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**Notes**

## Growth curve of *Aetosauroides scagliai* Casamiquela 1960 (Pseudosuchia: Aetosauria) inferred from osteoderm histology

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**Abstract:** Recent palaeohistological studies on paramedian osteoderms of aetosaurs revealed the presence of growth lines (lines of arrested growth or LAGs) and a minimal or nonexistent secondary remodelling in the bone matrix of these elements. This feature allows the age of individuals to be estimated through growth line count. In the present contribution we study the growth curve of the South American aetosaur *Aetosauroides scagliai*. We estimated the age (obtained from LAG counting) and body size (body length and body mass were used as proxies) of different aetosaur specimens in order to reconstruct the growth curve of the South American species. The data obtained for *Aetosauroides scagliai* were compared with that of other aetosaurs, such as *Neoaetosauroides engaeus*, *Aetosaurus ferratus*, *Aetobarkinoides brasiliensis*, *Typhothorax coccinarum* and *Paratyphothorax* sp. Our results indicate that, if body length is considered as proxy, all studied aetosaur specimens have a similar or almost identical growth rate. However, important variations arose among aetosaur taxa if body mass is considered as proxy, which would be related to a body morphology ranging from slender (e.g. *Aetobarkinoides brasiliensis*) to very wide (*Typhothorax coccinarum*) morphotypes. In comparison with extant pseudosuchians (i.e. crocodylians), *Aetosauroides scagliai* possesses a relatively lower growth rate.

Aetosaurs are a clade of quadruped pseudosuchian archosaurs from Upper Triassic continental beds of South and North America, Europe, Africa and India (e.g. Heckert & Lucas 2000; Parker 2008; Desojo & Ezcurra 2011). This group of diapsids, with a body length ranging from 1 to 6 m, is nested within Pseudosuchia, the crocodylian lineage of Archosauria. However, the high-level phylogenetic relationships of the group within Suchia are currently a matter of debate (e.g. Gower & Sennikov 1996; Nesbitt 2007, 2011; Brusatte *et al.* 2010; Desojo *et al.* 2012; see also Desojo *et al.* this volume, in press).

Aetosaurs are characterized by the presence of heavy armour composed of osteoderms covering most of the body. Recent palaeohistological studies on osteoderms of *Sierritasuchus macalpinii* Parker *et al.* (2008) and *Aetosauroides scagliai* Casamiquela 1960 (Cerde & Desojo 2011) have revealed important information about the growth pattern of the armour. The latter authors concluded that in

'Aetosaurine' aetosaurs (*sensu* Parker 2007) the osteoderm bone matrix lacks secondary remodelling and an estimate of individual age is possible by counting the lines of arrested growth (LAG) in these elements (Cerde & Desojo 2011). Similar studies in several dinosaur lineages were conducted in the last decade (e.g. Erickson *et al.* 2004, 2006, 2009) and shed light on the palaeobiology of these groups, as was the case in *Tyrannosaurus* (Erickson 2005). However, the study of growth dynamics in aetosaurs has been neglected despite the potentially important palaeobiological and evolutionary implications.

The LAGs in extant reptile osteoderms are correlated with annual interruptions of the individual's growth (Hutton 1986; Games 1990; Woodward & Moore 1992; Tucker 1997; Erickson & Brochu 1999; Erickson *et al.* 2003). This correlation has previously been used for age estimation in fossil archosaurs, including crocodylians (Erickson & Brochu 1999; Hill & Lucas 2006) and aetosaurs

(Parker *et al.* 2008; Cerda & Desojo 2011). Assuming that the preserved LAGs in the aetosaurian osteoderms were annually deposited, the age of individuals can be determined through counting the number of LAGs present in the cortical bone.

In order to contribute to the knowledge of growth dynamics in aetosaurs, in this contribution we reconstructed a growth curve for *Aetosauroides scaglii* employing age, body mass and total body length estimates. The recovered growth curve will allow comparisons with that of other aetosaurs.

## Materials and methods

### Analysed specimens

Although the present study is mainly focused on *Aetosauroides scaglii*, we also examined and discussed other taxa for comparison. The studied taxa comprise specimens assigned to six aetosaur species and an indeterminate Aetosaurinae (*sensu* Parker 2007) (Table 1). *Aetosauroides scaglii* was the best-represented taxon of our sample, with a total of four specimens from Argentina and Brazil representing different individuals (PVL 2073, PVL 2052, MCP 13 and UFSM 11070). The specimen PVL 2073 (holotype of *Aetosauroides scaglii*) has an almost complete armour and its total body length was estimated at about 2.4 m base on a quantitative analysis (Taborda 2011). The materials of *Aetosauroide scaglii*, identified as UFSM 11070 and UFRGS 11070, belong to the same individual but different elements were deposited in both institutions in Brazil. *Aetosaurus ferratus* Fraas 1877 is also used in this study, 16 of the 25 specimens included in the block SMNS5770 of Stuttgart, Germany (Schoch 2007) and the specimen SMNS12670 were studied. Although several specimens of *Aetosaurus ferratus* were examined, we studied a single thin section of this taxon. Besides *Aetosauroides scaglii*, two other South American aetosaurs were also studied: the holotype of *Neoaetosauroides engaeus* Bonaparte 1969 (PVL 3525). This specimen consists of complete skeleton and dorsal armour (Desojo & Báez 2005). The total length was measured and the body mass was estimated. The other South American aetosaur included is the holotype of the Brazilian *Aetobarbakinoides brasiliensis* Desojo *et al.* 2012 (CPE2 168), composed of several articulated vertebrae, a few poorly preserved dorsal osteoderms, ribs and some appendicular bones (Desojo *et al.* 2012). This material was used for body mass estimation and for thin sectioning. The total length of *Aetobarbakinoides brasiliensis* is estimated at 2 m (Desojo *et al.* 2012). Finally, we also included two taxa previously assigned to the Typothoracisinae (Parker 2007),

*Typothorax coccinarum* Cope 1875 (NMMNH P-56299) and *Paratypothorax* sp. (SMNS 1903). *Typothorax coccinarum* is currently known by fairly complete and articulated specimens from New Mexico (USA), and we employed recent published information from Heckert *et al.* (2010). Regarding the studied material of *Paratypothorax* sp., we examined a complete and articulated unpublished skeleton (SMNS 1903) from Stuttgart (Germany).

### Growth curve reconstruction

The growth curve reconstructions were first estimated by three different parameters: body mass ( $M$ ), total body length ( $TL$ ) and age.

**Body mass.** The most frequently employed equations for body mass estimates in reptiles are those obtained from the studies of Dodson (1975) and Anderson *et al.* (1985). The equation of Dodson (1975), employed previously for mass estimation in *Alligator mississippiensis* Daudin 1801 (equation 1), estimates  $M$  using  $TL$  as a parameter. This equation has been only employed for crocodylians and it can only apply in specimens composed of complete skeletons. In equation '1(a)' obtained by Anderson *et al.* (1985),  $M$  is estimated from femoral and humeral minimal circumferences ( $FC$  and  $HC$ , respectively) (equation 2). In the present contribution, we applied Anderson *et al.*'s (1985) equation because the equation of Dodson (1975) underestimates the weight of the aetosaur armour (Taborda 2011). The former equation (Anderson *et al.* 1985) is independent of the presence of body armour because the minimum diaphyseal circumference of the major weight-bearing bones (stylopedial bones) is strongly related to the mass of the animal, and weakly influenced by the varied forces exerted on the limbs (Campione & Evans 2012):

$$M = 0.97 \times 10^{-6} TL^{3.18} \quad (1)$$

$$M = 0.078 (FC + HC)^{2.73 \pm 0.09} \quad (2)$$

For the estimates of body mass, the equation of Anderson *et al.* (1985) uses the sum of the minimum circumferences of femur and humerus.

Blob (2000) noted that cursorial animals have a direct relationship between the limb bone's shape and the body mass, and mention a positive allometry in the circumference of limb's bones to compensate for the greater increase in stress with increases in body mass. Also, the femur and humerus are subcylindrical structures and slightly clepsydroid; therefore, their points of greatest weakness at the torsion and flexion are present in the area where their circumference is minimal. These

**Table 1.** Shows the measures of aetosaurs and estimated missing data (indicated with\*) used for this study, and the maximum number of LAGs counted in the histological cut and their estimated age

Taxon	Specimen No.	SL (mm)	FL (mm)	FC (mm)	HL (mm)	HC (mm)	TL (m)	M (kg)	M' (kg)	No. of LAGs	Age (years)
<i>Aetosauroides scagliai</i>											
	PVL 2073	–	157.26	59.56	99.58	33.2	1.39*	20.95	18.32	5	6
	PVL 2052	–	–	104.4	45.6	45.6	2.42*	78.7	68.05	21	22
	UFSM 11070	–	–	57.6	33.65*	–	1.34*	20.02	17.52	–	–
	UFRGS 11070	–	–	–	–	–	–	–	–	8	9
	MCP 13	–	–	–	–	–	1	–	–	1	2
<i>Aetobarbakinoides brasiliensis</i>											
	CPE 2 168	–	–	41.32	–	35.06	2*	12.27	10.78	>11	13
<i>Neoaetosauroides engaeus</i>											
	PVL 3525	–	172	80	99	42	1.86*	44.55	38.71	–	–
<i>Aetosaurinae</i> indet											
	PVL 2091	–	–	–	168	87	–	–	299.44	–	–
	MLP 61-VII-2-34	–	–	–	–	–	–	–	–	1	2
<i>Aetosaurus ferratus</i>											
	SMNS5770-S1	73	50	18.52*	–	12	–	0.98	0.88	–	–
	SMNS5770-S2	102	93	35.34*	56	20.09*	–	–	4.49	–	–
	SMNS5770-S3	73	64.99*	14	43	14.31*	–	2.41	2.15	–	–
	SMNS5770-S4	78	56.88*	13	45.12*	–	–	–	2.01	–	–
	SMNS5770-S5	96	79.03*	–	50	16	–	–	2.68	–	–
	SMNS5770-S6	–	77	13	–	–	–	–	–	–	–
	SMNS5770-S7	104	87	16	–	20	0.83	4.25	3.77	–	–
	SMNS5770-S8	81	60.84*	19	46.16*	–	0.73	–	4.12	–	–
	SMNS5770-S13	86	67.43*	–	47.89*	–	–	–	2.08	–	–
	SMNS5770-S16	101	87.21*	30.67*	47	16.09*	0.83	3.17	2.82	0	1
	SMNS5770-S17	108	96.45*	–	55.51*	–	–	–	4.75	–	–
	SMNS5770-S18	117	108.32*	–	58.63*	–	–	–	6.26	–	–
	SMNS5770-S19	87	68.75*	36	48.23*	–	0.79	–	3.9	–	–
	SMNS5770-S20	–	53	19.69*	–	–	–	–	–	–	–
	SMNS5770-S21	–	40	12	29	8.09*	–	0.31	0.28	–	–
	SMNS5770-S22	–	89	33.78*	–	–	–	–	–	–	–
<i>Typothorax coccinarum</i>											
	NMMNH P-56299	–	291.8	107	193	68	2.5	120.32	103.65	–	–
<i>Paratyphorax</i> sp.											
	SMNS 1903	–	–	–	–	–	2	–	–	17	18

Abbreviations: FC, femoral minimum mid-shaft circumference; FL, femoral length; HC, humeral minimum mid-shaft circumference; HL, humeral length; M, body mass using Campione & Evans' (2012) equation; M', body mass using Anderson *et al.*'s (1985) equation; SL, skull length; TL, total body length.

measurements are related to the body mass. Use of an equation based on femoral or humeral length could cause problems for individuals with different relationships between the limb length and body size. For instance, in *Aetobarbakinoides brasiliensis*, which has limbs relatively longer than other aetosaurs (Desojo *et al.* 2012), the body mass estimated as a function of femoral length is overestimated. Other equations use the snout vent length (SVL) (e.g. Blob 2000; Farlow *et al.* 2005); however, in palaeontology, this method is impossible to apply because, as opposed to living animals, in fossils the position of cloaca is unknown.

Recently, Campione & Evans (2012) showed, in their study of quadrupedal terrestrial tetrapods, a good correlation between the body mass and the total circumference of the stylopodia (humerus + femur). In contrast to Anderson *et al.*'s (1985) analysis, Campione & Evans (2012) used a more complete tetrapod sample in their analysis, with mammals, as well as reptiles and lissamphibians.

$$\log M = 2.754 \log(FC + HC) - 1.097. \quad (3)$$

To compare the result of Anderson *et al.*'s (1985) equation (equation 2) with that obtained by Campione & Evans' (2012) equation (equation 3), we can make two observations:

- the results obtained from equations (2) and (3) differed by approximately 10%;
- the result obtained using equation (3) is included within the error range of equation (2); likewise, the result obtained using equation (2) is within the error range of equation (3) (Fig. 1).

These two issues show that the results obtained by both equations are equally acceptable. However, in

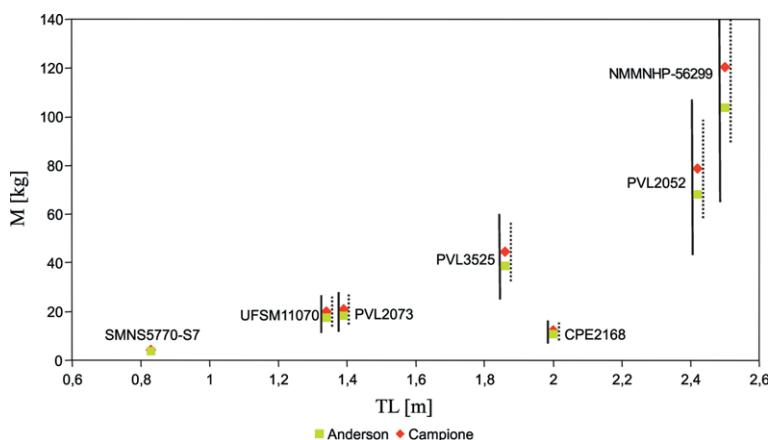
the present contribution we prefer to use Campione & Evans' (2012) equation to estimate the body mass of aetosaurs, as used for other reptiles.

Owing to the incomplete preservation and/or preparation of some specimens, we cannot obtain direct measurements of *FC* and *HC* in all of the sampled taxa. The missing data were estimated from linear regressions between different measurements of several skeletal sections. We use the data set of Farlow *et al.* (2005) for *Alligator mississippiensis*, in addition to the new data set of aetosaurs, in order to obtain a new equation. Employing our aetosaur (Table 1) and combined with Farlow's crocodylian data sets (Farlow *et al.* 2005, table 2 of supplementary data), we compared the femur length (*FL*) with *FC* and humerus length (*HL*) with *HC*. These comparisons revealed that the relationship between length and minimum midshaft circumference of these two stylopodial bones approached a lineal function in crocodylians and aetosaurs (Fig. 2). Linear regressions were obtained through the minimum squares method. The obtained equations are:

$$FC = 0.3913FL - 1.0479 \quad (4)$$

$$HC = 0.4536HL - 5.3306 \quad (5)$$

We employed these two equations to estimate the minimum midshaft circumference in specimens in which only femoral or humeral lengths could be measured. In *Paratyphorax* sp. (SMNS 1903), the appendicular skeleton is still unprepared, thus, we could not obtain measurements of any stylopodial bone (only the total body length of the individual).



**Fig. 1.** Comparison between results obtained with Anderson *et al.*'s (1985) equation (square) and Campione & Evans' (2012) equation (rhombus) for body mass estimations in aetosaur analyses. The lines indicate the range of error for body mass estimation in both equations (solid line for Anderson *et al.* 1985 and dotted line for Campione & Evans 2012).

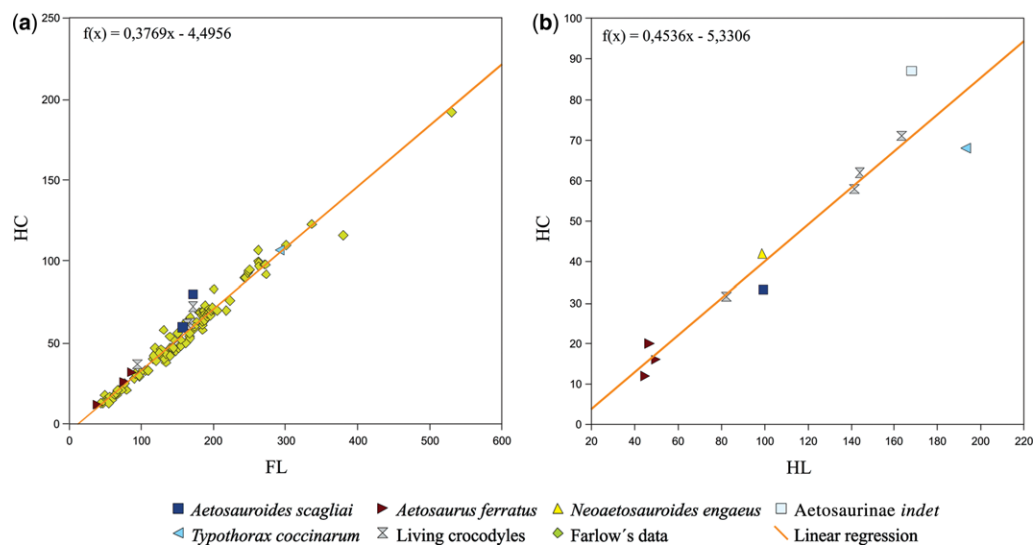
**Table 2.** *Crocodylians data taken and modified from Huchzermeyer (2003)*

Age (years)	TL (m)	M (kg)
0	0.24	0.08
0.08	0.36	–
0.83	0.45	0.24
1	0.34	1.84
1.25	0.72	2.15
1.7	0.75	1.41
1.75	0.81	1.74
2	1.1	5
2.7	1.12	4.1
3	1.39	8.7
3.8	1.46	9.18
4	1.65	13.18
6	2.07	37.75
9	2.52	62.3
10	2.78	106.45
11	2.86	118.75
6	1.68	15.45
9	2.05	39.3
10	2.19	51.35

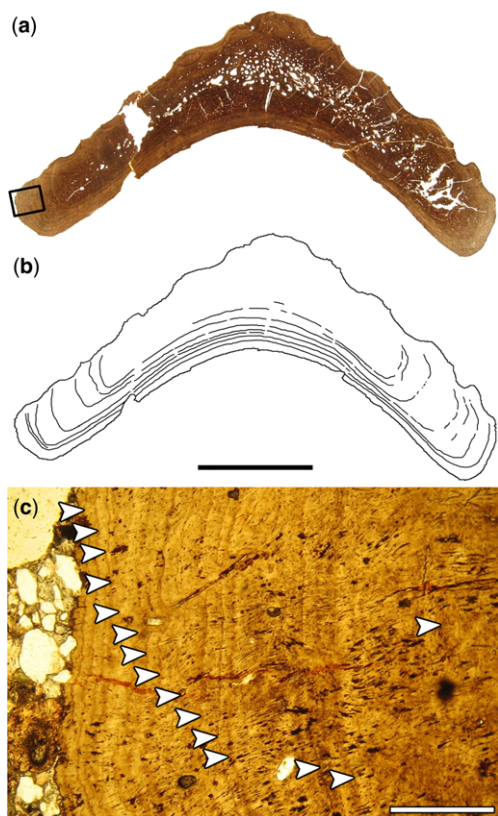
Abbreviations: TL, total body length; M, body mass.

**Age estimation.** The age estimation in aetosaurs was conducted by counting the number of LAGs (Fig. 3) in 18 osteoderms from different regions of the armour (paramedian, lateral, ventral and

appendicular) collected from Upper Triassic outcrops in Argentina and Brazil (Table 1). Palaeohistological preparations were made following the methodology described by Chinsamy & Raath (1992) at the Departamento de Geología of the Universidad Nacional de San Luis (Argentina). Osteoderm thin sections were studied under normal and polarized light through a binocular microscope housed at the Colección Nacional de Paleovertebrados of the Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ (Buenos Aires, Argentina). At least two transverse sections were obtained from each osteoderm. Since the LAG count varies in some individuals, even within the same osteoderm (see below), the age estimation was based on the maximum number of LAGs observed in each individual. The absence of intensive secondary remodelling in ‘Aetosaurinae’ osteoderms (Cerdeña & Desojo 2011) implies that all counted LAGs represent the complete set formed in an osteoderm during the life of the individual. However, given that extant crocodylians ossify their osteoderms about 1 year after hatching (Chiappe *et al.* 1998; Vickaryous & Hall 2008), an additional year was added to the counted age for a more accurate estimate. With the exception of the specimen assigned to *Paratypothorax* sp. (SMNS 1903) (for which the number of LAGs was obtained from Scheyer *et al.* 2011), all of the LAGs were directly counted from the thin section illustration by two of



**Fig. 2.** Relationships between length and minimum mid-shaft circumference (both in mm) for the femur and humerus. (a) Relationship between the femoral length (FL) and minimum mid-shaft circumference (FC) for aetosaurs and crocodylians. In both groups the relationships is linear. (b) Relationship between the humeral length (HL) and the minimum mid-shaft circumference (HC). The relationship between these variables is linear, and is similar for aetosaurs and crocodylians.

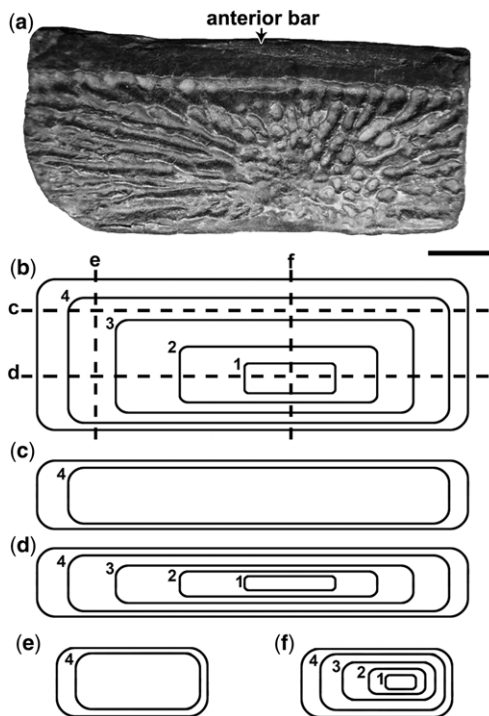


**Fig. 3.** Lines of arrested growth (LAGs) in a lateral osteoderm of *Aetosauroides scagliai* (PVL 2052). (a) Transversal thin section of the osteoderm. (b) Schematic drawing of the same specimen showing the position of nine of the 22 preserved LAGs. (c) Detail of the lateral cortex (box inset in a) showing the 15 outer LAGs. The scale bar equals 10 mm (a, b) and 0.5 mm (c).

the authors (J. B. Desojo & I. Cerda in Scheyer *et al.* 2011). We could not obtain thin sections from the articulated juvenile specimens of *Aetosaurus ferratus* preserved in block SMNS5770 but we took histological data from one paramedian osteoderm of SMNS12670. Although we could not take measurements from SMNS12670 because of its fragmentary condition, we considered that it had the same age as SMNS5770-16 because they are similar-sized individuals. (High-resolution versions of Fig. 3 are available from the authors on request.)

#### Problems with LAG counts

In some aetosaurian specimens the LAG count varies between different osteoderms, and even within the same element. This observed variation appears to be related to two major reasons,



**Fig. 4.** Photograph and drawing of an aetosaur paramedian osteoderm showing the best locations for thin sectioning. (a) Paramedian osteoderm of *Aetosauroides scagliai* (PVL 2073) in external view. (b) Schematic drawing of an aetosaur paramedian osteoderm. The internal numbered lines represent four deposited growth lines. Growth mark number 1 encloses the centre of ossification. Dashed lines indicate transversal (c, d) and parasagittal (e, f) sections. (c)–(f) Transversal and parasagittal sections showing variations in the LAG count. Note that the best sections are those that crossed the centre of ossification (d & f). The scale bar equals 10 mm.

excluding that of secondary remodelling because it was absent or minimal in our whole sample. The first reason is related to the histological preservation of the samples. For example, the diagenetic alteration observed in the sections obtained from the paramedian osteoderm of *Aetosauroides scagliai* PVL 2052 precluded the observation of the innermost deposited LAGs. The second reason for variation is related to the plane in which the osteoderms were sectioned. Owing to the different patterns of aetosaur osteoderm early development, particularly in the paramedian osteoderms (Cerda & Desojo 2011), the section plane would not include the centre of ossification of the element (which is enclosed by the first deposited growth mark). Thus, the number of LAGs is always underestimated (Fig. 4). The best areas for thin sectioning

of paramedian osteoderms (transversal or parasagittal) appear to be lateral to the dorsal eminence of the osteoderm because the centre of ossification is displaced towards this area (Cerdeña & Desojo 2011).

## Results and discussion

This is the first study of growth dynamics in aetosaurs, and provides new and substantial information about the mode and developmental differentiation of diverse taxa within the aetosaur lineage. In order to shed light on *Aetosauroides scagliai* growth dynamics, we reconstructed growth curves using the information obtained from mass ( $M$ ), total length ( $TL$ ) and age. For comparative purposes, we also plotted these variables for the other aetosaurian taxa examined here. In addition, we also plotted the same data for extant crocodylians (data obtained from Huchzermeyer 2003) to compare them with those in aetosaurian curves. The reason for this comparison is based on the fact that crocodylians are the closest extant relatives to aetosaurs (e.g. Gauthier 1986; Nesbitt 2011).

The *Aetosauroides scagliai* growth curves only represent a trend line because we considered that the sample size cannot indicate the real growth curve of *Aetosauroides scagliai*. Therefore, these curves are only descriptive and are not used to make predictions.

### TL–age

Both curves for *Aetosauroides scagliai* and crocodylians show a different trend for the relationships between  $TL$  and age (Fig. 5a). The slope of the aetosaur growth curve is lower than in crocodylians, which means a lower growth rate in *Aetosauroides scagliai*. This interpretation differs from that of previous studies of aetosaur bone histology (i.e. de Ricqlès *et al.* 2003, 2008; Cerdeña & Desojo 2011). Based on the LAG count, and comparing with extant and fossil crocodylians taxa, Cerdeña & Desojo (2011) proposed a similar growth rate between *Aetosauroides scagliai* and *Alligator mississippiensis*. In addition, de Ricqlès *et al.* (2003, 2008) proposed that phytosaurs, aetosaurs and poposaurs grew in a manner much more similar to crocodylians than ornithomirans.

Our results indicate that, compared with other pseudosuchian archosaurs, *Aetosauroides scagliai* was characterized by a relatively slow growth rate. If the reaching and maintaining of high growth rates through ontogeny was a basal characteristic of archosauriforms (de Ricqlès *et al.* 2003, 2008; Cubo *et al.* 2012), the relatively slower growth rate in *Aetosauroides scagliai* inferred from our

data indicated a derived condition in this taxon (and probably other aetosaurs), possibly gained independently from extant pseudosuchians. Interestingly, in a recent publication of Cubo *et al.* (2012), histological data reveal that another aetosaur (*Typothorax coccinarum*) also demonstrates a relatively slower growth rate compared with other non-ornithomiran archosaurs. The data obtained independently for *Aetosauroides scagliai* and *Typothorax coccinarum* suggest that aetosaurs were characterized by a lower growth rate in comparison with other pseudosuchian archosaurs.

We observed that the growth curve obtained for *Aetosauroides scagliai* also appears to be similar to *Aetosaurus ferratus*, *Paratyphorax* sp. and *Aetobarbakinoides brasiliensis*. This result indicates that these taxa possibly have a similar  $TL$  growth pattern independent of body shape. However, since these data are based in single individuals rather than an ontogenetic series, a more abundant sample of these other aetosaurian taxa is necessary for a more accurate comparison.

### M–age

The curve obtained for *Aetosauroides scagliai* has a very different trend to that of the extant crocodylians (Fig. 5b). The curves of body mass show a rapid increase in crocodylians, but a lower and almost constant rate for *Aetosauroides scagliai*. It seems that this constant increase in the body mass observed in *Aetosauroides scagliai* could differ from that of *Aetobarbakinoides brasiliensis*. The latter species exhibits the same relationship between  $TL$  and age to that of *Aetosauroides scagliai* but the estimated body mass depicted a lower value than expected compared to an *Aetosauroides scagliai* of the same age. As was previously mentioned, it is necessary to include more specimens of *Aetobarbakinoides brasiliensis* to corroborate this observation.

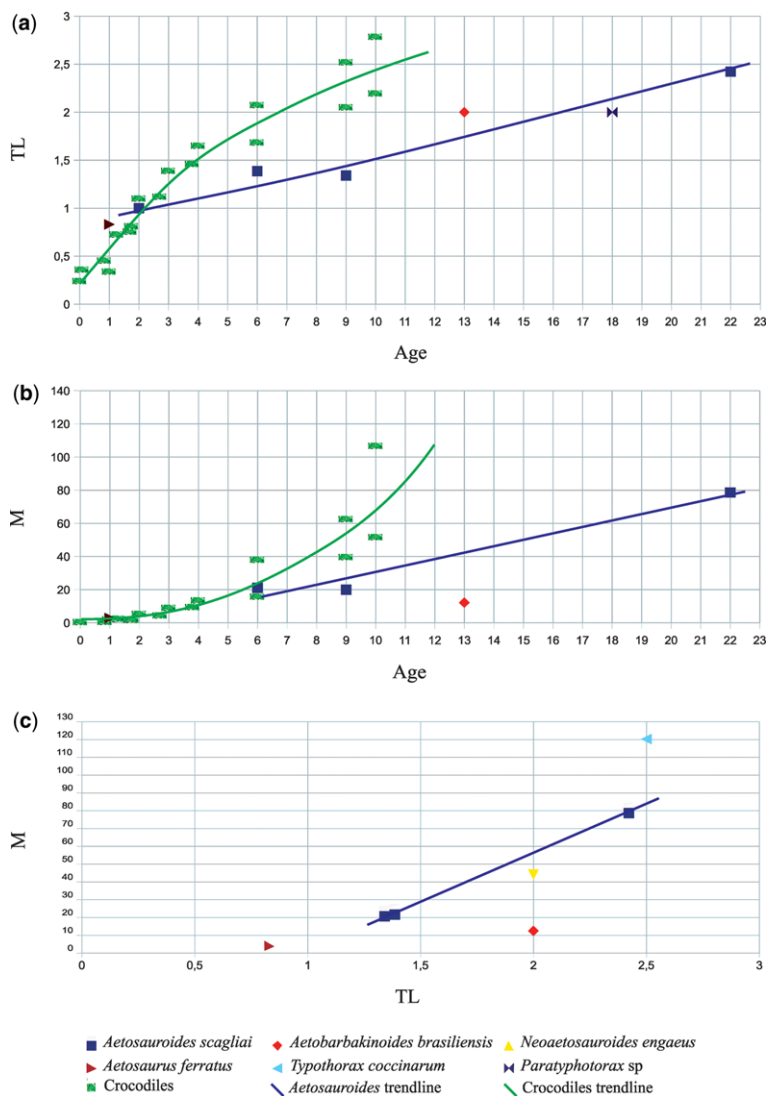
We can not compare *Aetosauroides scagliai*'s trend line with that of *Aetosaurus ferratus* because the data of the latter are located far from those of *Aetosauroides scagliai* (Fig. 5b).

### M–TL

Based on our results, we plotted the relationship between body mass and total body length for aetosaurs (Fig. 5c). Although we could not directly compare the aetosaur curve with that obtained for crocodylians (but both curves would be similar in shape), two individuals of the same size but lying on different curves can represent individuals of very different age (Fig. 5a).

We observed that the information available for *Neoaetosauroides engaeus* matches the curve for

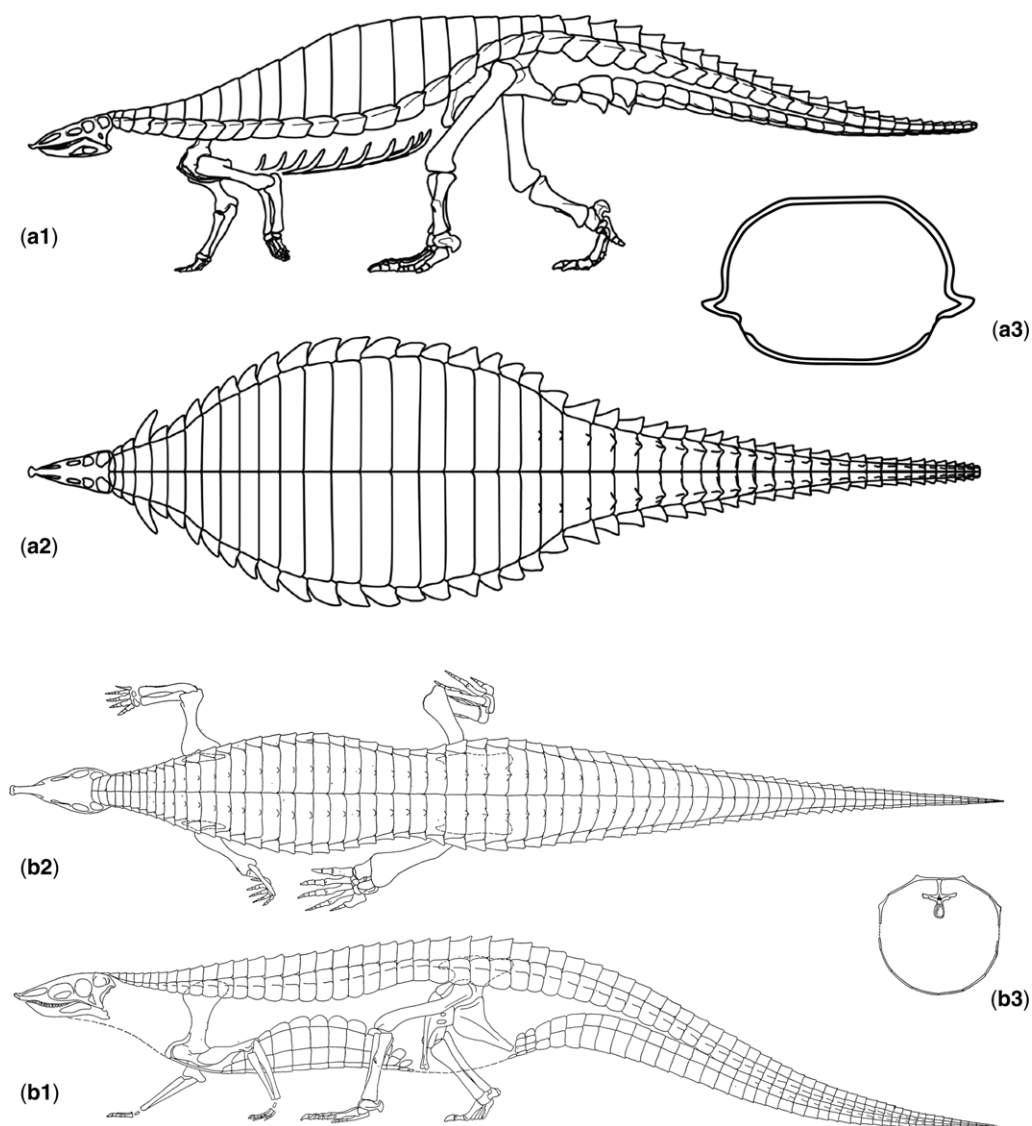




**Fig. 5.** Growth curves. The blue line indicates the relationship between body length, body mass and age in *Aetosauroides scagliai*, and the green line indicates the same relationship in crocodylians. (a) Relationship between corporal total length (TL) in metres and age in years. (b) Relationship between body mass ( $M$ ) in kg and age in years. Note that *Aetobarbakinoides brasiliensis* has a lower value of body mass than expected in an *A. scagliai* individual of the same age. (c) Relationship between  $M$  in kg and TL in metres. *Aetobarbakinoides brasiliensis* possesses a lower body mass value than expected for its total body length and *Typothorax coccinarum* is heavier than expected.

*Aetosauroides scagliai*. However, it is not the case for *Aetobarbakinoides brasiliensis* and *Typothorax coccinarum*. In the latter taxon, the estimated  $M$  is larger than that obtained for *Aetosauroides scagliai* at the same TL. By contrast, *Aetobarbakinoides brasiliensis* possesses a lower  $M$  value than was expected for *Aetosauroides scagliai* for an individual of the same age and TL. The deviations observed in *Aetobarbakinoides brasiliensis* and *Typothorax*

*coccinarum* would be the result of a different body shape. *Typothorax coccinarum* was a more robust animal than the other aetosaurs analysed, with an elliptical body in dorsal view and elliptical trunk cross-section. By contrast, *Aetosauroides scagliai* has a subrectangular, narrow body in dorsal view and a subcircular trunk cross-section. Accordingly, we can assume a proportionally greater body volume for *Typothorax coccinarum* than for other



**Fig. 6.** Schematic comparison of corporal morphologies between *Typothorax coccinarum* (a) and example of an aetosaur with a narrow body (b); in lateral view (–1), dorsal view (–2) and thoracic cross-section (–3). (Modified from Walker 1961 and Heckert *et al.* 2010.)

aetosaurs (Fig. 6). By contrast, *Aetobarbakinoides brasiliensis* was described as a gracile aetosaur (Desojo *et al.* 2012), a hypothesis that is here bolstered by a lower body mass than proportionally expected in other aetosaurs (Fig. 5b, c). As stated above, the data for *Aetosaurus ferratus* are not comparable with the trend line of *Aetosauroides scagliai* because *Aetosaurus ferratus* is away from the extrapolation zone.

## Conclusions

The distinct differentiation between the estimated body mass for *Aetobarbakinoides brasiliensis* and *Typothorax coccinarum* and that expected for an *Aetosauroides scagliai* individual of the same age and total length is evidence of a clear division into at least two aetosaurs morphotypes (i.e. narrow or wider forms). *Aetosaurus ferratus*, *Aetosauroides*

*scagliai* and *Neoaetosauroides engaeus* would share similar growth curves because they have the same body morphotype. By contrast, different body shapes (wider in *Typosuchus coccinarum* and slender in *Aetobarkinoides brasiliensis*) result in a deviation from the *Aetosauroides scagliai* growth curve. Finally, it is possible that all aetosaurs had rather similar growth rates when body length was employed as body size proxy, independent of the size of the animal. This aspect is purely speculative and needs to be supported by a larger sample to arrive at a more robust conclusion. The present work represents the first approximation of aetosaur growth dynamics. In the future, new data will allow us to construct a more precise growth curve that will contribute to the understanding of the growth model in this group of archosaurs.

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## Appendix

### *Institutional abbreviations*

CPE, Collection Municipal, São Pedro do Sul, RGS, Brazil; MPC, Museo de Ciências e Tecnologia, Porto Alegre, Brazil; MLP, Museo de la Plata, Buenos Aires, Argentina; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UFRGS, Universidad Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFSM, Universidad Federal de Santa María, Rio Grande do Sul, Brazil.

## References

- ANDERSON, J. F., HALL-MARTIN, A. & RUSSELL, D. A. 1985. Long-bone circumference and weight in mammals birds and dinosaurs. *Journal of Zoology*, **207**, 52–61.
- BLOB, R. W. 2000. Interspecific scaling of the hindlimb skeleton in lizards, crocodylians, felids and canids: does limb bone shape correlate with limb posture? *Journal of Zoology*, **250**, 507–531.
- BRUSATTE, S. L., BENTON, M. J., DESOJO, J. B. & LANGER, M. C. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology*, **8**, 3–47.
- CAMPIONE, N. E. & EVANS, D. C. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology*, **10**, 60.
- CERDA, I. A. & DESOJO, J. B. 2011. Dermal armour histology of Aetosaurinae aetosaurs (archosauria: Pseudosuchia) from the Upper Triassic for Argentina and Brazil. *Lethaia*, **44**, 417–428, <http://dx.doi.org/10.1111/j.1502-3931.2010.00252.x>
- CHIAPPE, L. M., CORIA, R. A., DINGUS, L., JACKSON, F., CHINSAMY, A. & FOX, M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature*, **396**, 258–261.
- CHIMSAMY, A. & RAATH, M. A. 1992. Preparation of fossil bone for histological examination. *Paleontologia Africana*, **29**, 39–44.
- CUBO, J., LE ROY, N., MARTINEZ-MAZA, C. & MONTES, L. 2012. Paleohistological estimation of bone growth rate in extinct archosaurs. *Paleobiology*, **38**, 335–349.
- DE RICQLÈS, A. J., PADIAN, K. & HORNER, J. R. 2003. On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. *Annales de Paléontologie*, **89**, 67–101.
- DE RICQLÈS, A., PADIAN, K., KNOLL, F. & HORNER, J. R. 2008. On the origin of high growth rates in archosaurs and their ancient relatives: complementary histological studies on Triassic archosauriforms and the problem of a 'phylogenetic signal' in bone histology. *Annales de Paléontologie*, **94**, 57–76.
- DESOJO, J. B. & BÁEZ, A. M. 2005. El esqueleto postcraniano de *Neoaetosauroides* (Archosauria: Aetosauria) del Triásico Superior del centro-oeste de Argentina. *Ameghiniana*, **42**, 115–126.
- DESOJO, J. B. & EZCURRA, M. D. 2011. A reappraisal of the taxonomic status of *Aetosauroides* (Archosauria, Aetosauria) specimens from the Late Triassic of South America and their proposed synonymy with *Stagonolepis*. *Journal of Vertebrate Paleontology*, **31**, 596–609.
- DESOJO, J. B., EZCURRA, M. D. & KISCHLAT, E. E. 2012. A new aetosaur genus (Archosauria: Pseudosuchia) from the early Late Triassic of southern Brazil. *Zootaxa*, **33**, 1–33.
- DESOJO, J. B., HECKERT, A. B., MARTZ, J. W., PARKER, W. G., SCHOCH, R. R., SMALL, B. J. & SULEJ, T. In press. Aetosauria: a clade of armoured pseudosuchians from the Late Triassic continental beds. In: NESBITT, S. J., DESOJO, J. B. & IRMIS, R. B. (eds) *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. Geological Society, London, Special Publications, **379**, <http://dx.doi.org/10.1144/SP379.17>
- DODSON, P. 1975. Functional and ecological significance of relative growth in *Alligator*. *Journal of Zoology*, **175**, 315–355.
- ERICKSON, G. M. 2005. Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology and Evolution*, **20**, 677–684.
- ERICKSON, G. M. & BROCHU, C. M. 1999. How the 'terror crocodile' grew so big. *Nature*, **398**, 205–206.
- ERICKSON, G. M., DE RICQLÈS, A., DE BUFFRÉNIL, V., MOLNAR, R. E. & BAYLESS, M. K. 2003. Vermiform bones and the evolution of gigantism in Megalania – how a reptilian fox became a lion. *Journal of Vertebrate Paleontology*, **23**, 966–970.
- ERICKSON, G. M., MAKOVICKY, P. J., CURRIE, P. J., NORELL, M. A., YERBY, S. A. & BROCHU, C. A.

2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature*, **430**, 772–775.
- ERICKSON, G. M., CURRIE, P. J., INOUE, B. D. & WINN, A. A. 2006. Tyrannosaur life tables – An example of non-avian dinosaur population biology. *Science*, **313**, 213–217.
- ERICKSON, G. M., MAKOVICKY, P. J., INOUE, B. D., ZHUO, C. & GAO, K. 2009. A life table for *Psittacosaurus lujiatunensis*: initial insights into ornithischian dinosaur population biology. *The Anatomical Record*, **292**, 1514–1521.
- FARLOW, J. O., HURLBURT, G. R., ELSEY, R. M., BRITTON, A. R. C. & LANGSTON, W. 2005. Femoral dimension and body size of *Alligator mississippiensis*: estimating the size of extinct mesoeucrocodylians. *Journal of Vertebrate Paleontology*, **25**, 354–369.
- GAMES, I. 1990. Growth curves for the Nile crocodile as estimated by skeletochronology. In: *Crocodiles. Proceedings of the 10th Working Meeting of the Crocodile Specialist Group, IUCN, Volume 1*. The World Conservation Union Gland, Switzerland, 111–121.
- GAUTHIER, J. A. 1986. *Saurischian Monophyly and the Origin of Birds*. California Academy of Sciences, Memoirs, **8**, 1–55.
- GOWER, D. J. & SENNIKOV, A. G. 1996. Morphology and phylogenetic informativeness of early archosaur braincases. *Palaeontology*, **39**, 883–906.
- HECKERT, A. B. & LUCAS, S. G. 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). *Zentralblatt für Geologie und Paläontologie*, Teil **I**, Heft, 11–12, 1539–1587.
- HECKERT, A. B., LUCAS, S. G., RINEHA, R. T., CELESKEY, M. D., SPIELMANN, J. A. & HUNT, A. P. 2010. Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Reueltian: early-mid Norian), eastern New Mexico, USA. *Journal of Vertebrate Paleontology*, **30**, 619–642.
- HILL, R. V. & LUCAS, S. G. 2006. New data on the anatomy and relationships of the Paleocene crocodylian *Akanthosuchus langstoni*. *Acta Palaeontologica Polonica*, **51**, 455–464.
- HUCHZERMAYER, F. W. 2003. *Crocodiles: Biology, Husbandry and Diseases*. CABI Publishing, London.
- HUTTON, J. M. 1986. Age determination of living Nile crocodiles from the cortical stratification of bone. *Copeia*, **1986**, 332–341.
- NESBITT, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History*, **302**, 1–84.
- NESBITT, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**, 1–292.
- PARKER, W. G. 2007. Reassessment of the Aetosaur '*Desmatosuchus*' *chamaensis* with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). *Journal of Systematic Palaeontology*, **5**, 41–68.
- PARKER, W. G. 2008. Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. *PaleoBios*, **28**, 1–40.
- PARKER, W. G., STOCKER, M. R. & IRMIS, R. R. 2008. A new desmatosuchine aetosaur (Archosauria: Suchia) from the Upper Triassic Tecovas Formation (Dockum Group) of Texas. *Journal of Vertebrate Paleontology*, **28**, 692–701.
- SCHOCH, R. R. 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie*, **246**, 1–35.
- SCHEYER, T. M., DESOJO, J. B. & CERDA, I. A. 2011. Comparative palaeohistology of Triassic rauisuchian and aetosaurian osteoderms (Archosauria: Pseudosuchia). 71 Annual Meeting of the Society of Vertebrate Paleontology, Las Vegas, USA. *Journal of Vertebrate Paleontology*, **31**, 49A.
- TABORDA, J. R. A. 2011. *Dinamica del crecimiento de Aetosauroides scagliai Casamiquela, 1960 (Archosauria: Aetosauria) del Triásico Tardío de América del Sur*. Master thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.
- TUCKER, A. D. 1997. Validation of skeletochronology to determine age of freshwater crocodiles (*Crocodylus johnstoni*). *Marine and Freshwater Research*, **48**, 343–351.
- VICKARYOUS, M. K. & HALL, B. K. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. *Journal of Morphology*, **269**, 398–422.
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London. Series B*, **244**, 103–204.
- WOODWARD, A. R. & MOORE, C. T. 1992. *Alligator Age Determination*. Florida Game and Fresh Water Fish Commission Bureau of Wildlife Research, Final Report, **7563**.