 (Tab. 4), so PVL 2073 is slightly shorter than PVL 2059.

ONTOGENY

Based on the closure of neurocentral sutures, PVL 2059 is the ontogenetically oldest specimen, with relatively tight closure of the cervical and anterior dorsal sutures (Brochu, 1996, 1999; Irmis, 2007). We concur with Irmis (2007) that PVL 2073 has open cervical and dorsal sutures, but disagree with him by considering the caudal sutures closed. By contrast, all vertebral sutures are open in MCP 13-a-b PV (Desojo and Ezcurra, 2011). A histological analysis (Cerdeña and Desojo, 2010) indicates that PVL 2073 has at least five LAGs (lines of arrested growth) and MCP 13a-b PV only one, suggesting that these specimens were at least six and two years old, respectively, at the age of death, assuming that aetosaurs were similar to modern crocodylians and began to ossify their osteoderms after their first year (e.g., Vickaryous and Hall, 2008). However, Parker *et al.* (2008 and references therein) suggested that it is probably inappropriate to estimate the age by adding one year to the LAG count, because histological studies of osteoderms in modern forms can show errors of several years over (or below) the total number of LAGs. In any case, the age difference between PVL 2073 (5 LAGs) and PVL 2059 (10 LAGs) is greater than the error of the estimation. Subsequent work determined that PVL 2059 has at least 10 LAGs and was therefore at least 11 years old (Cerdeña pers. comm.). The largest known specimen of *Aetosauroides*, PVL 2052, has 18–21 LAGs, indicating an age estimate of at least 19–22 years (Taborda *et al.*, 2013). Thus, the histological data independently supports the size and vertebral suture data and indicate that the larger specimens (PVL 2059 and PVL 2052) are ontogenetically more mature. What is confusing is that PVL 2059 appears to be skeletally mature (based on closed vertebral sutures), but is dramatically smaller in size (half the linear dimensions) of PVL 2052. We address this further in the Discussion section.

TABLE 3 - Width (in millimeter) of paramedian osteoderms of PVL 2073.

# Osteoderms	Right									Left									
	A			M			P			A			M			P			
	t	ma	la	t	ma	la	t	ma	la	t	ma	la	t	ma	la	t	ma	la	
Cervical 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cervical 5	-	-	-	-	-	-	-	-	-	-	-	-	-	*20,00	-	*57,00	*21,00	39,52	-
Cervical 6	-	-	-	-	20,44	-	-	22,26	-	-	-	-	-	*25,12	-	-	*26,72	-	-
Cervical 7	-	-	-	-	24,08	-	-	26,92	-	-	-	-	-	28,44	-	-	30,76	-	-
Dorsal 1	*67,02	*26,94	43,40	*69,58	*22,64	44,66	-	*29,26	-	-	-	-	-	*30,64	-	-	*33,30	-	-
Dorsal 2	-	-	-	-	-	-	-	-	-	-	*35,58	-	*81,28	*36,82	46,34	*81,00	*38,86	44,10	-
Dorsal 3	-	-	-	-	-	-	-	-	-	*84,82	*37,36	49,58	*87,00	*37,54	*49,42	-	*39,16	-	-
Dorsal 4	-	-	-	-	-	-	-	-	-	-	*37,36	-	-	*37,58	-	-	**39,00	-	-
Dorsal 5	-	-	-	-	-	-	-	-	-	-	-	-	-	*38,50	-	-	*40,16	-	-
Dorsal 6	-	31,78	-	-	33,46	-	-	*33,20	-	-	*37,44	-	-	*38,34	-	-	*41,00	-	-
Dorsal 7	-	34,12	-	-	34,52	-	-	36,04	-	-	-	-	-	*37,32	-	-	36,74	-	-
Dorsal 8	-	-	-	-	-	-	-	-	-	-	*39,38	-	-	*39,82	-	*92,16	*37,12	*55,44	-
Dorsal 9	-	-	-	-	-	-	-	-	-	*92,08	*34,34	*59,70	-	*32,94	-	-	-	-	-
Dorsal 10	-	*35,02	-	-	35,06	-	88,60	36,54	54,24	-	-	-	-	-	-	-	-	-	-
Dorsal 11	-	-	-	-	-	-	-	34,36	-	-	-	-	-	-	-	-	-	-	-
Dorsal 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dorsal 13	77,74	30,20	48,46	76,54	31,32	47,00	-	31,48	-	-	-	-	-	-	-	-	-	-	-
Sacral 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*42,50	-	-	*35,90	-
Sacral 2	-	26,54	-	-	27,58	-	-	29,78	-	-	-	-	-	-	36,76	55,92	28,10	31,22	-
Caudal 1	-	-	-	-	26,38	-	-	27,18	-	-	-	-	-	-	-	-	-	-	-
Caudal 2	-	-	-	-	27,64	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caudal 3	-	28,90	-	-	30,46	-	65,82	31,20	35,66	*64,00	29,28	*34,62	66,88	30,86	37,88	64,44	31,12	35,38	-
Caudal 4	-	28,60	-	-	31,00	-	-	31,68	-	69,96	31,76	*40,78	71,80	30,54	43,40	*68,44	30,84	*40,44	-
Caudal 5	73,36	29,22	30,98	75,24	30,40	45,92	72,66	31,88	42,44	-	31,54	-	-	29,80	-	-	29,08	-	-
Caudal 6	73,92	27,02	46,68	75,08	28,00	47,92	73,54	30,00	45,16	-	-	-	-	28,98	-	-	31,00	-	-
Caudal 7	*76,32	30,22	*47,86	77,06	30,64	47,72	72,82	30,56	44,98	-	-	-	-	-	-	-	*30,80	-	-
Caudal 8	76,84	31,30	46,64	77,46	30,38	47,78	72,16	31,32	43,68	-	-	-	-	-	-	-	32,94	-	-
Caudal 9	-	29,58	-	-	29,78	-	-	29,54	-	-	-	-	-	*30,38	-	-	30,12	-	-
29	-	-	-	-	-	-	-	-	-	-	-	-	-	28,38	-	-	29,88	-	-

A, anterior; M, medial; P, posterior; t, total; ma, medial area; ml, lateral area; * indicates imprecise measurement.

TABLE 4 - Vertebral length for aetosaurs analyzed.

PVL 2073														
Vertebra	C3/4	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15	D16
Length [mm]	13,7	21,2	22,0	22,9	23,7	24,4	23,1	22,9	23,2	24,7	23,4	24,0	22,5	23,4
Vertebra	S1	S2	Ca1	Ca2	Ca3	Ca4	Ca5	Ca6	Ca7	Ca*				
Length [mm]	-	30,8	21,7	22,1	23,4	24,3	24,2	22,6	24,7	21				
PVL 2059														
Vertebra	C2	C3	C4	C5	C6	C7	C8	C9	D1	D2	D3	D4	D5	D**
Length [mm]	14,6	15,3	17,0	19,1	18,5	21,1	22,4	21,2	21,8	23,8	22,6	22,7	23,3	26,8

C, cervical vertebra; D, dorsal vertebra; S, sacral vertebra; Ca, caudal vertebra; * caudal middle/posterior; ** dorsal middle/posterior.

OSTEODERM PROPORTIONS

There is general consensus among aetosaur workers that the proportions of the paramedian osteoderms, specifically the width/length (W/L) ratio, is taxonomically significant (Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 2000; Parker, 2007; Desojo *et al.*, 2013). However, most authors have not provided explicit criteria for measuring osteoderms. There are exceptions, such as Martz and Small (2006), who appear to have used protocols illustrated in Martz (2002) (see also Small and Martz, 2013). Casamiquela (1961) described the dorsal, ventral, and appendicular armour of the holotype of *Aetosauroides scagliai* (PVL 2073) in detail. However, few measurements of the osteoderms were provided. Casamiquela (1967) later described and compared a new specimen of *Aetosauroides scagliai* (PVL 2052), but again few measurements were taken (Casamiquela, 1967, p. 195). As noted by Heckert and Lucas (2002), the articulated carapace of PVL 2073 conceals the anterior bar in most osteoderms and hampers efforts to take complete measurements. Accordingly, we have taken multiple measurements of each relatively complete osteoderm in order to facilitate comparisons (Fig. 5).

Heckert and Lucas (2002) reported measurements of osteoderms showing that the left side of the anterior dorsal paramedian osteoderms in PVL 2073 appeared to be wider than the right ones. These enigmatic measurements are probably the result of the original restoration, which makes it difficult to determine the amount of reconstruction per-

formed on some osteoderms. It appears that the carapace was found exposed, broken, and very slightly disarticulated, and was removed in a single jacket. The postcranial elements were then prepared out of the bottom of the jacket, leaving the osteoderms. A plaster coat may have then been applied, and the top of the jacket removed and the carapace restored, including possibly the filling of a crack on the left side, resulting in “restored” osteoderms that were probably wider than they were in life. This restoration is not obvious even in first-hand observation, and extremely difficult to see in photographs, but becomes apparent when individual osteoderms are measured because the width of the mA on the left side is consistently wider than that of the right side for the same row of paramedian osteoderms.

We consider the first osteoderm row preserved in PVL 2059 as row 1, because it is articulated with the skull, but the first osteoderm row preserved in PVL 2073 should be row 6, middle cervical, matching the articulated vertebral series. After accounting for restoration, the widest osteoderms of both PVL 2059 and PVL 2073 are in rows 10–14, and their antero-posterior length is relatively constant (~22–26 mm). Thus, in both PVL 2059 and PVL 2073, the widest osteoderms have W/L ratios considerably larger than 3:1. Without including the anterior bar in the measurement (which is often ~10–20% of the total osteoderm length) this yields ratios of 3.8–3.9:1, but with the anterior bar included this ratio drops to below 3.5:1. Thus the osteoderms are relatively much wider than long, although

none are as wide as the widest armour in typhothoracisines, which possess a W/L ratio approaching or surpassing 4:1 (Long and Ballew, 1985; Parrish, 1993; Heckert and Lucas, 2000; Parker, 2007; Desojo *et al.*, 2013). Furthermore, these osteoderms are anterior to –and therefore not homologous with– the widest osteoderms of *Typhothorax coccinarum*, which are from the middle of the body rather than from the anterior dorsal series (*e.g.*, Heckert *et al.*, 2010). Because the presacral armour of PVL 2052 is not articulated, it is difficult to know which osteoderm positions are preserved. Although they are much wider, they are also longer and therefore appear to represent the posteriormost portion of the carapace (“waist”, sacrals, or anterior caudals), as W/L ratios of these are typically ~2.3:1 and do not exceed 2.5:1. Homologies of the osteoderms in MCP 13b PV (the anteriormost portion of the carapace) are not certain, but the widest osteoderms have a W/L ratio of ~3.5:1 exclusive of the anterior bar, which is again obscured by the overlying anterior osteoderm. Thus, all three carapaces exhibit the

same general proportions (maximum W/L of ~3.0–3.5 in the dorsal series), and the broadening of paramedian osteoderms from the cervical towards the dorsal series appears similar in all of them (Fig. 3). Similarly, the relative narrowing of the osteoderms along the caudal series is similar in MCP 13a PV and PVL 2073.

PATTERN

Desojo and Ezcurra (2011, p. 602) noted that the armour of the Brazilian specimen (MCP 13a-b PV) of *Aetosauroides scagliai* –and smaller specimens generally– consists primarily of “closed pits”, which they described as fully enclosed depressions, with few if any ridges. This contrasts with larger specimens, such as PVL 2052, which have more ridges. We observed that PVL 2073 is transitional between the two, with extensive, elongate ridges across many of the paramedian osteoderms, but retaining a large number of pits as well. Additionally, PVL 2059 exhibits less well-developed patterns (closer to anastomosing than radial) than in homologous osteoderms in PVL 2073. Because specimen MCP 13a-b PV is ontogenetically young, the ornamentation is poorly marked, making it difficult to correctly identify all ornamentation patterns. However, we identify an anastomosing pattern in the sacral region, similar to that present in PVL 2059 and PVL 2073.

DISCUSSION

The variation of the ornamentation pattern, osteoderm proportions, and size/age relations between the holotype and referred specimens of *Aetosauroides scagliai* can be explained by different factors (*e.g.*, taxonomic, taphonomic, ontogenetic, dimorphic, individual variation). As we described previously, the three specimens are referred to the same species –*Aetosauroides scagliai*– based on skeletal characters independent of the osteoderms (Desojo and Ezcurra, 2011). It is important to mention that, in contrast to typhothoracisines and desmatosuchines, osteoderms of more basal aetosaurs are much less informative taxonomically, and it is extremely problematic to use only those elements for species identification in these forms. For this reason, we consider the minor differences in osteoderm ornamentation between PVL 2073 and PVL 2059 to be less significant than the identical morphology of their presacral vertebrae. Accordingly, we invoke intraspecific variation to

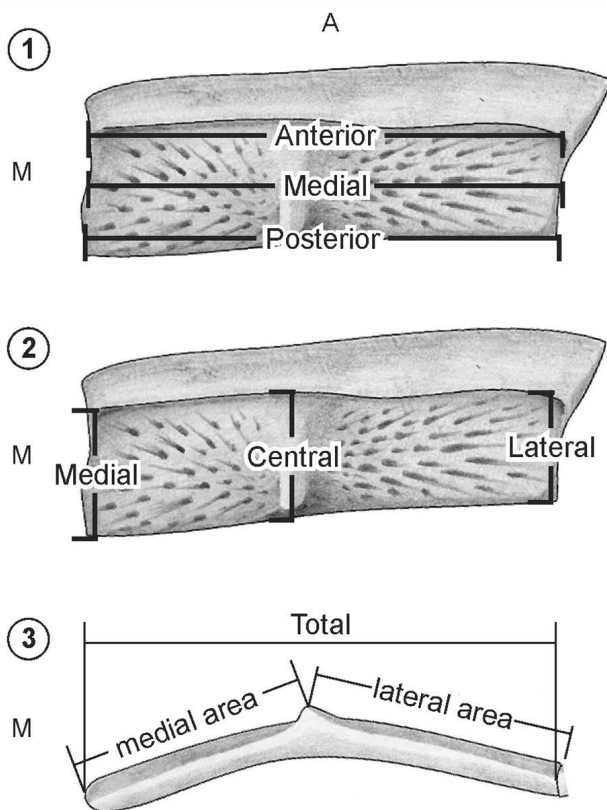


Figure 5. Variation in the proportions of “aetosaurine” paramedian osteoderms. **1**, Protocols for measuring width of paramedian osteoderms; **2**, Protocols for measuring length of paramedian osteoderms, **3**, Posterior view of osteoderm. Image modified from Schoch (2007).

explain the observed differences in osteoderm ornamentation, but a larger sample will contribute to test this hypothesis. Histological sections demonstrate that the external cortex is completely preserved; indicating that the osteoderm ornamentation is complete and not affected by weathering, diagenesis resulting from the fossilization process, or other taphonomic causes. Because the specimens are uniformly well-preserved, with no indication of damage or resorption of the external surface, and the histological sections also show no evidence of post-mortem damage, we reject the hypothesis of taphonomic variation.

Also, analyzing the patterns of absorption and deposition of bone in the external cortex of osteoderms, we observed the same patterns described by de Buffrénil (1982) and de Buffrénil *et al.* (2014) for crocodylians, which maintain a constant ornamentation pattern in the skull throughout ontogeny (see also Taborda *et al.*, 2013). The pattern of absorption and deposition of bone matrix corresponds to the displacement of grooves and pits during growth of the osteoderms. This displacement can explain the reorganization of pits, grooves and ridges in a larger osteoderm surface because growth maintained the same ornamentation patterns (Taborda, 2011; Taborda *et al.*, 2013). For this reason, the ontogenetic hypothesis to explain the difference in patterns is discarded, especially of similarly sized osteoderms (*e.g.*, PVL 2073 and PVL 2059).

Another possible explanation for the variation observed between PVL 2059 and the other two specimens is the presence of sexual dimorphism, which is supported by the relative ages and size of the individuals. This is because the younger specimen (PVL 2073, ~6 years) is of approximately the same size as the ontogenetically apparently older specimen PVL 2059 (~11 years), and both are considerably larger than specimen MPC 13 a-b PV (~2 years). In living crocodiles, male specimens typically are relatively larger (longer) than the females of the same age (Huchzermeyer, 2003; Barrios-Quiroz *et al.*, 2012). Similarly, female crocodiles are smaller than sexually mature males at the onset of sexual maturity (Barrios-Quiroz *et al.*, 2012). Unfortunately, it is not possible to know the gender, sexual maturity, and reproductive state of any of these specimens of *Aetosauroides scagliai*. Although with a small sample we cannot propose a male/ female size ratio, we know that the ontogenetically older specimen (PVL 2059) analyzed in this

paper does not define the maximum size for the species. Taborda *et al.* (2013) provided size and age estimates for the largest specimen assigned to *Aetosauroides scagliai* (PVL 2052), and determined that it has at least 21 LAGs and was probably 2.4 m long, approximately 1 m more than PVL 2073 and PVL 2059. Comparing this information with that previously mentioned for living crocodiles, we consider that PVL 2059 could be a female. Anyway, we cannot reject the possibility of non-sexually related individual variation. However, the anatomical evidence (*e.g.*, open neurocentral sutures, sequence of closure of the neurocentral suture of the vertebral series) suggests that PVL 2073 is not an adult, in correspondence with the histological data provided by recent analyses (Cerdeira and Desojo, 2011). Comparing the three analyzed specimens, intraspecific variation is mainly of two types. One is related to the size/age of the specimens (that cannot be explained by ontogeny, because some specimens, such as PVL 2073, show a size similar to ontogenetically older specimens such as PVL 2059). The other is related to the position of different ornamentation patterns along the armour.

One possibility for testing the hypothesis of sexual dimorphism in extinct archosaurs is to find evidence of medullary bone. This tissue appears in the female avians during reproduction (Dacke *et al.*, 1993), and was recognized in dinosaurs (*e.g.*, Chinsamy, 1990; Schweitzer *et al.*, 2005). However, living crocodiles apparently do not form medullary bone (Elsey and Wink, 1985), which is unknown in crocodile-line archosaurs. Unfortunately, we cannot determine if *Aetosauroides scagliai* preserves medullary bone because only the holotype (PVL 2073) preserves the femur, and may not be sampled with destructive methods.

Combining this information with the evidence of ontogenetic state and general body size of all the analysed specimens of *Aetosauroides scagliai*, and using the condition in living crocodiles as a proxy, we conclude that the intraspecific variation in *A. scagliai* is compatible with the hypothesis of sexual dimorphism. Unfortunately, sexual dimorphism has only been described in a few fossil archosaurs (*e.g.*, Raath, 1990; Molnar, 2005; Mallon and Holmes, 2006; Rinehart *et al.*, 2009; Barden and Maidment, 2011), and very few archosauriforms (*e.g.*, Zeigler *et al.*, 2003), and very difficult to test in paleontology. Nevertheless, we consider that it is the most parsimonious hypothesis to ex-

plain the observed variation in the armour of *Aetosauroides scagliai*. We note that Walker (1961) held sexual dimorphism as a possible explanation for differences in caudal vertebra morphology in *Stagonolepis robertsoni* and the distribution of osteoderms around the cloacal opening in *Aetosaurus*, but not in the overall pattern of preserved osteoderms. Similarly, Parker and Martz (2010) dismissed Elder's (1978) unpublished hypothesis that osteoderms used to identify *Lucasuchus* and *Longosuchus* are actually sexual dimorphs.

This study demonstrates that it is necessary to evaluate the patterns of paramedian osteoderms in aetosaurs beyond the simplistic "random" versus "radial" dichotomy used by most previous authors. Careful documentation of osteoderms in articulated carapaces reveals a greater diversity of patterns, which may not only help understanding intraspecific variation, as suggested here, but also improve the accuracy of comparisons of incomplete material, such as isolated osteoderms, with articulated carapaces.

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