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LAMINAE TERMINOLOGY APPLIED TO CERVICAL VERTEBRAE OF PELOMEDUSOIDES (TESTUDINES, PLEURODIRA)

Dias Campos de Andrade
Magister Scientiae

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Dissertation submitted to the Animal Biology Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

Adviser: Pedro S Ribeiro Romano

Co-adviser: Thiago Fiorillo Mariani

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Assent:

Dias Campos de Andrade
Author

Pedro Seyferth Ribeiro Romano
Adviser

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"To my beloved little dog, Pretinha. Your untimely loss leaves a void, but your memory will forever be a part of me. R.I.P."

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To my parents, who have always tried to give me the best opportunities despite the hardships of life.

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"*Life is an open chemical system that increases the entropy of its environment to minimize its own entropy production and maintain a state far from equilibrium while sustaining the capacity for self-replication.*" (Erwin Schrodinger)

ABSTRACT

ANDRADE, Dias Campos de, M.Sc., Universidade Federal de Viçosa, September, 2024. **Laminae terminology applied to cervical vertebrae of Pelomedusoides (Testudines, Pleurodira)**. Adviser: Pedro Seyferth Ribeiro Romano. Co-adviser: Thiago Fiorillo Mariani.

The nomenclatural basis for identifying anatomical components of the cervical vertebrae in turtles is still non-standardized and incomplete. With that in mind, we propose an adaptation of laminae in the cervical vertebrae of Pelomedusoides derived from the well-established nomenclature used for sauropod dinosaurs. This approach is a landmark-based serial analysis to examine the appearance of the laminae along the neck, i.e., identifying their presence or absence and the changes in length, height, width, and orientation. We established the anatomical demarcations using traceable landmarks and identified twelve types of laminae: four of which are Apophyseal laminae, linking the transverse apophyses to the zygapophyses and centrum; Two Spinal laminae continuum to the prezygapophyses articulation fossae and the postzygapophyses articulations; Two Zygapophyseal laminae linking to the centrum; and four Hypapophyseal laminae that link the Cranial and Caudal hypapophysis together or to the vertebral centra. Applying such precise topological terminology improves the potential phylogenetic assessments of turtle interrelationship and morphofunctional adaptations of living and extinct taxa.

Keywords: comparative anatomy; neck; osteology; turtle.

RESUMO

ANDRADE, Dias Campos de, M.Sc., Universidade Federal de Viçosa, setembro de 2024. **Terminologia laminar aplicada à vértebras cervicais de Pelomedusoides (Testudines, Pleurodira)**. Orientador: Pedro Seyferth Ribeiro Romano. Coorientador: Thiago Fiorillo Mariani.

A base nomenclatural para identificar componentes anatômicos das vértebras cervicais em tartarugas ainda é despadronizada e incompleta. Com isso em mente, nós adaptamos a bem estabelecida nomenclatura laminar dos Saurópodes nas vértebras cervicais de Pelomedusoides. Esta abordagem é uma análise seriada baseada em marcos para examinar a aparência das lâminas ao longo do pescoço, ou seja, identificando sua presença ou ausência e as mudanças no comprimento, altura, largura e orientação. Estabelecemos demarcações anatômicas usando marcos rastreáveis e identificamos doze tipos de lâminas: quatro das quais são lâminas apofiseais, ligando as apófises transversas às zigapófises e ao centro vertebral; duas lâminas espinais que se estendem até as fossas de articulação da pré-zigapófise e às articulações das pós-zigapófises; duas lâminas zigapofiseais ligando ao centro vertebral; e quatro lâminas hipapofiseais que ligam a hipapófise cranial e caudal entre si ou ao centro vertebral. A aplicação de tal terminologia topológica e menos arbitrária é uma base para avaliações filogenéticas das relações entre tartarugas e as adaptações morfofuncionais de táxons vivos e extintos.

Palavras-chave: anatomia comparada; osteologia; pescoço; tartaruga.

SUMMARY

INTRODUCTION

Testudines comprise sea turtles, freshwater turtles, and tortoises. It is highly diversified, consisting of 13 living families and approximately 300 species distributed across all continents except Antarctica (Turtle Taxonomic Group, 2017). Two major living groups are recognized: Cryptodira and Pleurodira (e.g., Gaffney, 1975; Gaffney, 1988; Turtle Taxonomic Group, 2017; Joyce et al., 2021). The former group includes species of turtles that retract their necks vertically into their shells between the shoulder girdles, while in the latter, retraction occurs horizontally beneath the anterior margin of the carapace (e.g., Williams, 1950; Gaffney, 2006; Werneburg et al., 2014a,b, 2015). Two extant clades, Cheloides and Pelomedusoides, are recognized within Pleurodira (Joyce et al., 2021), which can be distinguished, among other features, by the articular formula of the cervical vertebrae (CV). Cheloides has the fifth and eighth CV biconvex, while Pelomedusoides has the second CV biconvex (e.g., Williams, 1950; Gaffney et al., 2006; Joyce, 2007). Therefore, the vertebrae morphology is crucial for characterizing the two groups of Pleurodira.

At the onset of the group's evolution, the neck of turtles became increasingly specialized due to the development of the shell (Werneburg et al., 2014a,b; Anquetin et al., 2017; Lyson & Bever, 2020). Consequently, it is one of the body's most mobile and specialized parts (e.g., Williams, 1950; Aerts et al., 2001; Anquetin et al., 2017). The neck is generally associated with feeding habits (e.g., van Damme & Aerts, 1997; Aerts et al., 2001; Lemell et al., 2002; Herrel et al., 2008; Anquetin et al., 2017; Werneburg et al., 2015), and it also functions as a defensive structure, as individuals retract it when threatened (e.g., Williams, 1950). In addition to the neck's relationship with feeding habits, there are taxonomic differences in their cervical, a taxonomic value that has been relatively underexplored (Williams, 1950; Mariani, 2016;), generally not being the principal aim of the studies (e.g., de Broin, 2007; Bona & de la Fuente, 2005; Gaffney et al., 2006, 2011).

Part of the difficulty in acquiring vertebral anatomical data, whether for taxonomic or morphofunctional purposes, lies in the terminology (Romer, 1956) used to describe the basic structures of turtle vertebrae. Romer terminology is very useful when tracking the general aspects of vertebrae in reptiles, but it neglects some specific morphologies inside inclusive taxa. Also, the same structure is commonly described with different names depending on the researcher. The cranially positioned hypapophysis is named such as ventral keel (Williams, 1950; Hoffstetter & Gasc, 1969; Gaffney, 1990), ventral crest (de Broin, 2007; Lapparent de Broin & Prasad, 2020), or ventral spine (Hoffstetter & Gasc, 1969; de Broin, 2007). The caudally positioned hypapophyses are mentioned as posteroventral tubercles, posterior tubercles, and sometimes only tubercles (de Broin, 2007; Lapparent de Broin & Prasad, 2020); posterolateral keels (Cadena, 2015); and in Cryptodires as ventrocaudal projections broadly referred to as knobs (Jasinski, 2018). Additionally, they are not referred to as apophysis, as hypapophyses suggests, with only Werneburg (2015a) mentioning the cranial hypapophysis as a "hypophyseal process."

The first step to acquiring data is to delimit categories that fit with the object of study, and the present nomenclature either overlooked or poorly describes the continuities between the basic components of CV and the angular shape created by the continuum of links. For instance, the transverse Apophyses has up to four continuities between them and other structures, but the terms used to categorize their morphology are too broad as "wing-shaped" or "broad-based" (e.g., Lapparent de Broin et al., 2007; de Broin & Prasad, 2020) not reflecting the full range of possible morphologies. The continuity of the transverse apophyses to other structures was only mentioned as "borders" (Lapparent de Broin et al., 2007). Nonetheless, as warned by T. Mariani (pers. comm.), we have discussed the possibility of these continuities being laminae and confirmed with B. Navarro (pers. comm.) that the nomenclatural system for Sauropods (Janensh, 1929) is compatible with these continuities and angular shapes.

Janensch (1929), in sauropods, created a landmark-based criterion to deal with the continuities between structures, which is precise and repeatable. This Laminae terminology has been used to do phylogenetic research among fossil groups, saurischian dinosaurs primarily, but also other groups inside crown Diapsida (e.g., Rodolfo A Coria, 1998; Martín D. Ezcurra et al., 2014; Martín D. Ezcurra, 2016). It was also applied to Squamata, a highly diverse extant taxon (Tschopp, 2016). As Testudines are included in crown Diapsida, the present work intends to adapt the laminae nomenclature to provide detailed descriptions to solidify a basis for osteological comparisons of the neck, starting with Pelomedusoides.

Therefore, to fulfill the necessity of fully characterizing most of the aspects in the basic structures of the CV in Testudines, it is necessary to establish a nomenclatural terminology between structures that adds enrichment of detail to the descriptions. Accordingly, in the herein-studied taxon, Pelomedusoides, I propose the establishment of a laminae nomenclature adapted from the vertebrae of sauropods and other saurischians (Janensch, 1929; Wilson, 1999). For these reasons, the objective is to identify, describe, and compare the cervical laminae of each family of Pelomedusoides to track the differences between vertebrae of the same neck and between its within lineages. It was necessary to adapt some basic structures' names to fit the terminology to reach this purpose.

MATERIAL & METHODS

The present material accounts for all the great groups in Pelomedusoides: Araripemydidae with *Araripemys barretoi* (AMNH22550; AMNH 22556; AMNH 24453; AMNH 24454; MNRJ6637-V; MNRJ6949); Bothremydidae with *Cearachelys placidoi* (BSPG1976-160); Euraxemydidae with *Euraxemys essweini* (FR4922); Pelomedusidae with *Pelomedusa subrufa* (USNM40248; USNM63099; USNM222469), *Pelusios chapini* (AMNH10065), *Pelusios gabonensis* (AMNH10053), *Pelusios sinuatus* (USNM42144), and *Pelusius subniger* (AMNH71188; USNM220896); and Podocnemididae with *Podocnemis expansa* (AMNH46174; AMNH6597; AMNH46250), *Podocnemis unifilis* (INPA10020; INPA10021; MZSP2708), *Podocnemis* sextuberculata (INPA5402; INPA8936), *Podocnemis erythrocephala* (INPA10261; INPA10266; INPA12413), *Erymnochelys madagascariensis* (AMNH63579), *Peltocephalus dumerilianus* (INPA21940; INPA22887; INPA25560). Specimen data from the AMNH, MNRJ, FR, and USNM were acquired by photography, and those from INPA and MZUSP were taken in hand.

QUALITATIVE DESCRIPTIONS

Osborn (1899) coined the term laminae to describe the ridges that, according to him, are built to counteract the stress applied in vertebrae, and his nomenclature takes into account only the planar orientation. Janensch (1929) maintains the first described function of the laminae, briefly adding the specificity of weight reduction. Also, improve the nomenclature by adding the landmarks that they connect to the name of the laminae to make it precise and repeatable. Over time, discussions about the formation of laminae emerge with a dichotomy: (1) Does the laminae emerge by the stress forces applied by the muscles or (2) by the formation of soft tissue as pneumatic diverticula? For instance, Bonaparte (1999) is adept at the first approach, while some are at the second (e.g., Britt, 1997; Wilson, 1999; Wedel, 2003a, 2003b; Salgado, 2006). Despite this difference, other saurischians dinosaurs that do not contain such adaptations as pneumatic diverticula are treated as having laminae, so it is clear that laminae can emerge by the action of muscle forces and the presence of diverticula influences their enormous development. Unlike Sauropods and other saurischians dinosaurs, turtles are tremendously small and do not present air sacs, so the present study aimed only to apply the laminae nomenclature as a way to characterize the angular shape of the vertebrae, consequently be a reference for muscular attachment and consider their formation only by the stress applied by the muscles on the bone surfaces. Therefore, in the present study, laminae have nothing to do with diverticula or gravity force resistance.

Following Wilson’s nomenclature, every lamina name has two landmarks, and the preferential landmark is always the second to appear in the name. The sequence of arbitrary preferential landmarks is Transversal Apophyses, Prezygapophyses, Postzygapophyses, Neural spine, Hypapophyses, and Centrum, with the first being the most preferential (Table 1). The serial description of the cervical laminae was made in two ways: (1) Tracking the presence and absence through the series (Table S2-5); (2) Tracking the changes of the present ones along the neck, considering three principal aspects of height, width, and length (Fig.1) and taking into account the changes in anatomical landmarks positions. After the descriptions of the laminae, comparisons were made laminae by laminae to elucidate the morphological range of differences in each family within Pelomedusoides. The neck of only one specimen of each family was described, but all specimens studied were analyzed for the presence and absence of the laminae.

Table 1: Each Laminae with its abbreviation and morphological landmarks

LAMINAE	Abbreviation	LANDMARK 1	LANDMARK 2
Cranio Centroapophyseal	CRCAL	Tranverse Apophysis	Most dorsolateral part of centrum cranial articulation
Caudo Centroapophyseal	CACAL	Tranverse Apophysis	Most dorsolateral part of centrum caudal articulation
Prezygapophyseal	PRAL	Tranverse Apophysis	Prezygapophysis
Postzigapophyseal	POAL	Tranverse Apophysis	Postzigapophysis
Prespinal	PRSL	Neural Spine base	Neural Spine summit
Spinopostzygapophyseal	SPOL	Neural Spine sumit	Postzygapophysis
Centropostzygapophyseal	CPOL	Postzygapophysis	Most dorsolateral part of centrum caudal articulation
Centroprezygapophyseal	CPRL	Prezygapophysis	Most dorsolateral part of centrum cranial articulation
Cranio Hypapophyseal	CRHL	Cranial Hypapophysis	Most ventromedial part of centrum cranial articulation
Caudo Hypapophyseal	CAHL	Cranial Hypapophysis	Most ventromedial part of centrum caudal articulation; Medial portion of the centrum
Cranio Posthypapophyseal	CRPHL	Caudal Hypapophysis	The medial portion of the centrum; The medial portion of the CAHL
Caudo Posthypapophyseal	CAPHL	Caudal Hypapophysis	Most ventromedial part of centrum caudal articulation

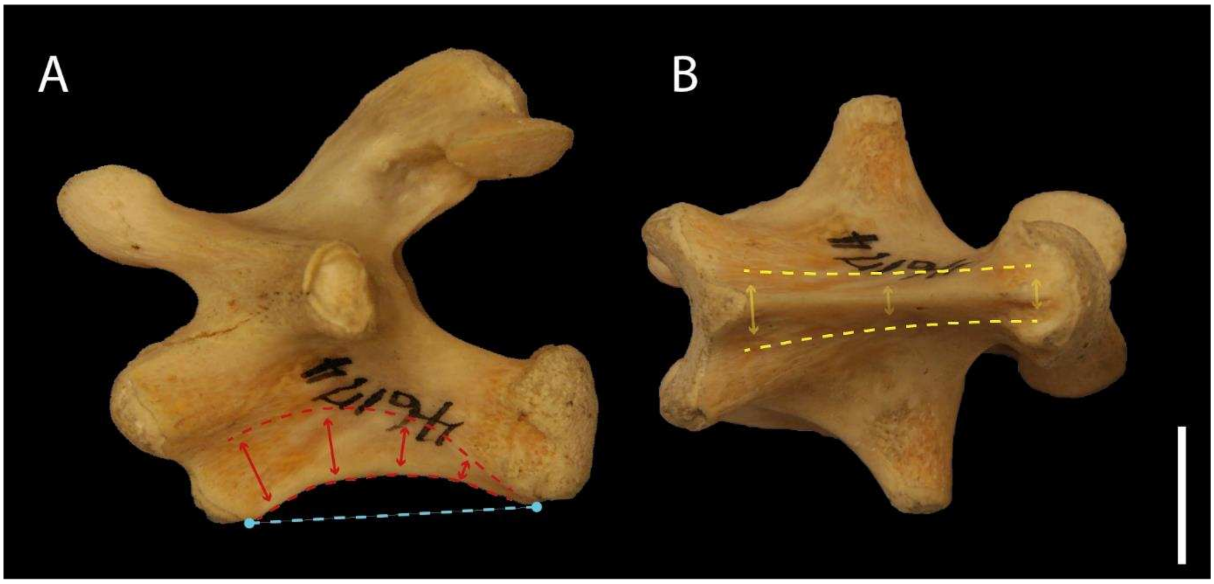

Figure 1: Three main descriptive parameters: Length in blue, height in red, and width in yellow. Seventh cervical of *Podocnemys expansa* (AMNH46174) in lateral view (A) ventral view (B).

TERMINOLOGY AND CHANGES

The anatomical orientation followed Smith & Dodson (2003), and the terminology of primary vertebrae components followed Romer (1956), which was applied in previous studies that described turtle cervical vertebrae (e.g. Williams, 1950; Hoffstetter & Gasc, 1969; Gaffney, 1990; de Broin, 2007; Sereno & ElShafie, 2013; Jasinski, 2018; Lapparent de Broin & Prasad, 2020). Nomenclatural adaptations in some primary vertebral components were necessary to define these structures better and remove ambiguities and generalizations that could hide some features needed to standardize the Laminae nomenclature.

The transversal process is a general and ambiguous term because it is given to any process that is transversal to the centrum and neural arch (Kardong, 2017). The term “apophysis,” coined by Owen, is used to refer to the different processes found in a vertebra (Owen, 1860) without the intention of being a specific term, in the present study, was preferred over “process,” as other researchers already have used for Pleurodira (Antunes & de Broin, 1998; de Broin, 2007; Lapparent de Broin & Prasad, 2020).

In Archosauria, generally, two transversal apophyses are recognized in the cervical region, the diapophyses and parapophyses, the first articulating with the tuberculum (dorsal head) and the second with the capitulum (ventral head) of the ribs (Romer, 1956; Hoffstetter & Gasc, 1969), and both can be named with certainty when the cervical ribs are present. In Lepidosauria, the cervical parapophysis and diapophysis of the same side can be fused, and the name of the resulting apophyses is synapophysis (Romer, 1956; Hoffstetter & Gasc, 1969). Within Sauropoda, in which the present approach was developed, and Crocodylia, an outgroup of present work, it is easy to state the nomenclature of these structures because these animals have cervical ribs and the diapophysis and parapophysis are well separated, with the first originating from the neural arch and the second on the intercentrum (Romer, 1956; Hoffstetter & Gasc, 1969). The same could be said for some fossil Testudinata (Gaffney, 1985, 1990). However, in Pelomedusoides, the so-called transverse process has portions of the neural arch and the centrum divided by the neurocentral suture (Pers. obs.), added to the absence of the cervical ribs, I could not assume the same terminology used for either Archosauria or Lepidosauria would apply in the herein-studied taxa without further investigation.

The term hypapophysis refers to an apophysis that emerges from the ventral part of the vertebrae and is treated as a modified intercentrum (Romer, 1956; Hoffstetter & Gasc, 1969), although it is ambiguous given that outgrowths of the centrum have been treated as hypapophysis too (Hoffstetter & Gasc, 1969). Within Crocodilia, this apophysis is always cranially positioned, which is conspicuous in the trunk region (Hoffstetter & Gasc, 1969). Within Lepidosauria, Rhynchocephalia the intercentra appear as intercentral wedges in the cervical region, but only in Squamata is the hypapophysis well differentiated and could be cranially or caudally positioned, fused, or sutured to the centrum or even individualized between the centrum of adjacent vertebrae, see Hoffstetter & Gasc (1969) fig.46.

In Testudinata, several names have been used to refer to hypapophyses in cervical vertebrae. In the Cranial aspect of the centrum: Ventral keel (e.g., Williams, 1950; Hoffstetter & Gasc, 1969; Gaffney, 1990; Sterli et al., 2007; Sereno, 2012); ventral crest (de Broin, 2007; Lapparent de Broin & Prasad, 2020); and ventral spine (Hoffstetter & Gasc, 1969; de Broin, 2007). Only Werneburg (2014) mentioned it as a “hypophyseal process.” In the Caudal aspect: Posteroventral tubercles, posterior tubercles, sometimes only tubercles (de Broin, 2007; Lapparent de Broin & Prasad, 2020); posterolateral keels (Cadena, 2015); In Cryptodires, ventrocaudal projections or knobs (Jasinski, 2018). In the herein-studied group, these terms do not fit because there are changes in the position of these structures among taxa and even in the same cervical series that are not covered. First, the already cited terms for cranial hypapophysis encompass the caudal hypapophyses in some vertebrae. Second, the terms for caudal hypapophysis do not consider that they can be ventromedially or ventrally positioned, single or paired, and assume morphologies from low tubercles to conspicuous projected apophysis.

These two distinct structures, Transverse apophyses and Hypapophyses, together with their synonyms, are not standardized throughout the turtle literature. The cervical vertebrae of Pelomedusoides do not have cervical ribs, and their transverse apophyses were not tracked along their evolutionary path, so they can not be assumed as diapophyses, parapophyses, or synapophyses. Even if the transverse apophyses have portions of both neural arch and center, thinking of it as synapophyses is superficial because of the lack of study. For Hypapophyses, except for the hypophyseal process (Werneburg, 2015a), the other terms do not consider them apophyses. They could refer to more than one structure, ignoring the presence of laminae, consequently missing the full range of morphological differences. To avoid confusion related to these names' meanings and track all the variations among taxa, the preference is to (1) use the term transversal apophyses over diapophyses, parapophyses, or synapophyses and (2) use the term hypapophysis with the distinction of the Cranial and Caudal ones over keels, crests, and tubercles. These preferential terms and the distinction of laminae between them cover far more different morphologies that the older ones cannot (Fig. 2; Fig.3).

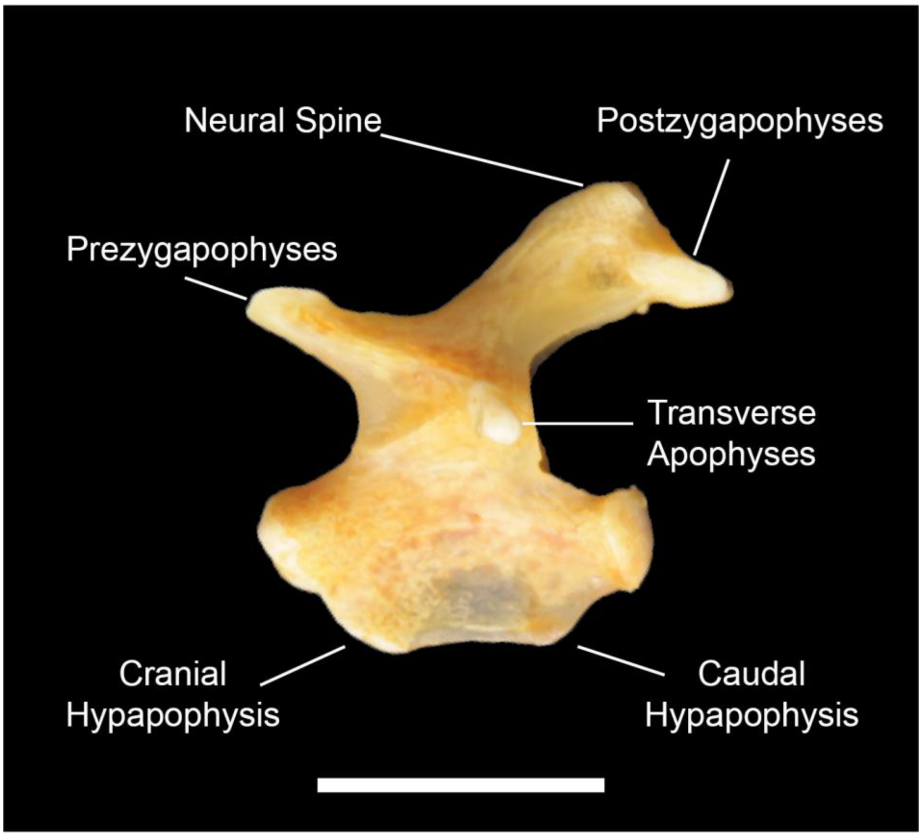

Figure 2: Basic anatomical components of the CV of Pelomedusoides. Eighth cervical of *Podocnemis sextuberculata* (INPA8936).

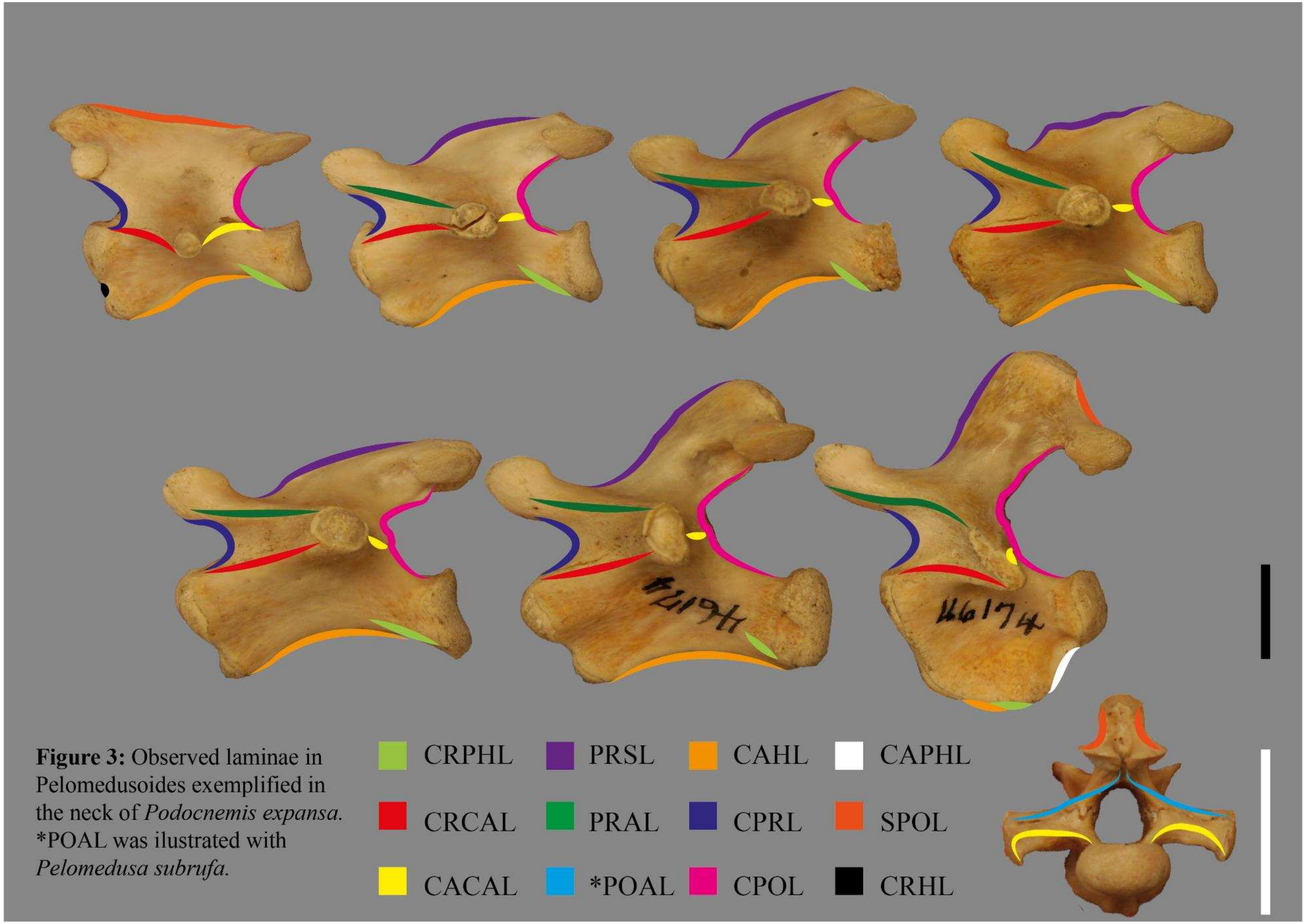

Figure 3: Observed laminae in Pelomedusoides exemplified in the neck of *Podocnemis expansa.* *POAL was ilustrated with *Pelomedusa subrufa.*

RESULTS

DESCRIPTION OF CERVICAL LAMINAE

Cranio-centroapophyseal Laminae (CRCAL)

The CRCAL connects the ventrocranial aspect of the transversal apophyses with the centrum in the most dorsolateral part of the cranial centrum articulation. Because the transverse apophyses originate in the middle length of the centrum and are caudolaterally projected, the CRCAL is always longer than the caudo-centroapophyseal laminae (CACAL) in Pelomedusoides

In *Podocnemis expansa* and *Cearachelys placidoi,* this lamina is thick and does not reach the second landmark (fig.1S; Fig. 21S). The CRCAL of *Araripemys barretoi* and *Euraxemys essweini* appear remarkably thin (fig.11S; fig.16S). In *Pelomedusa subrufa,* it is thin and gets lower along his path, not reaching the second landmark. In addition, in ventral view, the height of the CRCAL of *A. barretoi* and *E. essweini* are different from other Pelomedusoides because they are almost straight from one landmark to another (fig.12S; fig.17S), straighter in the first. Meanwhile, *P. expansa*, *P. subrufa,* and *C. placidoi* have a strong curvature, with the lowest height in the middle of the landmarks(fig.2S; fig.7S). Smother curvatures in *C. placidoi*.

In *A. barretoi,* the CRCAL almost overlaps with the prezygapophyseal laminae (PRAL), and only near the second landmark do the two laminae split into different paths. This feature is exclusive of this taxon.

Caudo-centroapophyseal Laminae (CACAL)

The CACAL connects the transversal apophyses with the most dorsolateral part of the centrum caudal articulation. Once the transversal apophysis is caudolaterally projected, the CACAL is shorter than CRCAL in all species studied. The CACALs of *E. essweini* and *C. placidoi* slowly change their length along the neck without a conspicuous pattern. In contrast, from C6 to C8 of *P. expansa,* the CACAL gets gradually shorter (fig.1S). In *P. subrufa,* the CACAL does not change serially; they are shorter in C4, C5, and C8 (fig. 6S). *A. barretoi* have the shortest CACALs due to having the most caudolaterally projected transversal apophysis, only in the C8 the CACAL is longer because the transverse apophyses origin is a little bit more cranial and are less caudolaterally projected (fig.16S).

In every taxon, the CACAL is low. In *P. expansa*, *A. barretoi*, and *C. placidoi* the CACALs are thick. The CACAL of the first increases in width towards the second landmark in every cervical. This occurs at a point that is not possible to distinguish the CACAL from the centropostzygapophyseal (CPOL) and postzygapophyseal laminae (POAL) in caudal view; however, it is possible to observe the continuity of these laminae to their respective landmarks (fig.5S). The CACALs are the thinnest in *E. essweini* and *P. subrufa* (fig.15S; fig.10S). There are two remarkable differences between the two species; first, *P.subrufa* is the only taxon whose POAL and CACAL can be distinguished from one another in all vertebras, at least on one side (fig.10S), which makes an exclusive fossa; second, in *E. essweini,* the CACALs are so low that from C5 to C7 they're almost absent, restricted to a smooth elevation right on the top of the neurocentral junction (fig.11S).

Prezygoapophyseal Laminae (PRAL)

The PRAL connects the apophyses with the ventrolateral margin of the prezygapophyses, and they appear only when the prezygapophyses are projected. Because the transverse apophyses are caudolaterally projected, they are longer than the CACAL and almost the same size as CRCAL. In *E. essweini* and *C. placidoi,* the PRAL does not show major differences in length throughout the series. However, in *P. expansa,* the PRAL becomes notably longer throughout the neck, while in *P. subrufa,* they are longer in C3, C7, and C8 without a serial pattern (fig.1S; fig.6S). In *A. barretoi,* the PRAL is shorter in the C8, and the other cervicals are generally the same size.

Whereas the PRAL is the thickest in *C. placidoi* and *P. expansa*, yet in the latter, these laminae become increasingly thicker, more near the first landmark (fig.1S), they are the thinnest in *A. barretoi* and *E. essweini*, followed by an intermediary width in *P. subrufa*. Again, in *A. barretoi,* they almost overlap with the CRCAL, at least from C6 to C8 (fig.16S; fig.19S). In dorsal view, *A. barretoi*, *C. placidoi*, and *E. essweini* have the highest and most straightened craniomedially projected PRAL, with the first being the most straight and the latter showing a smooth curvature (fig.18S; fig.13S). In contrast, *P. expansa* and *P. subrufa* have a more accentuated curvature and lower laminae. In *P. expansa,* they vary serially along the neck, increasingly higher until C5 (fig.3S), while *P. subrufa* does not show a clear pattern. The PRAL of *P. expansa* is higher than its own CRCAL from C4 to C8, whereas in *P. subrufa,* the PRALs are lower from C5 to C7 (fig.7S). In other taxa, the PRAL and CRCAL have similar heights along the neck.

In almost all taxa, the PRAL is straight dorsocranially projected in lateral view. In *A. barretoi* near the prezygapophyses, the projection becomes significantly dorsal, contrasting with the C8 of *P. expansa,* the PRAL significantly becomes dorsal near the transversal apophysis, consequently curved with the concavity downwards (fig.1S; 16S).

A conspicuous lateral expansion occurs in C7 and C8 of *Podocnemys expansa* near the prezygapophyses (fig.3S). The PRAL begins typically in the most craniolateral region of the transverse apophyses in dorsal view, but in the C6 and C7, this landmark is slightly caudally dislocated, which is more clearly observed in C7 (fig.3S).

Postzygoapophyseal Laminae (POAL)

The POAL connects the transverse apophyses with the postzygapophyses in its ventral or ventrolateralmost part (caudal view). Since one of the landmarks is the postzygapophyses, the POAL is longer than the other apophyseal laminae.

In *P. subrufa,* it occurs from C3 to C8, but in C6 and C7, on one side, the CACAL is higher and thicker than the POAL (fig. 10S). Only in *P. subrufa* does a fossa appear between the well-separated CACAL and POAL. In C7 and C8, remarkably, the POAL and CACAL interrupt the path of the centropostzygapophyseal laminae (CPOL) (fig.10S), which makes the fossae between the CACAL and POAL continuous to the inside of the neural arch, different to the others that the CPOL delimitates.

In the C5 to C7 of *E. essweini*, the POAL begins as the CACAL remarkably becomes very low (fig.11S). It's possible to see that between the POAL and the very low CACAL of *E. essweini*, a shallow fossa appears, but it is not conspicuously like in *P. subrufa*.

In *A.barretoi*, *C. placidoi,* and *P. expansa*, the POAL is not recognized due to the absence of or the fusion with the CACAL.

Prespinal Lamina (PRSL)

The PRSL links the summit of the neural spine to its base medially. This lamina only appears when the neural spine is more dorsally projected than the postzygapophyseal pedicel. The pedicel is dorsocaudally projected along the neck in all taxa, so when the neural spine gets more dorsally projected than the pedicel, principally in the back of the neck (C6 to C8), the PRSL gradually becomes more visible until C8 when it is conspicuous. The PRSL can be conspicuous without the gradual changes in the neural spine. In *P. expansa* and *P. subrufa,* the C5 has conspicuous PRSL; in *E. essweini* from C3 to C5; and in *C. placidoi* from C4 to C6. *A. barretoi* does not show significant changes in the projection of the pedicel and the neural spine even in the back of the neck (e.g. Meylan, 1996; Broin et al., 2007?), and so on the PRSL vary from a line to its absence.

The height of PRSL is generally the same between landmarks in most cervicals of herein studied taxa. However, the PRSL has a remarkable rise in the base of postzygapophyseal pedicel, next to the prezygapophyses, in C4, C5, and C6 of *C. placidoi* (fig.21S); in the C3 of *E. essweini* (fig.16S); in the C5, C7 and C8 of *P. subrufa*, but with less intensity in the last two (fig.6S); and in the C5 of *P. expansa* (fig.1S). This lamina is thin in *E. essweini* and *A. barretoi*, and thicker in *P. expansa*, *P. subrufa*, and *C. placidoi*. In *A. barretoi,* it appears to be low or absent in the analyzed specimens. In the lateral view, the PRSL is dorsocaudally projected, following the projection of the pedicel.

Remarkably, in C7 and C8 of *P. expansa*, this lamina is relatively thicker, as if the whole extension of the postzygapophyseal pedicel is lateromedially constricted (fig.3S). In addition, the PRSL of the C5 splits into two, with a shallow slit between the split. It is also observed in *E. essweini* but from C3 to C5 and in C8 but more separated.

The PRSL is absent in the C2 of *P. expansa* and *P. subrufa*. In the other taxa, it could not be addressed because the C2 was absent.

Spinopostzygapophyseal Laminae (SPOL)

The SPOL links the neural spine with the postzygapophyses. They are present only in C2, C7 and C8 of *P. expansa* and *P. subrufa* and in the C8 of *E. essweini* (fig.1S; fig.5S; fig.6S; fig.10S; fig.11S; fig.15S). The SPOL is absent in every other taxa.

The SPOL is conspicuous, thick, high, and craniodorsally projected in C2 in every taxon that has C2 in this study, unlike the C8 in which they are low and caudoventrally projected (fig.1S;fig.6S) in every taxon that possesses it. The presence of these laminae in C7 and C8 is related to the rise of the neural spine above the pedicel of postzygapophyses.

Centroprezygapophyseal Laminae (CPRL)

The CPRL links the ventral part of the prezygapophyses with the centrum in the most dorsolateral part of the cranial central articulation.

There are no significant changes in the length of CPRL along the cervical series in *A. barretoi* and *E. essweini* (fig. 16S; 11S). In *C. placidoi,* asserting some characteristics is difficult due to the fossil's preservation. The CPRL is thinner in *A. barretoi* and *E. essweini,* thicker in *P. subrufa*, and thicker in *C. placidoi* and *P. expansa* (fig. 6S, 21S, 1S). The laminae are higher in *E. essweini*, followed by *P. subrufa*, the lowest in *P. expansa* and *A. barretoi*. The CPRL elongates along the neck in *P. subrufa* and *P. expansa* due to the separation of the landmarks. *A. barretoi*, *E. essweini*, and *P. subrufa* own laminae ventromedially projected (fig. 19S, 14S, 9S), while in *P. expansa,* the CPRL has a ventral projection with a slight curvature (fig 4S).

Centropostzygapophyseal Laminae (CPOL)

The CPOL links the ventral part of postzygapophyses to the dorsolateralmost part of the caudal central articulation. In almost all taxa herein studied, the CPOL elongates through the series as the pedicel of the postzygapophyses is more dorsocaudally projected (fig. 1S, 6S, 11S, 16S, 21S). Evidently, these changes are more prominent in the back of the neck, with *P. expansa* and *P. subrufa* possessing the more intense elongation and *A. barretoi* the lesser.

In *E. essweini*, *A. barretoi,* and *P. subrufa,* the laminae are conspicuous, thinner, and higher in all cervicals. In *P. expansa* and *C. placidoi,* they are thick and low; in the midlength between their landmarks, they are even lower, almost vanishing (fig. 5S, 21S). The regions near the postzygapophyses are thinner and higher because of the pedicel's articulation fossae with the posterior vertebra's prezygapophyses.

In *P. subrufa*, they are high and thin from C3 to C6, but in C7 and C8, the CPOL is continuous with both POAL and CACAL, creating an exclusive fossa of this taxon. Still, the other cervicals are also continuous but are not interrupted by POAL and CACAL, showing a fossa that is not continuous to the visceral part of the neural arch, as in C7 and C8 (fig. 10S). In addition, in *P. expansa,* the CPOL is indistinguishable from the POAL and CACAL in all vertebrae but the C2, thus being fused (fig. 5S).

Cranio-hypapophyseal Lamina (CRHL)

The CRHL links the cranial aspect of the hypapophysis to the ventralmost part of the cranial central articulation. It is present only in C2 to C4 and frequently only in C2 (fig. 1S, 4S). The presence of CRHL is restricted to the *Pelusios* genera of Pelomedusidae and in all podocnemidid genera herein studied. These features depend on the cranial hypapophysis projection, so the more ventrally projected the latter, the more developed this lamina is. The height and width of CRHL do not change significantly among taxa.

Caudo-hypapophyseal Lamina (CAHL)

The CAHL links the hypapophysis to the caudal articulation of the centrum. However, the second landmark changes depending on specific characteristics. In *P. expansa*, they vanish near the midlength of the centrum from C2 to C6, but in C7, the lamina runs up to caudalmost part of the centrum medially while in the C8, by the ventralization of the caudal hypapophysis, it is continuous to the unique cranio-posthypapophyseal lamina (CRPHL) so the second landmark changes to most cranial portion of the caudal hypapophysis (fig. 2S). In *P. subrufa,* the CAHL links with the pair of CRPHL in almost every cervical vertebra but is discontinuous in the C7 and C8 (fig. 7S). In *E. essweini* and *A. barretoi*, the CAHL runs further caudally to 2/3 of the length of the centrum (fig. 12S, 17S). In C7 of *A. barretoi,* the CAHL runs between the two CRPHL, reaching the most ventromedial part of the caudal centrum articulation. In *C. placidoi*, these laminae are all continuous to the CRPHL.

In *A. barretoi*, *E. essweini,* and *C. placidoi,* they vary less along the cervicals in width, generally thinner and thickest in the latter (fig. 17S, 12S). *P. expansa* and *P. subrufa* vary along the neck and are thick. In the former, they are thinner in C7 and thicker in C8, while in the latter, because they are doubled cranially from C7 to C8, they become thinner (fig. 2S, 7S). The height of CAHL changes by the projection of the cranial hypapophyses in *P. expansa,* and *C. placidoi* is taller because the cranial hypapophyses are highly projected. In contrast, lower projected ones, such as *A. barretoi* and *E. essweini,* show lower laminae, while *P. subrufa* shows an intermediary state (fig. 1S, 21S, 16S, 11S, 6S). The CAHL runs caudodorsally, except in the C8 of *P. expansa*, because the CAHL links with the CRPHL being slightly ventrocaudal and is remarkably covered with an articular surface (fig. 1S).

Cranio-posthypapophyseal Laminae (CRPHL)

The CRPHL links the caudal hypapophyses to the mid-length of the centrum or is continuous to the CAHL. It is continuous in *C. placidoi* in every cervical, *P. subrufa* from C3 to C6 (fig. 7S), C8 of *P. expansa* (fig. 2S), and uncertainty in C8 of *E. essweini* due to the cervical fracture (fig. 12S). This continuity appears in two ways: (1) when the caudal hypapophyses are separated and lateral in the ventral part of the centrum, and in this case, this pair of laminae meet the CAHL, as in *P. subrufa*, *E. madagascariensis*, and *C. placidoi*; or (2) when the caudal hypapophysis is single and medial, so the CRPHL runs straight to the CAHL, as in C8 of *P. expansa*, *E. essweini* and C7 of *C. placidoi*. The CRPHL are not continuous to the CAHL in the C7 of *A. barretoi* (fig. 17S); the C7 and C8 of *P. subrufa*; the C3 and C4 of *E. essweini,* from C5 to C7 of *E. essweini* due to fractures are impossible to define*;* and from C2 to C7 of *P. expansa*.

The CRPHL are thick in *P. expansa*, *P. subrufa*, and *C. placidoi*, and thinner in *A. barretoi* and *E. essweini*. It is highest in *P. subrufa* and *C. placidoi,* but in the C8 of the podocnemidids, they are higher than any other. They do not show major changes in width and height along the series of all studied taxa.

Caudo-Posthypapophyseal Laminae (CAPHL)

The CAPHL emerges only in the C8 of the genus *Podocnemis* and connects the ventralmost part of the centrum to the caudalmost part of the extreme ventrally projected caudal hypapophysis. In *P. expansa,* (fig. 1S, 5S) it is conspicuous, short, thin, and relatively high despite its size. The only exception out of the *Podocnemis* genus is in the C8 of *Pelusios chapini*, but in a different way because in *P. chapini,* the caudal hypapophyses are two separated structures, and they are very brief, thick, and low.

SERIAL DESCRIPTION

Euraxemys essweini

Apophyseal laminae

Along the neck, the apophysis' origin is in the midlength of the centrum and is slightly caudolaterally projected, with no discrepant changes. However, they gradually become laterally projected and thicker, except in the C8, in which they are relatively thick and shorter. The prezygapophyses are projected dorsocranially; in the C3, C4, and C8, they are more cranially projected. The postzygapophyses are dorsocaudally projected. From C3 to C4, they become more dorsal, then remain the same until C6, with a second rise from C7 to C8. The centrum length increases until C7, and in C8 the centrum is shorter.

The CRCAL becomes longer with low intensity due to the apophysis's lateral projection and the centrum's elongation, except in the C8 due to a shorter centrum. The width remains the same, and the height decreases from C3 to C4 and increases from C5 to C7, with C6 being the highest.

Due to the projection of the prezygapophysis, the PRAL is slightly longer than the CRCAL. The width of the PRAL does not change; it becomes higher from C3 to C6 and then decreases until C8.

The CACAL is short and visible only in the C2 to C4. Although the origin of the apophysis is virtually centrally positioned in the centrum, the caudolateral projection makes these laminae shorter than their cranial counterparts. Along the series, they become lower when restricted to a sheet running upon the neurocentral junction, from C5 to C7, and the width does not change.

POAL are the longest apophyseal laminae due to the relative position of the postzygapophyses to the apophysis. They exist only from C4 to C8 and become slightly longer until C8. Even though the postzygapophyses of C7 are less caudally projected than C6, this increase in the dorsal projection and the lateralization of the apophysis make the POAL longer in C7 than in C6. The pedicel of the postzygapophyses in C8 is curved, which adds length to the lamina. The width is similar along the series, and the height increases until C6, then gradually lower from C7 to C8. The POAL are all higher where the articulation fossae of the pedicel of postzygapophyses appear.

Prezygapophyseal laminae

The CPRL does not show significant differences in length, width, and height despite slight changes in the prezygapophysis projection and elevation along the series. The CPRL is short because the prezygapophysis and the cranial central articulation are close. The thickness is slightly different along its path, being thinner closer to the centrum. Here the curvature of the laminae is related to the height, so deeper curvatures are lower laminae.

Postzygapophyseal laminae

The SPOL is present only in the C2 and C8. Because only the posteriormost portion is preserved in the C2, all aspects of the SPOL cannot be studied. In C8, they are thin, low, and short.

The CPOL, with minor changes, is shorter from C2 to C4 and longer from C6 to C8. In C4, they are longer than in C3 and C5, which are the same size. The width remains equal in all the series, and it is thinner next to the postzygapophyses, where the articular fossae of the pedicel for the prezygapophyses are located. The CPOL is slightly higher in C3, C6, and C7.

Hypapophyseal Laminae

The cranial hypapophysis is projected ventrocranially from C3 to C8, being more projected from C3 to C5 (it achieves its most projection in C5), and then from C6 to C7, it remains the same but decreases in C8. In turn, the caudal hypapophyses are tiny, discrete, and ventrolateral; they are more developed in C3, C5, and C7. The caudal hypapophyses ventromedially pair in C7 and in C8 a fused fully ventralized apophysis. In these two vertebrae, the caudal hypapophysis interferes with the shape of caudal central articulation, in caudal view the central articulation is expanded on the position of the caudal hypapophysis. Because caudal hypapophyses are more ventral in C8, being fused medially, the bottom expansion of the centrum articulation is a little sharper compared to the expansion of C7.

The cervicals of *E. essweini* do not have CRHL and CAPHL. Once both the cranial and caudal hypapophysis join with the cranial and caudal central articulation.

The CAHL of C3 and C4 run through two-thirds of the length of the centrum, but in the other cervicals, the ventral aspect is damaged, so it was impossible to address the length of the laminae with precision. It increases in height from C3 to C5, where it achieves the apex (at least in the cranial-most part), then it becomes slightly lower in C6 and C7 but still higher than C3 and C4, and finally decreases in C8. Its width is generally similar along the neck, but it appears thicker in the C4, at least in the cranial part.

The length of CRPHL is challenging to state because they are very low. In the C3, it is possible to state that they run to the midlength of the centrum but in the C7, they certainly do not, while in the remaining vertebrae, it does not reach the middle of the centrum. They are generally low, slightly higher in C3, C5, and C7. The C3 has thinner ones, and the others are the same width. In C8 the CRPHL and CAHL fuse continuously to each other.

Spinal Lamina

The neural spine lies down on the top of the neural arch pedicel, which bears the postzygapophyses in the same structure (Broin et al., 2007); however, the caudalmost part projects dorsocaudally in different degrees along the series: it is more dorsal from C3 to C5, decreases in C6, subsequently rises in C7, and remains the same height in the C8.

The PRSL is remarkably bifurcated from C3 to C5 and in C8. In C3, it runs to the caudomedial portion of the articular fossae of the prezygapophyses, becoming shorter until C5. Due to breakage, the length of the laminae of the remaining vertebrae cannot be addressed with certainty. It is thinner in C3 and C4, then it remains with the same width until C7 and becomes thicker in C8. The height differences are remarkable, with the C3 having the highest laminae, then decreasing until C6, and increasing until C8. In the C3, the PRSL arises dorsocranially with intensity in its cranialmost part and continues caudally. Despite becoming more dorsal after the first great rise, the PRSL lowers towards the postzygapophyses because the pedicel extends dorsocaudally and reduces the relative height of the lamina.

Araripemys barretoi

Apophyseal Laminae

The origin of the apophyses is caudal on two-thirds of the centrum length, except in the C8 in which the apophyses' origin is in the midlength of the centrum. They are caudolaterally projected from C2 to C7, but in C8, they are more lateral than caudal. The apophyses appear to increase in extension along the neck, a feature that is intensified from C6 to C8. They increase in thickness from C6 to C8. The prezygapophyses are poorly projected dorsocranially from C6 to C7, broken in C8. The postzygapophyses are dorsocaudally projected, more caudal than dorsal, at least from C6 to C8.

The CRACAL and PRAL almost overlap in the C6 and C7 of MN6949 and C8 of AMNH24453, fused in the C7 of the latter. Both laminae can be distinguished, whether fused or not because they run through different paths when the PRAL climbs toward the prezygapophysis. They are the longest laminae among herein studied taxa, proportionally to the size of the cervicals, with no major differences from C6 to C7; however, as the apophyses projects from the midlength of the centrum of C8, they are shorter in this vertebra. In MN6949, the prezygapophyses are poorly projected, so the CACAL and PRAL are almost the same size. In AMNH24454, the tendency in the height of the PRAL along the neck is to be increasingly higher and longer from C2 to C7 due to the lateralization of the apophyses, but in C8, the PRAL is shorter and lower. In all specimens, both laminae are thin.

The CACAL is proportionally the shortest one of all taxa studied herein. They are remarkably low in AMNH24453, and from C6 to C7, they are not observable close to the tip of apophyses, only in its base, where they may be fused with the POAL. In the C8, the CACAL is visible close to the apophyses but vanishes in the middle of their length. The specimen AMNH24454 is not fully prepared, so only the dorsal half of the cervicals can be studied, while the rest is within the rocky matrix. Therefore, it was impossible to state whether the CACAL and POAL are separated or fused. The POAL is only seen in the C8 of AMNH24453, where they are distinguished and separated from the CACAL. The POAL is low, and they do not climb too much towards the postzygapophysis.

Prezygapophyseal Lamina

The length of the CPRL grows from C6 to C7 because the prezygapophyses are more dorsal in the latter. In MNRJ6949, the laminae of the C7 appear in the margin of the neural canal and are thicker laterally to the neural arch, whereas they are higher in the C6 than the C7.

Postzygapophyseal Laminae

The CPOL elongates from C6 to C8, is thin, and does not show differences in height. The SPOL is absent in all cervical vertebrae of the analyzed specimens.

Hypapophyseal Laminae

The cranial hypapophysis is cranioventrally projected with no major differences in all present vertebrae, and the caudal hypapophyses are ventrolaterally projected. In the C7 of MNRJ6949, both are more developed than in C6. They appear in the C8 of MNRJ6637 but not in the C8 of AMNH24453 because they may have joined the caudal centrum articulation or disappeared.

The CAHL are similar in C6 and C7 of MNRJ6949, low, thin, and running through two-thirds of the centrum length. In AMNH24453, the CAHL runs all the way, reaching the ventralmost portion of the caudal central articulation of the C7. In turn, it vanishes close to the caudal central articulation in the C8. In the C6, this lamina is thicker than the C8.

The CRPHL of MNRJ6949 is low, thick, and short from C6 to C7. The C7 of AMNH24453, compared to the others, is thin, higher in the most caudal portion, and goes further to the middle length of the centrum. The C8 of MNRJ6637 and AMNH24453 are absent. Both CRHL and CAPHL are lacking in this species.

Spinal Lamina

The neural spine is not easily recognized in the cervicals of *A. barretoi*, being only a tiny projection in the caudalmost part of the pedicel in C6 and C7 of MNRJ6949. In AMNH24454, the dorsal aspect of the cervicals is hardly altered by the fossildiagenesis, so tracking the neural spine's and its lamina's morphology is unreliable.

The PRSL is absent in the dorsal view of MN6949 but is visible in the C7 of AMNH22556. It is very low and thin, looking like a line, and vanishes close to the middle distance between the neural spine and the articulation fossa of prezygapophyses.

Cearachelys placidoi

Apophyseal laminae

The apophyses originate in the midlength of the centrum, are caudolaterally projected, and remain the same size along the neck, with no increase in lateralization. They are relatively thick in all cervicals. The prezygapophyses are dorsocranially projected in all present vertebrae, but even though the C5 appears dorsally projected, a fossildiagenesis artifact causes this feature. The present Postzygapophyses are all dorsocaudally projected, and because C5 is damaged, they are not so caudally projected like in the plate; from C3 to C6, they get longer. The centrum is shorter in C3 and C4, becomes longer in C5, and in C6, they are slightly short, but not as in the first two present cervicals.

The CRCAL is thick in all present vertebrae. It is high in C3, loses height in C4, and achieves the lowest height in C6; the C5 is damaged so that the neural arch is disconnected from the centrum, which prevents establishing the CRCAL morphology. Because the apophyses do not increase in lateralization, they remain the same length through the series.

The PRAL is thick, with no variation in the series. It is increasingly higher from C3 to C6 (uncertain due to distortion of C5), being longer in C6 than in C3 and C4 (broken C5 and C7), with no variation between C3 and C4. The PRAL and CRCAL are thick at a point that the fossae between them are shallow. In C3 and C4, the CRCAL is more apparent than the PRAL, but in C5 and C6, it is the opposite.

The CACAL is less developed than the CRCAL, and the PRAL appears as a sheet at the base of the caudal portion of the apophysis. It is thicker, lower, and shorter than its counterparts, showing no differences in the series. The POAL and CACAL are fused.

Prezygapophyseal Laminae

The CPRL is thick and low, and the length remains the same in all present vertebrae. The C5 is broken so that no assertive assessment can be done.

Postzygapophyseal Laminae

The CPOL increases in length through the series because of the increase in the projection of postzygapophyses. They are all thick and low, but closer to the LM1 they are higher and thinner due to the deep articulation fossae of the postzygapophyses pedicel. The SPOL is not present in any of the vertebrae, but the conditions of the 3D model could be hiding it, so the presence of these laminae could not be safely assessed.

Hypapophyseal Laminae

The Cranial hypapophysis is present in all preserved vertebrae. It is cranioventrally projected and shows no major differences throughout the series. The Caudal hypapophyses are caudolaterally projected in C3 and become gradually ventralized until C7, in which they become medially fused.

The CAHL is present from C3 to C7 and is thick in all cervicals, but it decreases in width from C6 to C7. This lamina is increasingly higher until C7, when the CAHL is almost straight between the two LMs. The length is directly related to the size of the centrum, so C3, C4, and C7 are the shorter ones, whereas C5 and C6 are the longest.

The CRPHL is fused with the CAHL. They are higher near the LM1 and lower until the fusion with the CAHL along the series. The exception is the C7, both laminae the same height. The CRHL and CAPHL are not present.

Spinal Lamina

The neural spine is projected with low intensity and is recognized over the caudalmost part of the pedicel of the neural arch in all present vertebrae, being more developed in the C6.

The PRSL is present from C3 to C6. It increases in height from C3 to C4, remains the same in C5, and then decreases in C6. Its higher portion is close to the fossae of articulation of the prezygapophyses, and in C4 to C5, it is remarkably dorsally projected alongside the fossae, followed by a less intense subsequent dorsocaudal increase until the summit of the pedicel. It is thick along the series, and the base of the pedicel of postzygapophyses limits its length.

Pelomedusa subrufa

Apophyseal Laminae

The apophyses originate in the middle length of the centrum. They are caudolaterally projected, becoming more caudally projected from C3 to C5, then decreasing in caudalization until C7, which is almost as laterally projected as in the C3, and in the C8, they end more caudolaterally projected as in the C5. They are also more ventrally projected in the C6 and C7 and become slightly longer along the series. The prezygapophyses are dorsocranially projected and increasingly more dorsal from C3 to C5, remaining the same in C6, and rising dorsally again until C8. The postzygapophyses are dorsocaudally projected, increasing with intensity from C5 to C7 and decreasing in C8. The centrum remains the same length from C3 to C5, elongates from C6 to C7, and is shorter in C8.

The CRCAL near the LM2 lowers and thickens in all vertebrae. Their length slightly increases with the projections of the apophysis, so they become slightly longer from C3 to C5, reduce in C6, and expand until C8, with the C5 and C8 being the same length. The CRCAL are thin and do not vary along the neck. From C3 to C5, they become increasingly higher, lowering on C6 and rising again until C8.

The PRAL is generally the same size from C3 to C6; in C7 and C8, it is equally elongated. The PRAL becomes increasingly higher from C3 to C4, lowering and remaining low in the same amount in C5 and C6, then higher until C8. The width does not vary along the neck.

CACAL and CPOL are continuous to the dorsolateralmost part of the caudal centrum articulation. CACAL are the shortest laminae and are even shorter when the apophysis becomes more caudally projected. They increasingly shorten from C3 to C5, longer from C5 to C7, and decrease again in C8. The width does not show a pattern along the neck, but in C6 and C7, they are thicker asymmetrically (on the left side of C6 and on the right of C7). They are all low laminae.

Both POAL and CPOL link to the postzygapophyses. The POAL is bigger than CACAL but smaller than the other apophyseal laminae. Because of the articulation fossae of the postzygapophyses pedicel, these laminae increasingly become higher as they run towards the LM2. They do not show tendencies in both height and width changes along the neck.

The CACAL and POAL are remarkably continuous to the CPOL from C4 to C8 in different ways along the neck. In C4 and C5, CACAL and POAL become closer along their way when both become continuous to CPOL. In C6, on the left side, only the CACAL is thick and continuous on the medium length of CPOL, and on the right side, the POAL and CACAL are continuous with CPOL. On the right side of the C7, only the thick CACAL is continuous to CPOL. Still, on the left, both laminae are continuous to CPOL, interrupting it and presenting an exclusive fossa connected to the neural canal's visceral aspect. Lastly, in C8, both POAL and CACAL are continuous at the medium length of CPOL on the two sides.

Prezygapophyseal Lamina

The length of CPRL is the same until C6, increasing from C7 to C8 as the prezygapophyses become more dorsal. They have the same width in all cervicals and are higher from C3 to C5 but become lower until C8.

Postzygapophyseal Laminae

The SPOL is present only in C7 and C8. They are low and thick, lower at C8, and thicker in C7; on C8, they are longer. The CPOL elongates from C5 to C7, with more intensity in C6 and C7, and slightly shortens in C8. Close to the LM1, they are higher, and in their middle length, they become lower with a slight rise near the LM2, which does not reach the dorsolateralmost part of the caudal central articulation. The CPOL is slightly lower until C5, higher in C6, and from to C8, they are continuous to CACAL and POAL on only one side in C7.

Hypapophyseal Laminae

The cranial hypapophysis is cranioventrally projected. They become slightly thicker from C3 to C6, then split into two in C7 and C8, with both projections thinner. The caudal hypapophyses are ventrolaterally projected and thicker in its caudalmost region. They are equally thick from C3 to C4, increasing in C5 and slightly thinner until C8. They are less apparent in C7 to C8.

The length of CAHL changes with the increase in centrum length, so they have the same length from C3 to C5 and elongate from C6 to C7 with a slight decrease in C8. They have the same height until C6 and lower until C8. The CAHL follows the thickness of the cranial hypapophysis, thickening until C6, then becoming thinner until C8. Such an alteration in width in the last two is due to the split of the Cranial hypapophysis.

The CRPHL are fused with the CAHL until C7, where they become discontinuous, more in C8 but still as long as in the other cervicals. In C7 and C8, they barely reach the medium length of the centrum. The CRPHL are the same width from C3 to C6, thinner in C7 and C8, get higher until C6, then slightly lower until C8. CRHL and CAPHL are not present.

Spinal Lamina

The neural spine is low, projected only in the caudalmost part of the pedicel. It is more projected in C3, slightly less in C4 to C5, and increases from C6 to C8; in C7 and C8, it is much more projected than the others.

The PRSL is equally low in C3 to C4, highest in C5, reduced to a tiny line on the curvature of the postzygapophyseal pedicel in C6, and increasingly higher until C8. It is equally thick throughout the series. Its length changes as the projection of the postzygapophyses becomes dorsocaudally longer after C5, being more elongated in C7 and C8 but longer in C7.

Podocnemis expansa

Apophyseal Laminae

The apophyses’ origin is on the medium length of the centrum. They are laterally projected in C2, and then they get caudolaterally projected, less in C5 and C7. The prezygapophyses are dorsocranially projected and become dorsal from C4 to C5, with a decrease in C6 and subsequent rise until C8. The postzygapophyses are dorsocaudally projected, more dorsal in C4, and from C5 to C8, they increasingly become more dorsally projected. The centrum size increases from C2 to C3, remains the same until C5, and then increases until C7 with a subsequent decrease in C8.

The CRCAL elongates from C2 to C6 due to the increase in the apophyses projection's height and the centrum's length. C3, C4, and C7 do not reach the second landmark, which becomes lower throughout its path. The width slightly increases from C2 to C8, thicker closer to the apophysis. The CRCAL are higher in C2, lower until C4, then rise until C6 with a subsequent decrease in C7, when they are barely seen. Already in C8, they are slightly higher.

The PRAL slightly becomes longer until C8. Thickens from C3 to C5 decreases in C6 with a subsequent increase in C7, and is the thinnest in C8. The PRAL becomes higher from C3 to C5 and then decreases until C8.

The CACAL and the POAL are fused. The resulting lamina is thick and low, becoming thicker until C8 and having the same height until C6, then lowering in C7 and C8. Their length increases as the apophyses become more lateral from C2 to C7 and are shorter in C8.

Prezygapophyseal lamina

The CPRL becomes longer until C5, decreasing in C6 with a subsequent increase until C8. They are thinner in C2 and increasingly thicker until C7; in C8, they become slightly thinner. Their height decreases gradually from C2 to C8.

Postzygapophyseal Laminae

The CPOL is indistinguishable from both POAL and CACAL because they are all thick and adjacent continuous. The length of CPOL increases from C2 to C4 and decreases in C5, followed by elongation until C8. They are higher and thinner in all vertebrae near their landmarks, but in the mid-lenght they are very low and thick, more from C6 to C8. They are higher and thinner, close to the postzygapophyses, due to the pedicel articulation fossae.

The SPOL appears only in C2, C7, and C8. In C2, they are high, thick, and very long, but in C7 and C8, they are short, low, and thick, longer in C8.

Hypapophyseal Laminae

The cranial hypapophysis is cranioventrally projected and more developed from C2 to C4 and C6 to C8. The caudal hypapophyses are caudolaterally projected and very small from C2 to C6. In C7, they are more ventromedial; in C8, they are completely fused medially and ventralized. They become slightly bigger from C2 to C5, smaller in C6, and more prominent until C8.

The CRHL is present only in C2, where it is possible to note a constriction between the cranial hypapophysis and the central articulation. The CAHL runs to two-thirds of the centrum length until C7, where it goes through the caudal centrum articulation, but in C8, it links to the ventralized caudal hypapophysis. It is higher in C2, lowering until C5, then being higher until it achieves the highest in C8. They all have the same width except for C7, which is the thinnest.

The CRPHL are shorter in C5 and C7, whereas they show the same size in the other vertebrae. They are extremely low and equally thick along the series, making tracking along the neck challenging. The CAPHL appears only in C8 and is short, thin, and relatively high for its size.

Spinal Lamina

Only the caudalmost part of the neural spine is projected, with low intensity, from C3 to C6, but in C7 and C8, it is strongly dorsocaudally projected, being higher in C8.

The length of PRSL changes as the postzygapophyses are more projected. It is shorter from C3 to C5 and longer from C6 to C8. It becomes thicker from C3 to C5, thinner in C6, and dramatically thickens until C8. PRSL is low, but in C5, it becomes higher close to the prezygapophysis with a dramatic rise followed by a subsequent slow dorsocranial rise. In addition, the C5 has the PRSL bifurcated.

VARIATION THROUGHOUT THE SERIES

In all studied taxa, the variability of the structures from C3 to C5 is minor compared to the variation from C2-C3 and C6-C8 (fig. 4), with the C2 and C8 being the most differentiable cervicals. In *E. essweini*, due to the exceptional conservation of the fossil, it is possible to state that their neck has more similar cervicals, all generally having the same shape, except for C2 and C8. The same could be noted in *A. barretoi*, with some differences, because the cervical series studied (AMNH24454) has only the dorsal view partially preserved and with many alterations. Even so, the cervicals are more similar in the series than the other extant taxa and *C. placidoi*.

In *P. expansa*, *P. subrufa*, and *C. placidoi*, this pattern of similarity between C3 and C5 is less evident, with more changes than in *E. essweini*. However, the crescent pattern of change in the back of the neck (C6 to C8) of the extant taxa is even more pronounced (fig. 4, 5, 7). In addition, this concentration of variability in the last three cervicals is shared with all taxa but less in *E. essweini* and *A. barretoi*.

The principal shared differences in the last three cervicals (C6-C8) are in the centrum, the pedicel of postzygapophyses, and the neural spine. Therefore, laminae connected with these structures in these vertebrae change more. The CAHL varies in length with conformity to the length of the centrum, being longer in C7, shorter in C6, and shortest in C8. In *P.subrufa* and *E. essweini,* the POAL changes conform to the variation of postzygapophysis projection, longer in C7, shorter in C8, and the shortest in C6 of the former. Yet, in the latter, the length increases from C6 to C8. The CPOL elongates from C6 to C8 because of the increase in length of the centrum and postzygapophyses; even if the centrum decreases in C8, this lamina is longer than in C7 because from C7 to C8, the postzygapophyses increase in size with more intensity. In the C8 of *P. subrufa,* the postzygapophyses are less projected than in the C7; added to the decrease of the centrum length, this species is the only one to have a reduction in CPOL length from C7 to C8 (fig. 4; 5; 7).

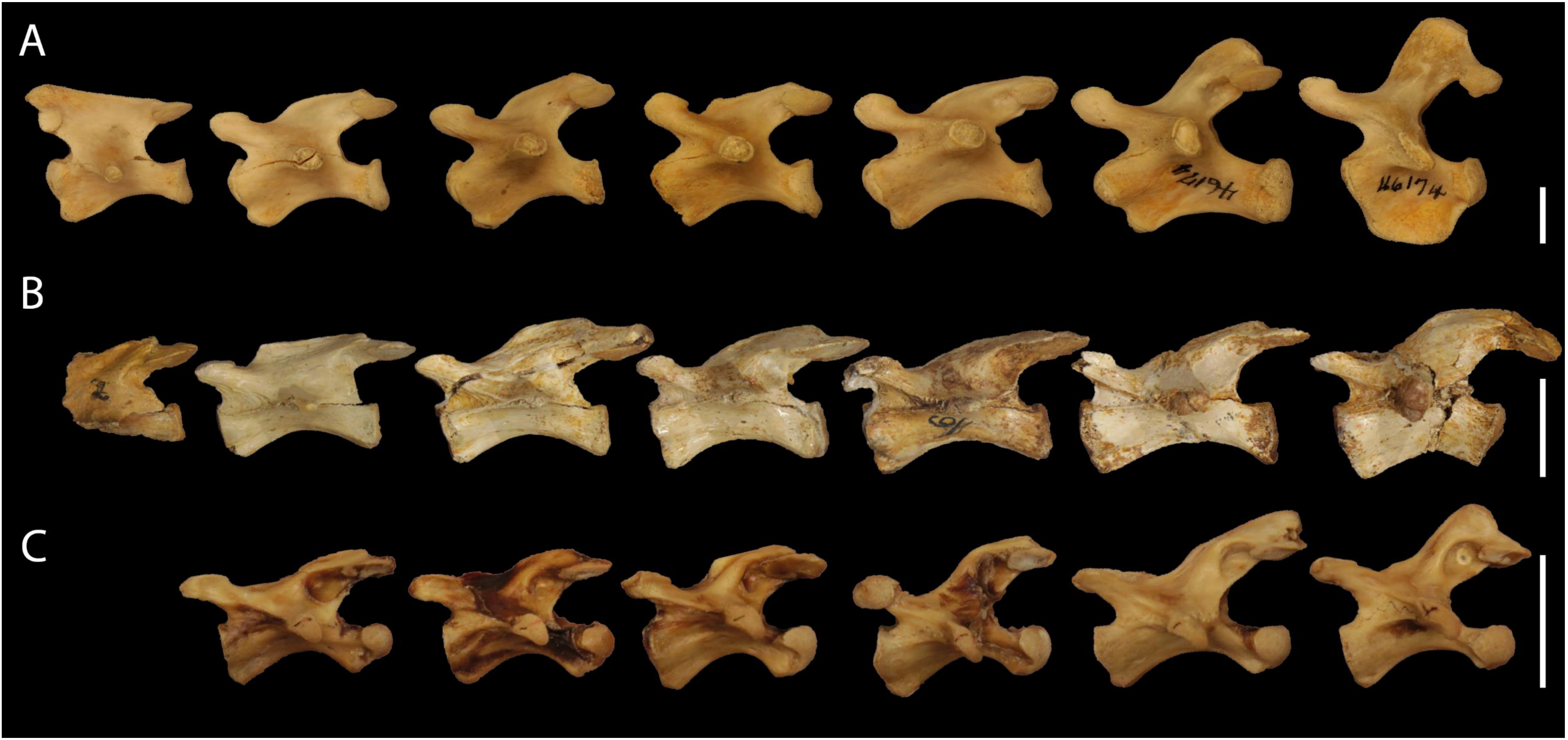

Figure 4: Comparisons among the neck of *Podocnemis expansa* (A; AMNH46174), *Euraxemys essweini* (B; FR4922), and *Pelomedusa subrufa* (C; USNM40248) showing similar patterns between cervicals in different taxa. Minor changes occur in C3 to C5, whereas changes from C6 to C8 are more pronounced.

The neural spine is more dorsally projected from the C6 to C8, but the SPOL is present in the C7 and C8 of Pelomedusidae, Podocnemididae, and the C8 of *E. essweini*. In turn, despite the neural spine of *C. placidoi* and *A. barretoi* also changes in projection from C6 to C8, the SPOL is absent.

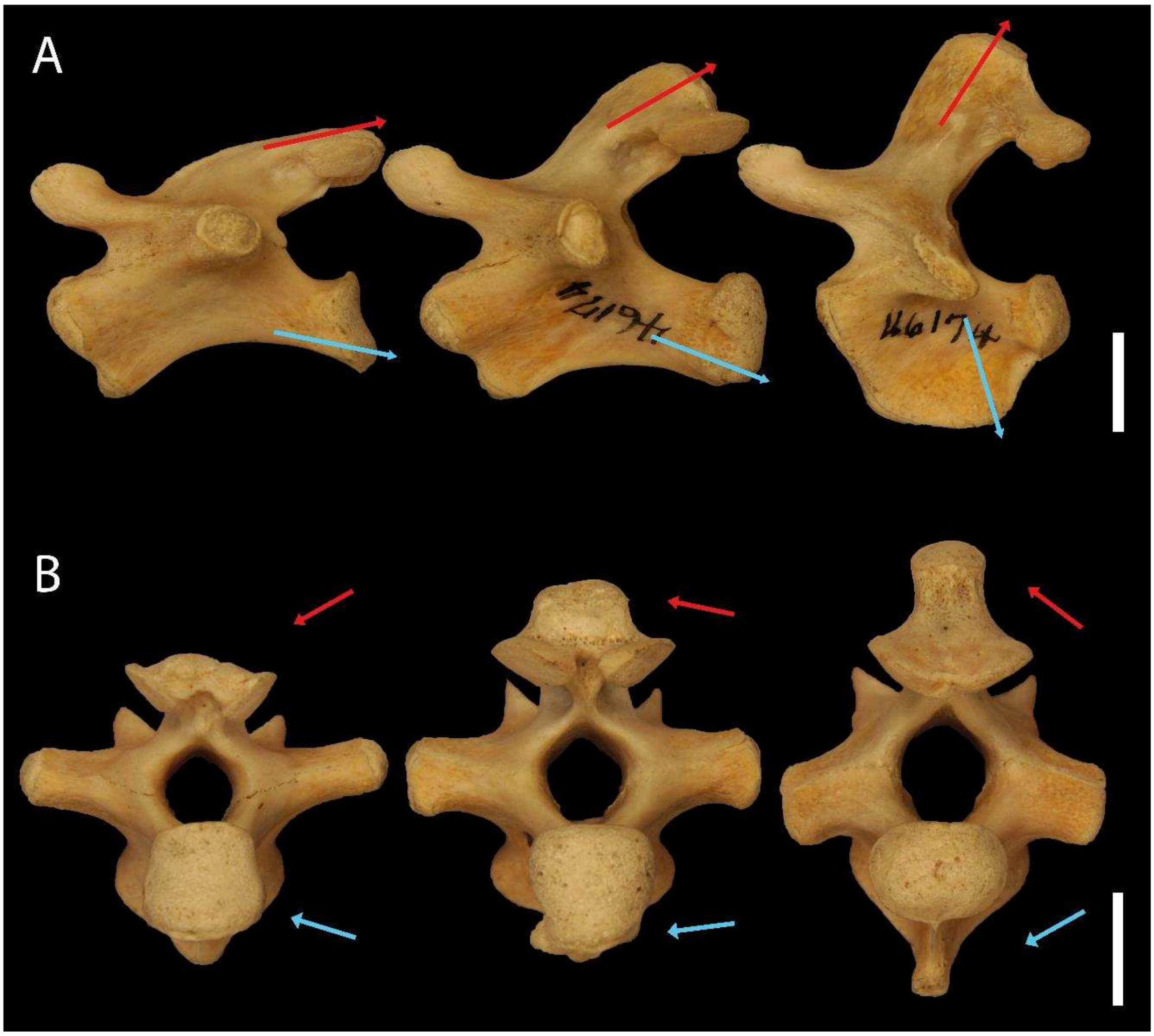

Figure 5: Changes in the projection of both neural spine and caudal hypapophyses from C6-C8 of Pelomedusoides exemplified by *Podocnemis expansa* (AMNH46174). Blue arrow = hypapophyses projection; Red arrow = neural spine projection

The other laminae that do not share landmarks with these structures (neural spine, postzygapophysis, centrum) do not show a concentration of variability in the back of the neck but occur along the neck. The ones that share these landmarks have the variability spread throughout the neck

DISCUSSION

NOMENCLATURAL CHANGES AND LAMINAE IMPLICATIONS

This work did not intend to change the usual terminology, even though some nomenclatural adaptations were necessary, but rather to propose names for cervical features that have been overlooked in anatomical comparisons of turtles by applying an already established system (i.e., Wilson, 1999). Therefore, the bony structures described here are not a novelty either to the anatomists or turtle specialists but an attempt to clarify morphologies that have been loosely described or referenced through the years (e.g. Shah, 1963; Hoffstetter & Gasc, 1969; Pritchard, 1984; Gaffney, 1985, 1990; Broin et al., 2007; Mariani, 2016), which ultimately reduced the accuracy of both the terminology and position of the anatomical features, whether these are bony or muscles.

For instance, Shah (1963) described and compared the neck muscles between cryptodiran and pleurodiran turtles and, when doing so, he described muscular origins and insertions using expressions such as “on the diapophysis,” “on the posterior end of the diapophysis,” “from the anterior border of the diapophysis” and even “posterior diapophysis.” Herrel et al. (2008) followed by using similar broad expressions such as “posterior aspect of the transverse process” and “ventral aspect of the transverse process.” These locations could be more accurately described using the apophyseal laminae (Fig 6). Therefore, the distinction of laminae as a whole can be a solid criterion for muscular attachment references, whether these are origins or insertions.

Within Testudines, Pleurodira, the morphology of the transversal apophyses has been commonly referred to either as wing-shaped (i.e., de Broin et al., 2007; de Broin & Prasad, 2020) or triangular transverse processes (Hoffstetter and Gasc, 1969). In the present study, all cervicals show wing-shaped transverse apophyses, a morphology caused by up to four laminae: CRCAL, PRAL, CACAL, and POAL. Yet, all have unique differences along the neck and between groups in at least one of three laminae that rely on the transversal apophyses.

Araripemys barretoi, Euraxemys essweini, and *Pelomedusa subrufa* have the thinnest apophyseal laminae, but the three differ from one to another in the cranial portion. *Araripemys barretoi* pursue the CRCAL very near the PRAL, almost overlapped, with a shallow slit between them. *Euraxemys essweini* possesses the CRCAL near the PRAL, only next to the tip

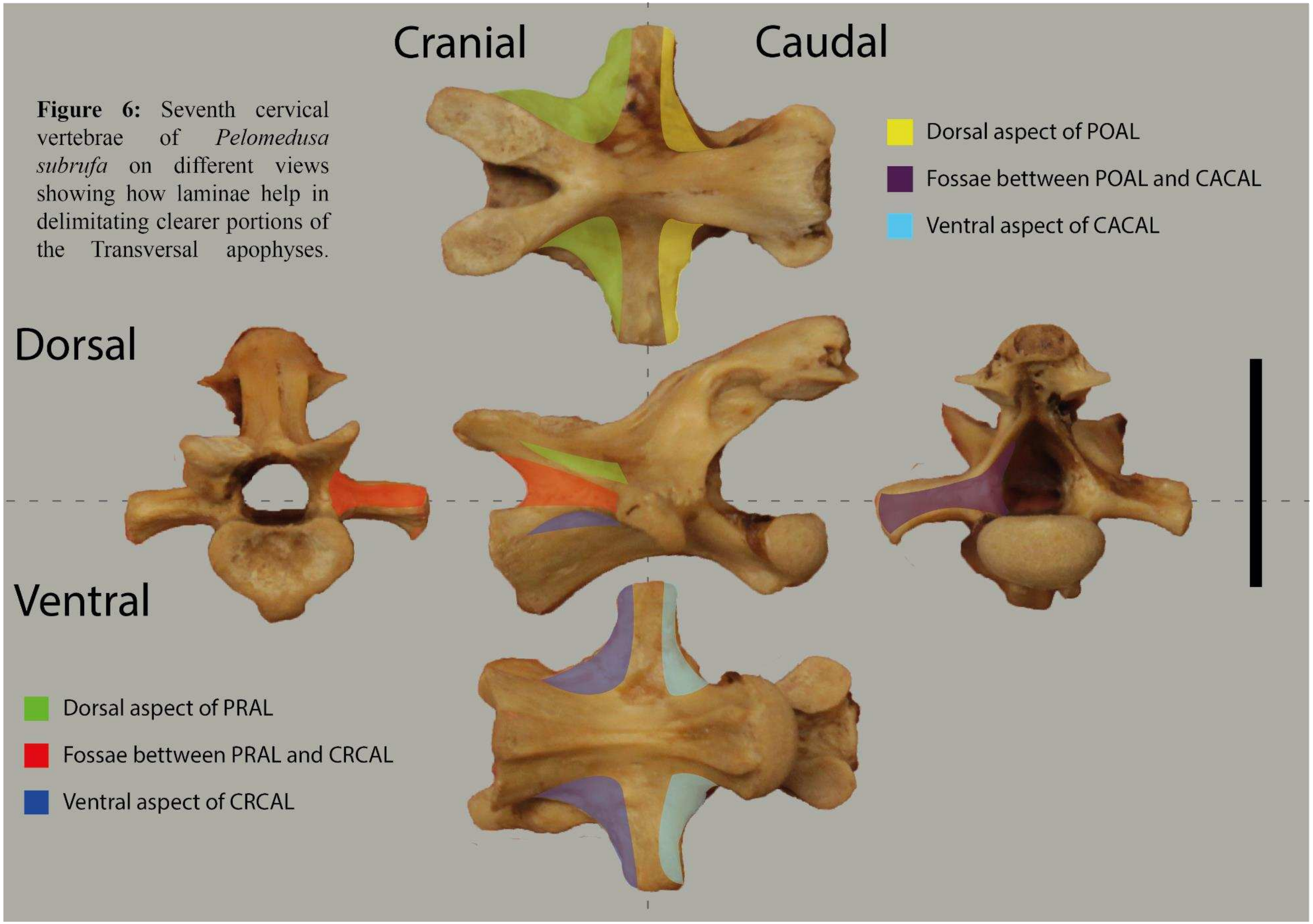

Figure 6: Seventh cervical vertebrae of *Pelomedusa subrufa* on different views showing how laminae help in delimitating clearer portions of the Transversal apophyses.

of the apophyses. However, along their path throughout their respective second landmarks, they are widely separated with a pronounced fossa between them. In *P. subrufa*, the fossa between CRCAL and PRAL is even more pronounced, with the two laminae being widely separated, even though some of them are asymmetrically very near each other next to the summit of the apophysis. *Cearachelys placidoi* and *Podocnemis expansa* have the thickest, even though they are different. The fossae between their CRCAL and PRAL are very shallow in the former and deep in the latter because these laminae are, respectively, higher and lower.

In the caudal aspect of the transversal apophyses, *Pelomedusa subrufa* and *Euraxemys essweini* have unique POAL, which is conspicuous and separate from CACAL. The difference is that in the former, they are present in all cervical vertebrae, while in the latter, only from C4 to C8. In *Podocnemis expansa*, *Araripemys barretoi*, and *Cearachelys placidoi*, the fusion of the POAL with the CACAL is hard to establish. Still, in the former, the fusion of both seems more plausible because of the evident continuity of the fused laminae close to their respective landmarks.

The Cranial and Caudal hypapophyses are not broadly treated as similar processes in Testudines. Still, in Pelomedusoides, they are remarkably similar in projection, as Broin (2007) has taken into account. Nonetheless, in disconformity with Broin, which treats the hypoapophyses as tubercles, I treat them as apophyses, considering their projection (fig. 5). In addition, they play a role by changing the shape of the cervical joints, as Broin (2007) mentioned. She considered that the reduction of the posterior tubercles (caudal hypapophyses) is associated with the formation of saddle-shaped joints; in the herein-studied group, I consider the changes in the projection of the cranial and caudal hypapophyses related to changes in almost all the joints depending on its morphology.

In all compared taxa, the cranial hypapophysis is always ventrally and medially positioned under the anterior cranial articulation of the centrum and continuous to the articulation, forming a cuspid morphology to the ventral aspect of it (resembling a heart). In *E. essweini*, the difference is that the general shape of the articulations is more circular. In the C2 of *P. expansa*, the cranial hypapophysis is slightly more ventrally projected and, thus, is not continuous to the central articulation. When this occurs, the CRHL emerges between these structures and can occur up to the C4 in the extant forms (Table.S3-5)

In *P. expansa,* the caudal hypapophyses, ventrolaterally projected from C2 to C6, give the caudal centra articulation the saddle-shaped joint morphotype (Broin, 2007), larger in its base. From C6 to C8, the ventralization of the caudal hypapophyses changes the morphology of the central articulation: in C7, it is saddle-shaped but with its base shorter, while in C8, with the intense ventralization of the caudal hypapophyses, the continuity with the posterior articulation of the centrum is interrupted, having an oval morphology. This intense ventralization in C8 is similar to the ventralization of the cranial hypapophysis in C2, and when it occurs, CAPHL emerges between caudal hypapophysis and centrum articulation. This happens only in the C8 of some Podocnemidids (Table.S5)

In *P. subrufa,* these two structures are continuous from C4 to C6, so the caudal articulation has a morphology of a trapezium with a short base, while the other cervicals have oval, wider than high articulations. *Euraxemys essweini* has a subtriangular central articulation from C3 to C6, but when the ventralization of the caudal hypapophyses intensifies from C6 to C7, the central articulation becomes oval, higher than wide. In C8, with the fusion of the two hypapophyses, the ventral aspect of the articulation is sharper and, added to the expansion in the mid part, has a morphology similar to that of a lozenge. In the *A. barretoi* caudal portion, the hypapophyses remain ventrolaterally projected, and the center articulations remain triangular. *Cearachelys placidoi*, in contrast to all the other taxa, have the caudal articulations of the center all oval, higher than wide, due to caudal hypapophyses being more ventromedially positioned in every cervical.

The terms wing-shaped (for transversal apophyses), tubercles (for hypapophyses), and crests (for laminae) are not wrong but not the best way to fully describe the morphology of cervical vertebrae across taxa. In contrast, the distinction between laminae has more power to seek differences. Furthermore, these distinctions clarify the role of laminae formation and the changes in the shape of central articulations.

The neural spine is always in deep relation with the postzygapophysis pedicel in Pelomedusoides, making it difficult to track throughout the neck. From C3 to C5, the neural spine is fused with the postzygapophysis pedicel, making it challenging to differentiate. Only from C6 to C8 is it possible to see that the projection of the neural spine becomes more dorsal than the pedicel. Consequently, it becomes more visible until C8, which is conspicuous (Fig. 5; 7). In C2, the neural spine is conspicuous but has shifted craniodorsally. Broin (2007) argues that the neural crest (=neural spine) in Eupleurodiran turtles becomes a tubercle above the pedicel on the seventh and eighth vertebrae, but in Pelomedusoides, the Neural spine projects itself caudodorsally from the two-thirds of the pedicel length, and do not resemble a tubercle (fig 5; 7). Because of the translucency of the PRSL in *Peltocephalus dumerilianus*, it is possible to see this difference clearly (Fig. 7).

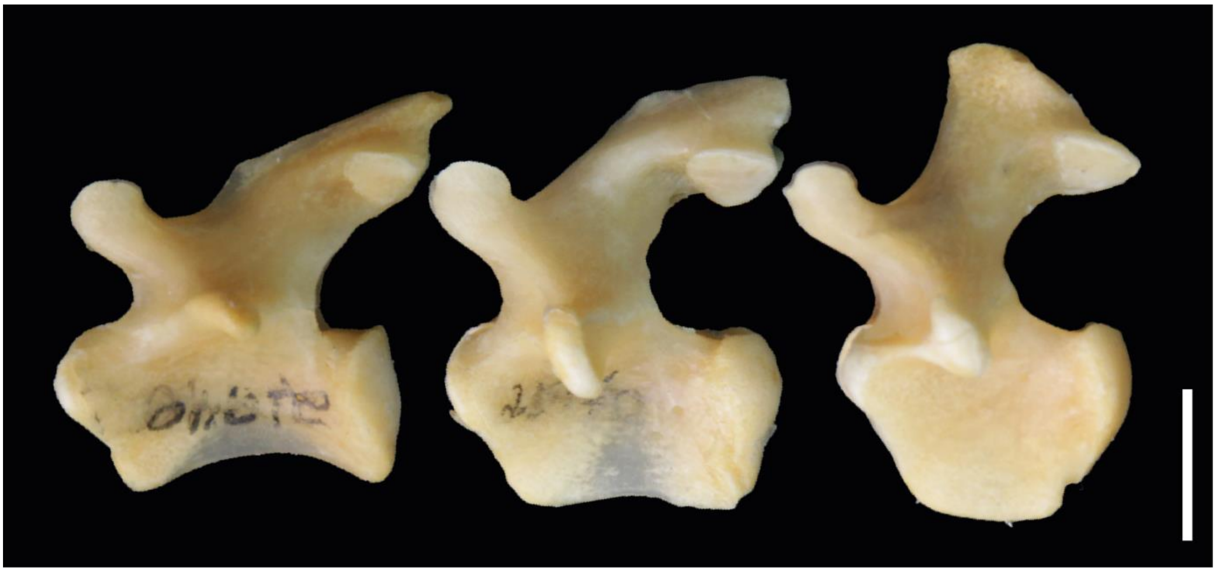

Figure 7: Changes in the projection of both PRSL and neural spines from the C6 to C8 of Pelomedusoides, exemplified by *Peltocephalus dumerilianus* (INPA21940). There is a clear distinction between the PRSL and the neural spine.

The PRSL occasionally was treated as the neural spine in fossil specimens (Lapparent de Broin et al., 2007; Sterli et al.,2007), though these fossils are not remarkably well-preserved so that the neural spine could be easily differentiated from the PRSL as in living species (e.g. *P. dumerilianus*; Fig. 7). Still, it was possible to differentiate them in the fossil pelomedusoids *Cearachelys placidoi* and *Euraxemys essweini* (table S1; fig. 4B, S21). This distinction is helpful because the changes in the neural spine are different from the differences in the laminae; for instance, the PRSL could be highly developed and the neural spine not as in C5 of *P. expansa* or the neural spine well developed and the PRSL not, as in C6 of *P. dumerilianus*.

TAXONOMIC IMPLICATIONS

The taxonomic implications of laminae in sauropods have been developed since Osborn (1899) first created a system to characterize them (Wilson, 1999). Recently, in Squamata, applying laminae terminology was also helpful in distinguishing groups (Tschop, 2016). Indeed, the herein-studied group possesses some implications.

There are remarkable differences in *Araripemys barretoi* and *Euraxemys essweini* that are not found in any other species within Pelomedusoides, only based on laminae morphology up to two laminae. *Euraxemys essweini* has an exclusive, strongly developed PRSL in C3, and *Araripemys barretoi* have the PRAL and CRACAL overlapped with a shallow slit between them. Besides these unique differences, only a combination of numerous characteristics can distinguish the other taxa. For instance, all the members of *Podocnemis* genera herein studied have an exclusive hypapophyseal laminae morphology in the C8, where the cranial hypapophysis is more ventralized, and the caudal hypapophyses fused in a single ventral projection, so the CAHL fuses with the CRPHL, and the CAPHL emerges in the caudal region. However, some of these conspicuous differences must not be taxonomical because exceptions of these characteristics are found in distantly related groups; for instance, in all herein studied species of Pelomedusidae, the CV has a single cranial hypapophyses and a pair of caudal hypapophyses, in which the CAHL fuses to the pair of CRPHL. This same morphology is found in *Cearachelys placidoi* and Erymnochelys madagascariensis.

The presence and absence of laminae and the changes in each lamina are sufficient to distinguish some taxa within Pelomedusoides, but some differences are not. Despite these conspicuous differences, many are very slight but certainly compatible with quantitative approaches such as geometric morphometrics because of landmark-based terminology (fig. 7). Including these landmarks proposed by the establishment of laminae terminology helps cover more of the general shape of the cervical vertebrae used in previous works (i.e., Wernenburg, 2014).

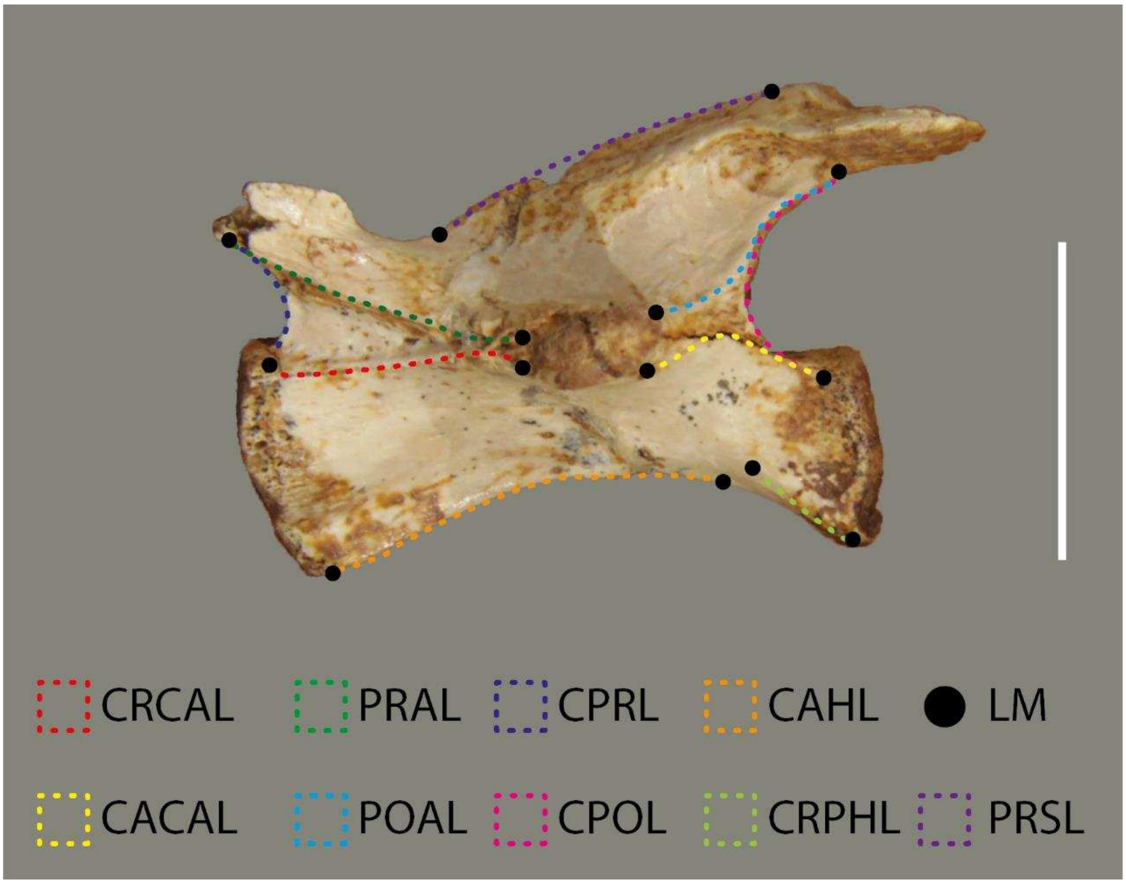

Figure 8: The laminae terminology aids in delimiting new landmarks and may also serve for applying semi-landmarks for geometric morphometrics, as exemplified by *Euraxemys essweini* (FR4922).

CONCLUSION

In this work, the laminae nomenclature proposed by Wilson (1999) was efficiently applied to the cervical vertebrae of Pelomedusoides so that 12 laminae were identified and named for the group. Moreover, it was the first time such features were identified for turtles. Because this is a landmark-based terminology, it can be precise and repeatable with few arbitrary inconveniences, granting a trustworthy set of landmarks that bring confidence and enrichment of details in further descriptions and osteological comparisons. This opens a new way for understanding cervical modifications along the turtle evolution by covering aspects of the CVs' morphology that have been overlooked and paving the way for studying relevant morphofunctional aspects of the turtle neck.

Differences were found within Pelomedusoides between taxa, suggesting that specific laminae morphology may be specific for some clades. They may be of phylogenetic importance, such as the morphology of the cranial apophyseal laminae of *Araripemys barretoi* and the pattern of hypapophyseal laminae of the C8 in *Podocnemis* genera. Nonetheless, in the same way, some very conspicuous patterns of well-established clade can be found in distantly related taxa, which may evoke morphofunctional shared differences, for instance, the pattern of hypapophyseal laminae in Pelomedusidae that is found in *Erymnochelys madagascariensis* and *Cearachelys placidoi*.

Also, some morphological differences and patterns are more compatible with quantitative approaches because a significant amount of this variation is very discreet. Since the method for naming laminae is landmark-based, it is possible to "establish the first criterion of homology, that of similarity" (Wilson, 1999, p. 639). It could also be assessed using quantitative techniques, such as geometric morphometrics. Therefore, one implication of this work lies in the compatibility of the terminology with quantitative approaches, which are essential for testing hypotheses.

Additionally, naming both laminae and other cervical parts helps in a more stable osteological nomenclature but also provides a more precise osteological and topological region for the study of muscle anchorage onto the cervical vertebrae, which may ultimately aid in the identification of muscular homologies in morphofunctional analyses (e.g., biomechanics of neck retraction and feeding habits), and in looking for osteological correlates of fossil species (i.e., muscle reconstruction).

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APPENDIX

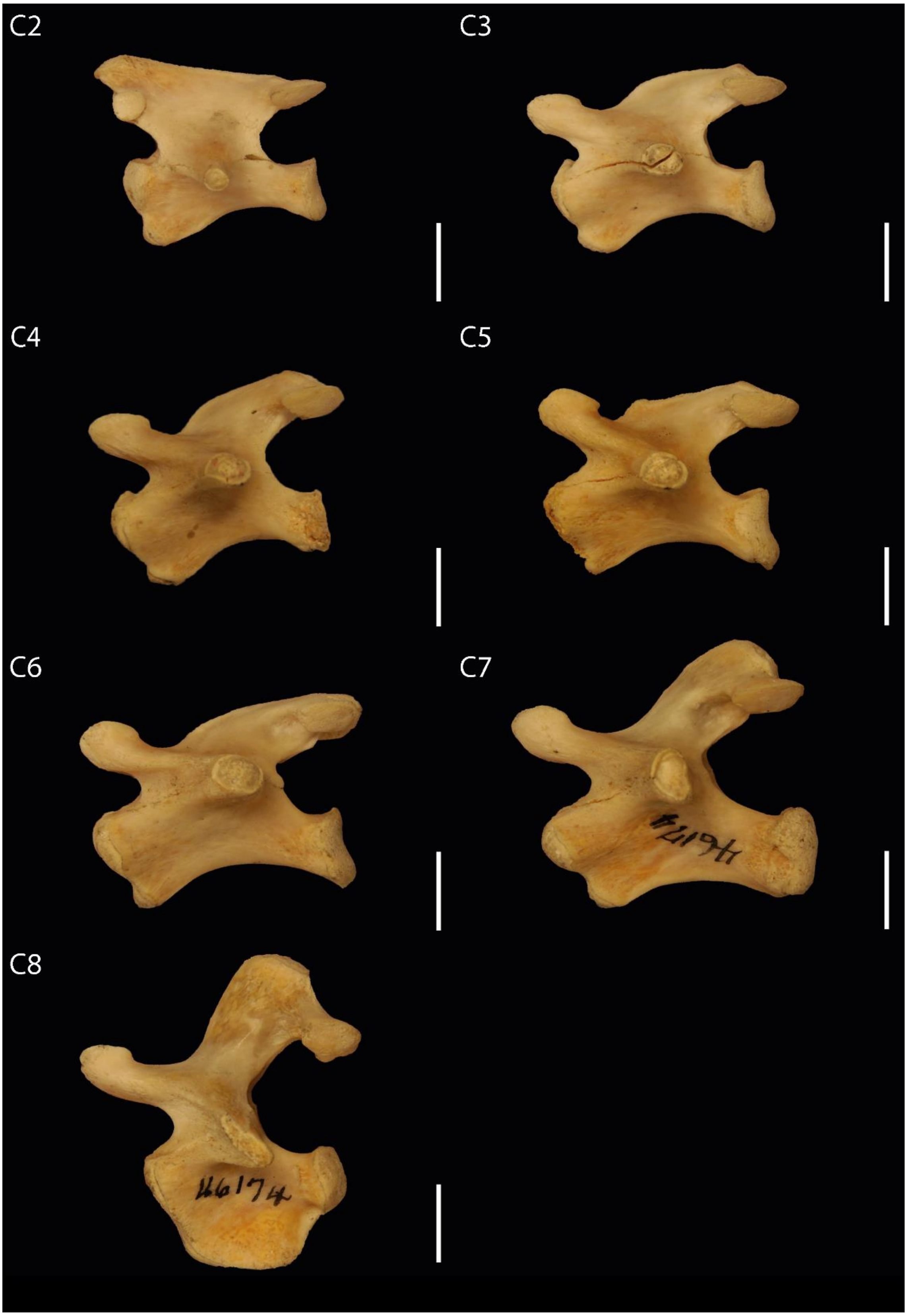

FIG1S: Lateral view of *P. expansa* (AMNH46174).

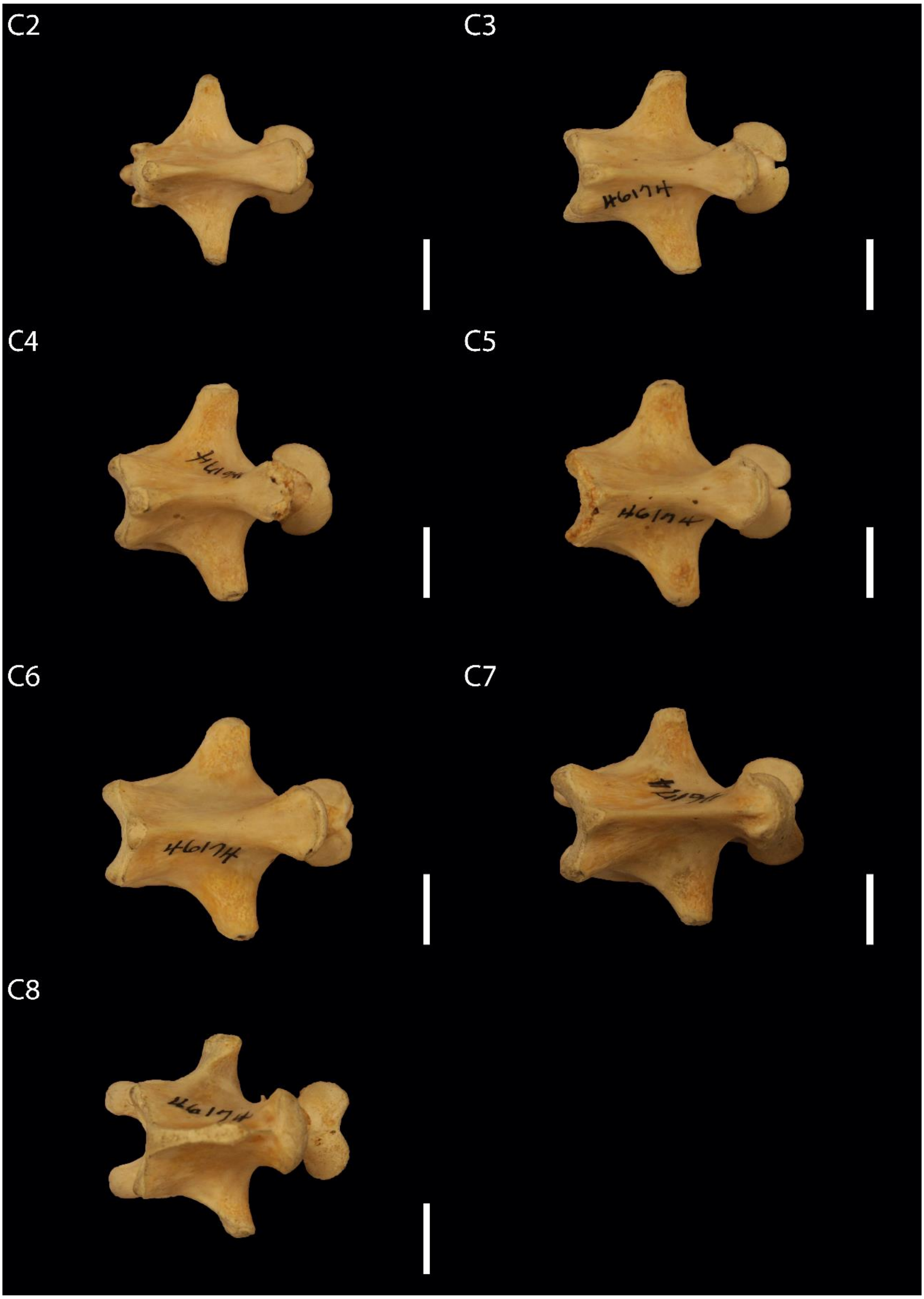

FIG2S: Ventral view of *P. expansa (AMNH46174).*

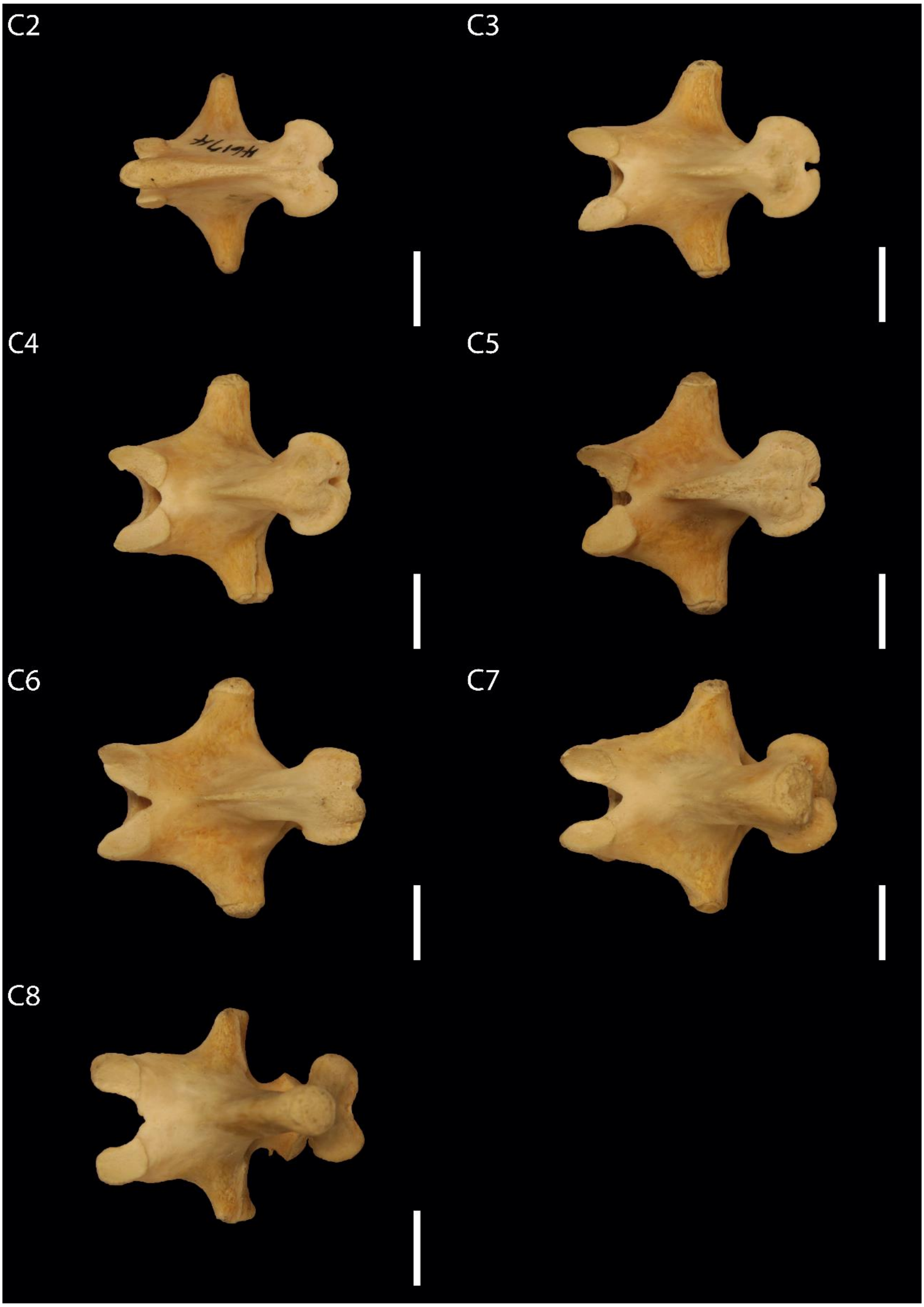

FIG3S: Dorsal view of *P. expansa (AMNH46174).*

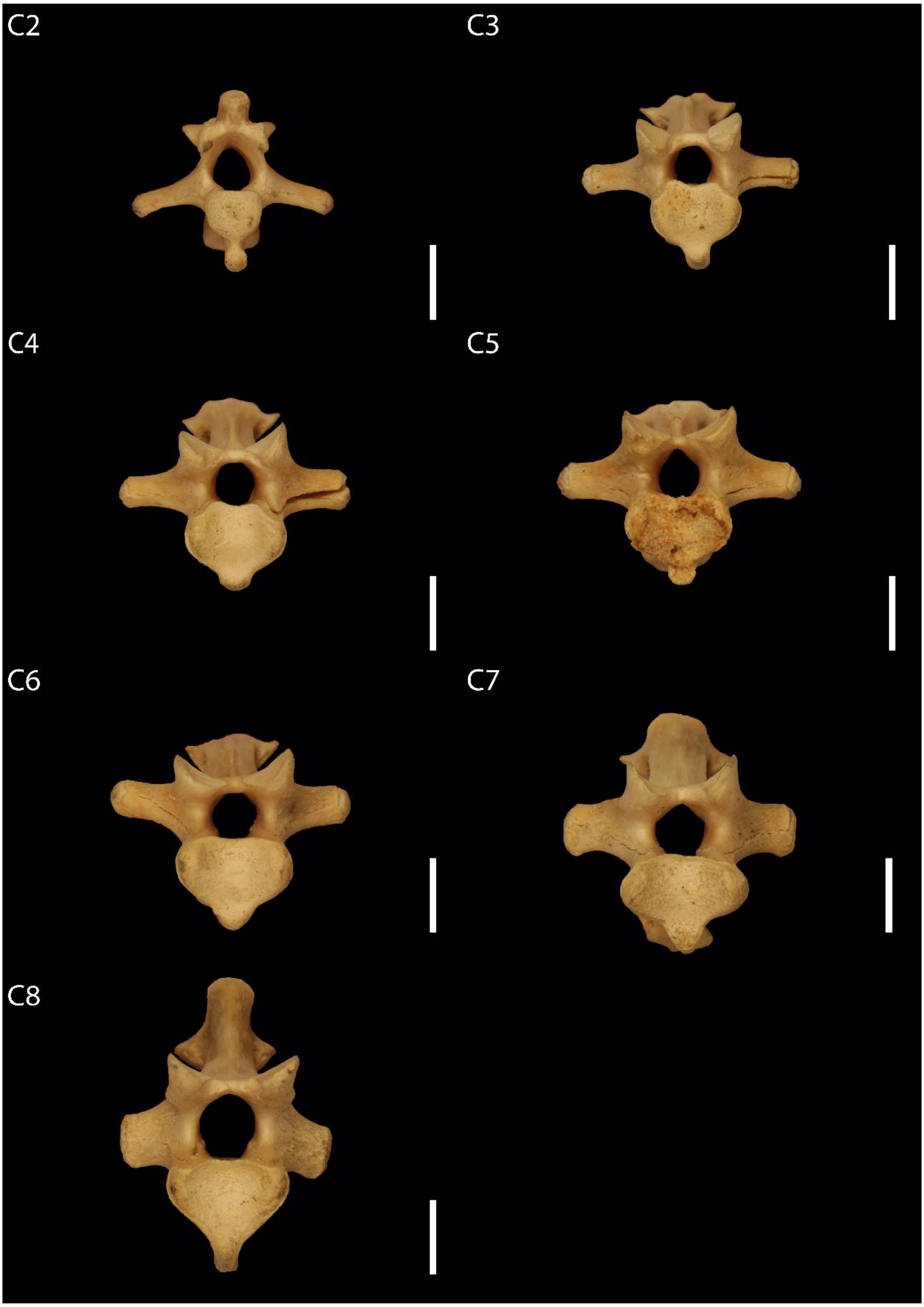

FIG4S: Cranial view of *P. expansa* (AMNH46174).

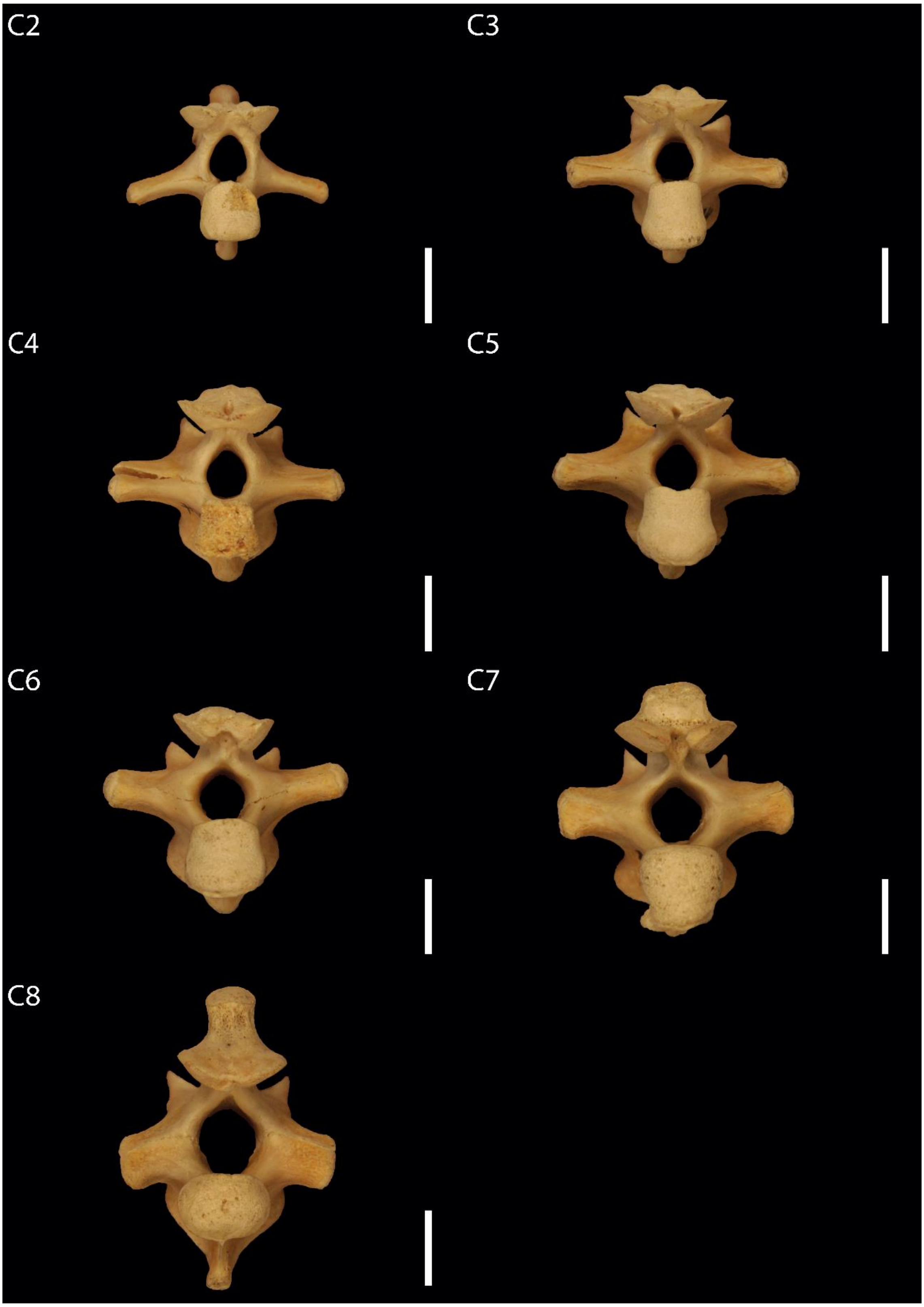

FIG5S: Caudal view of *P. expansa* (AMNH46174).

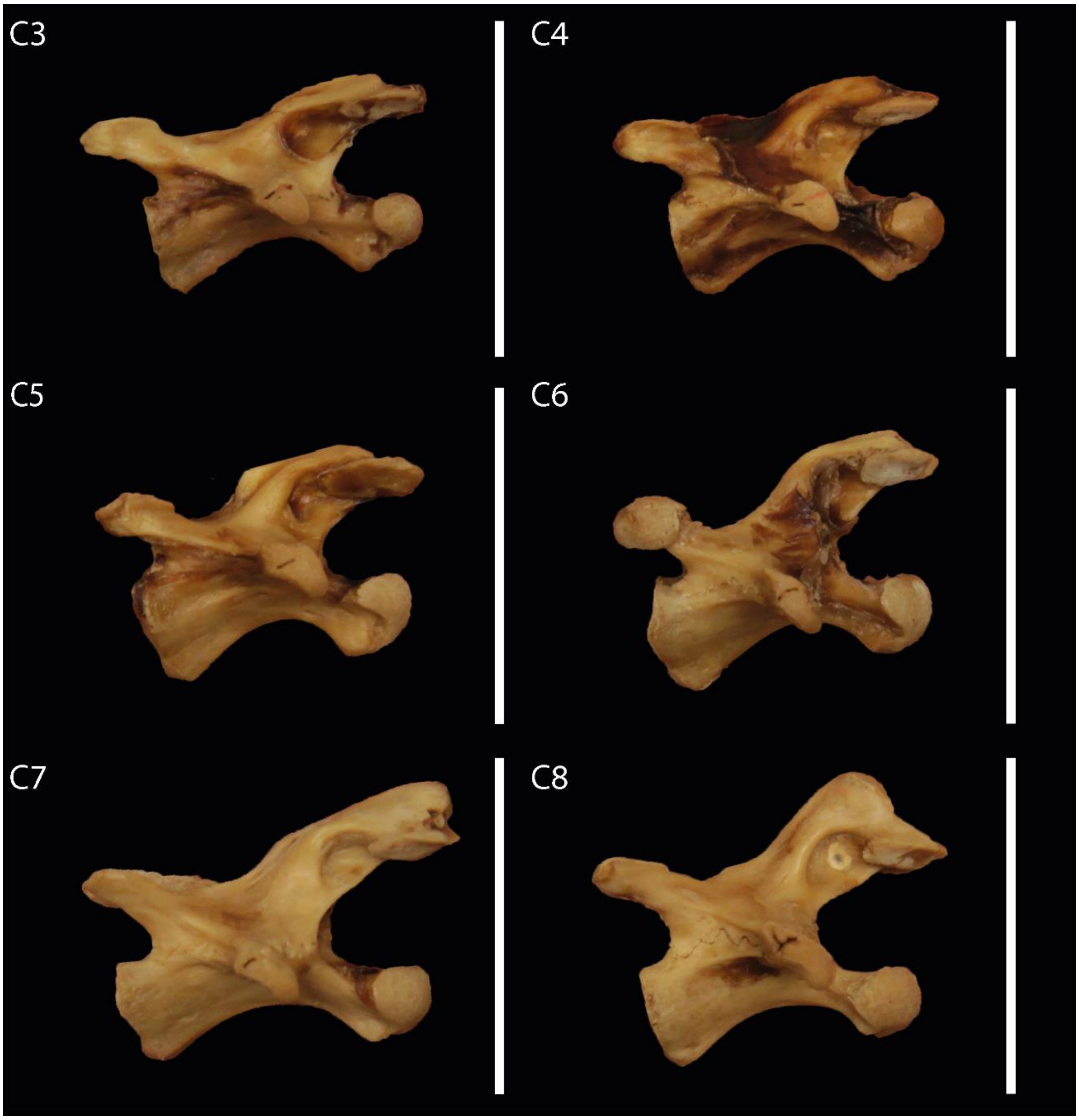

FIG6S: Lateral view *P. subrufa* (USNM40248).

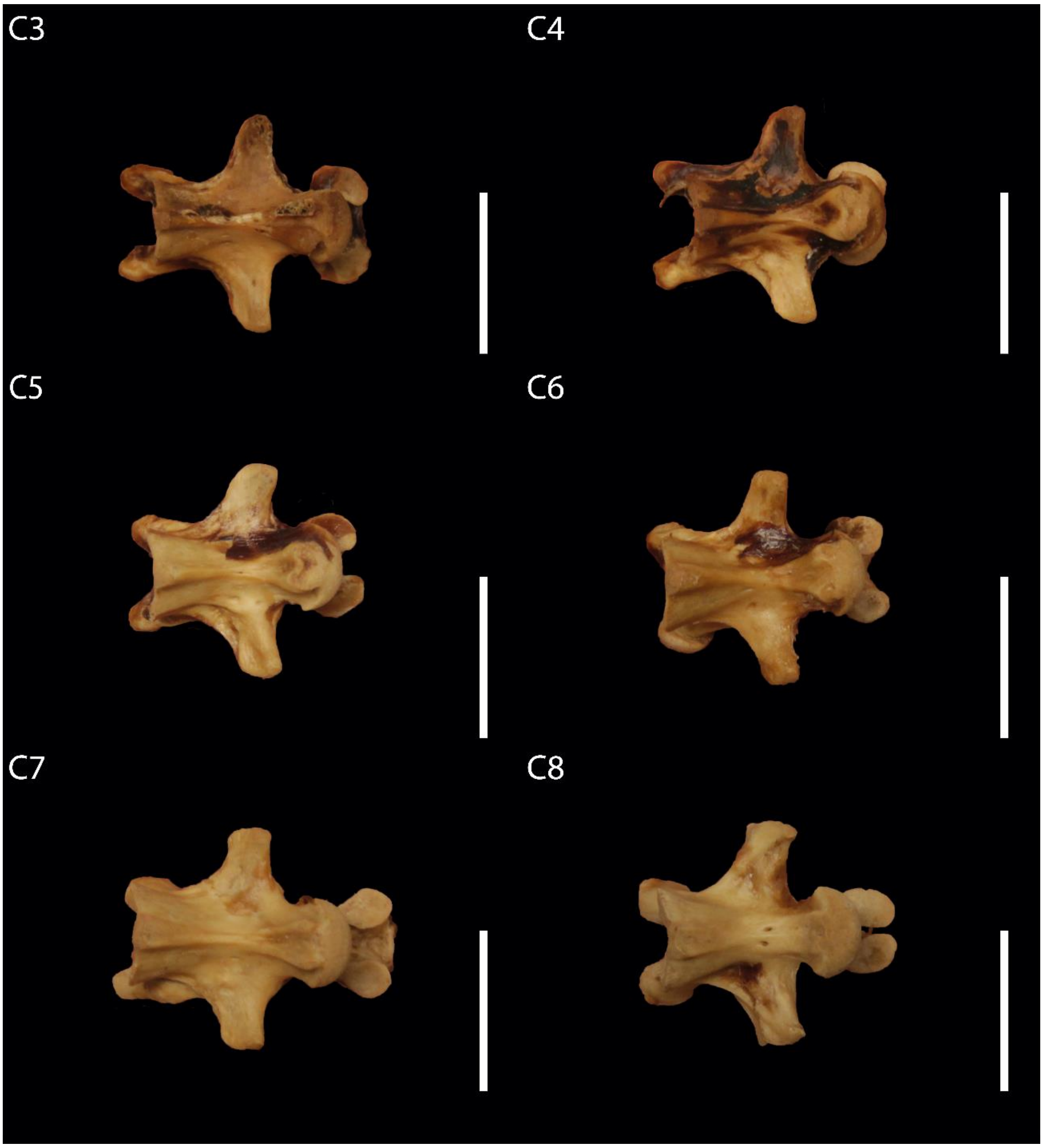

FIG7S: Ventral view *P. subrufa* (USNM40248).

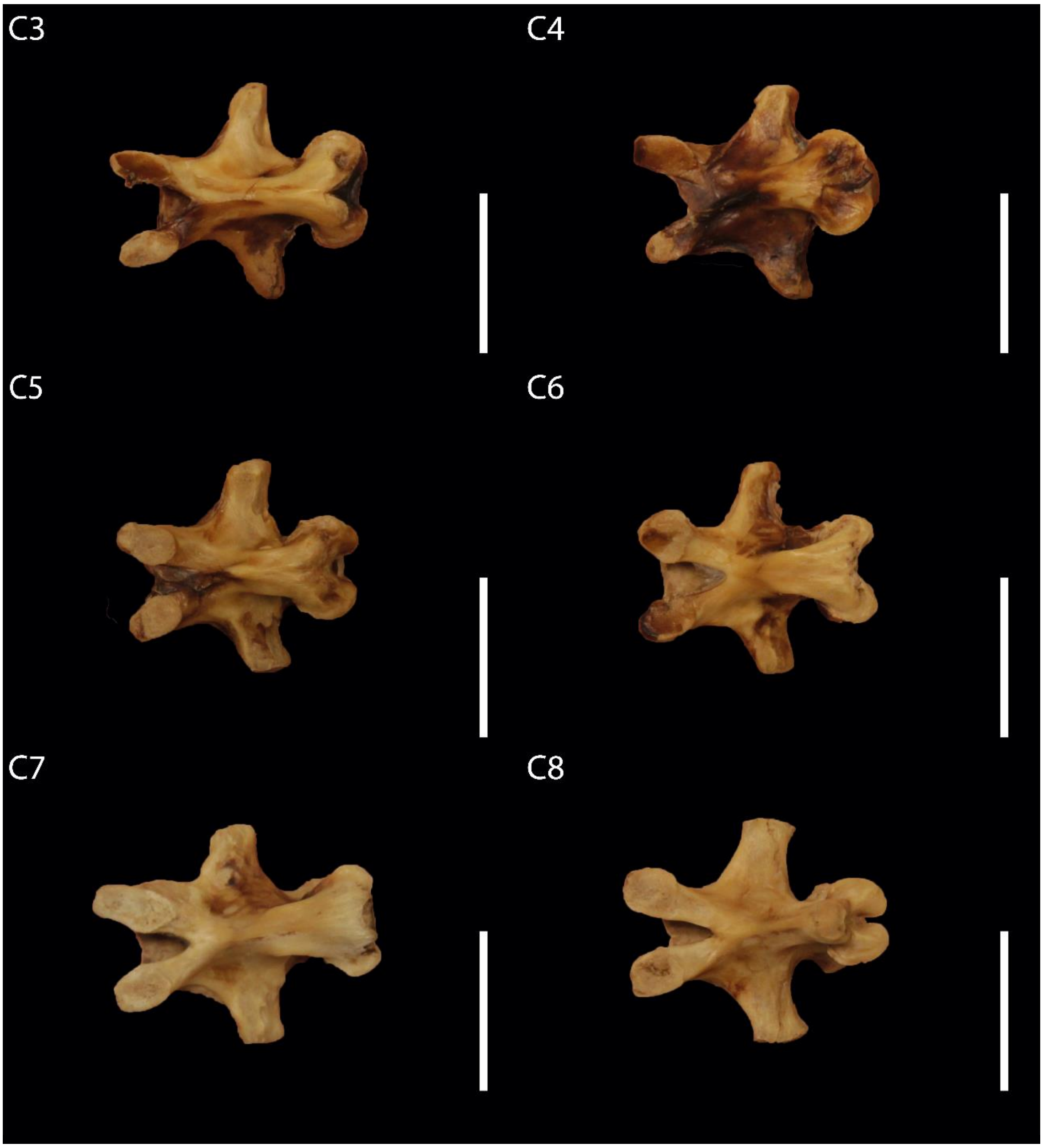

FIG8S: Dorsal view *P. subrufa* (USNM40248).

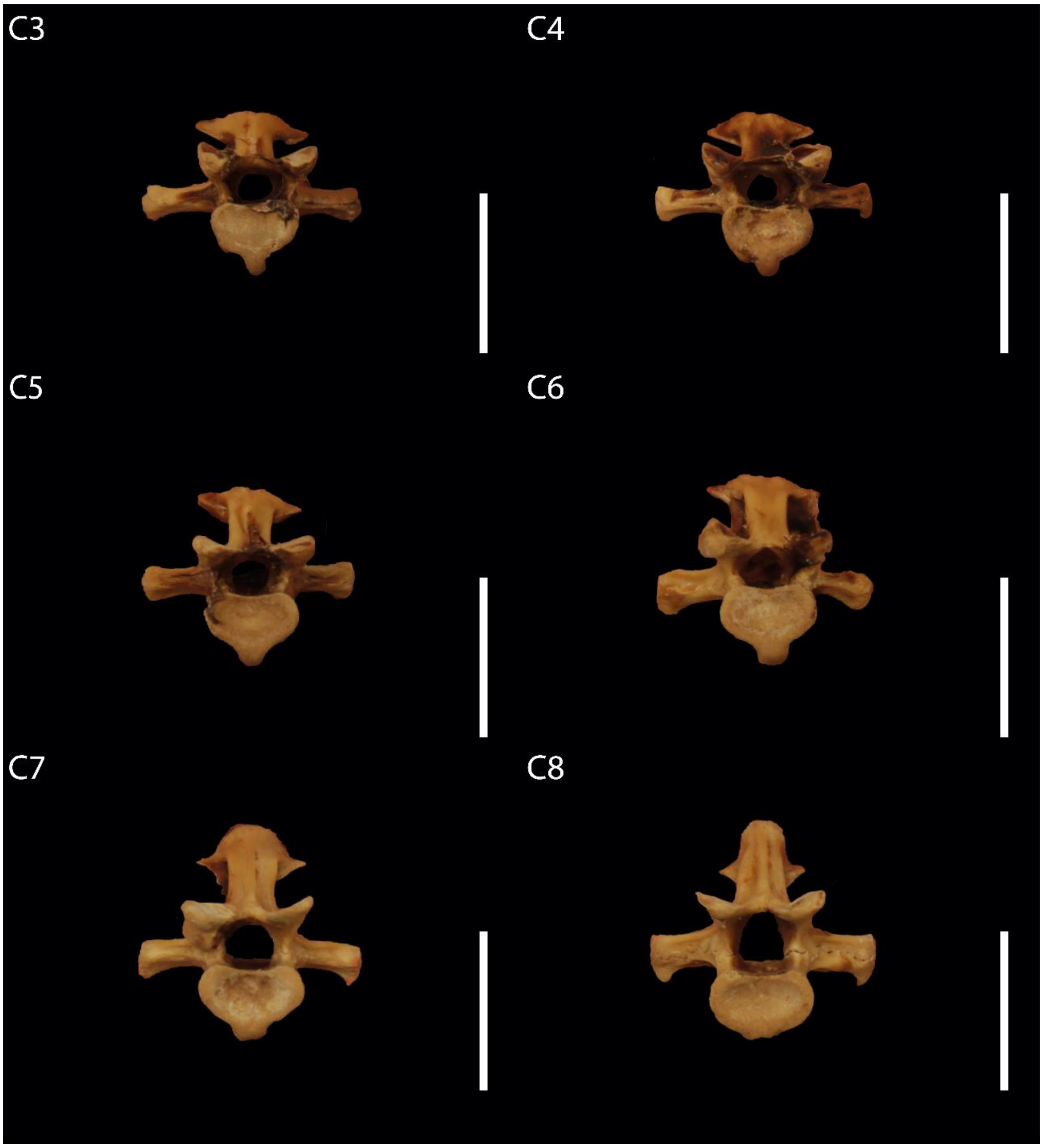

FIG9S: Cranial view *P. subrufa* (USNM40248).

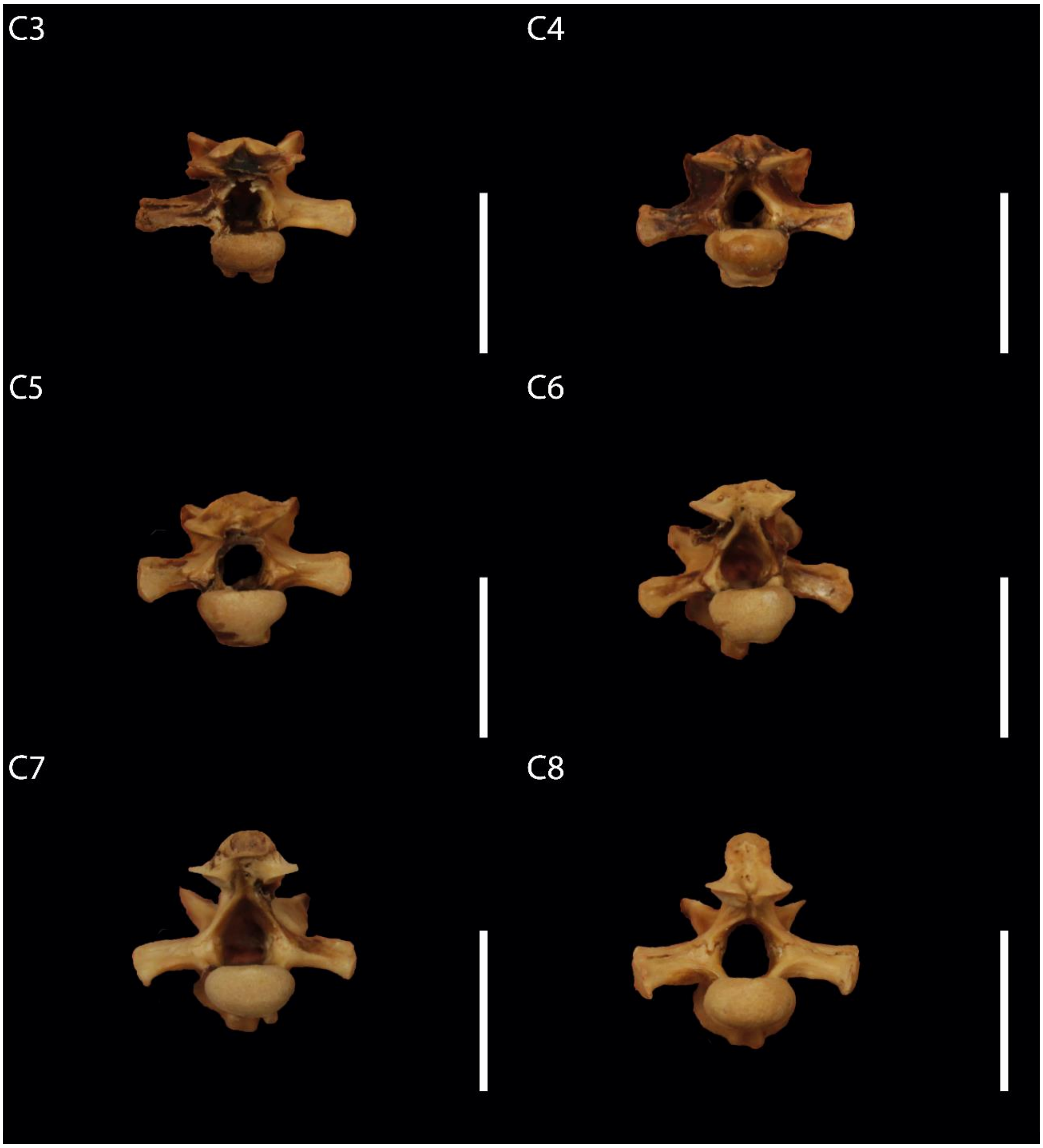

FIG10S: Caudal view *P. subrufa* (USNM40248).

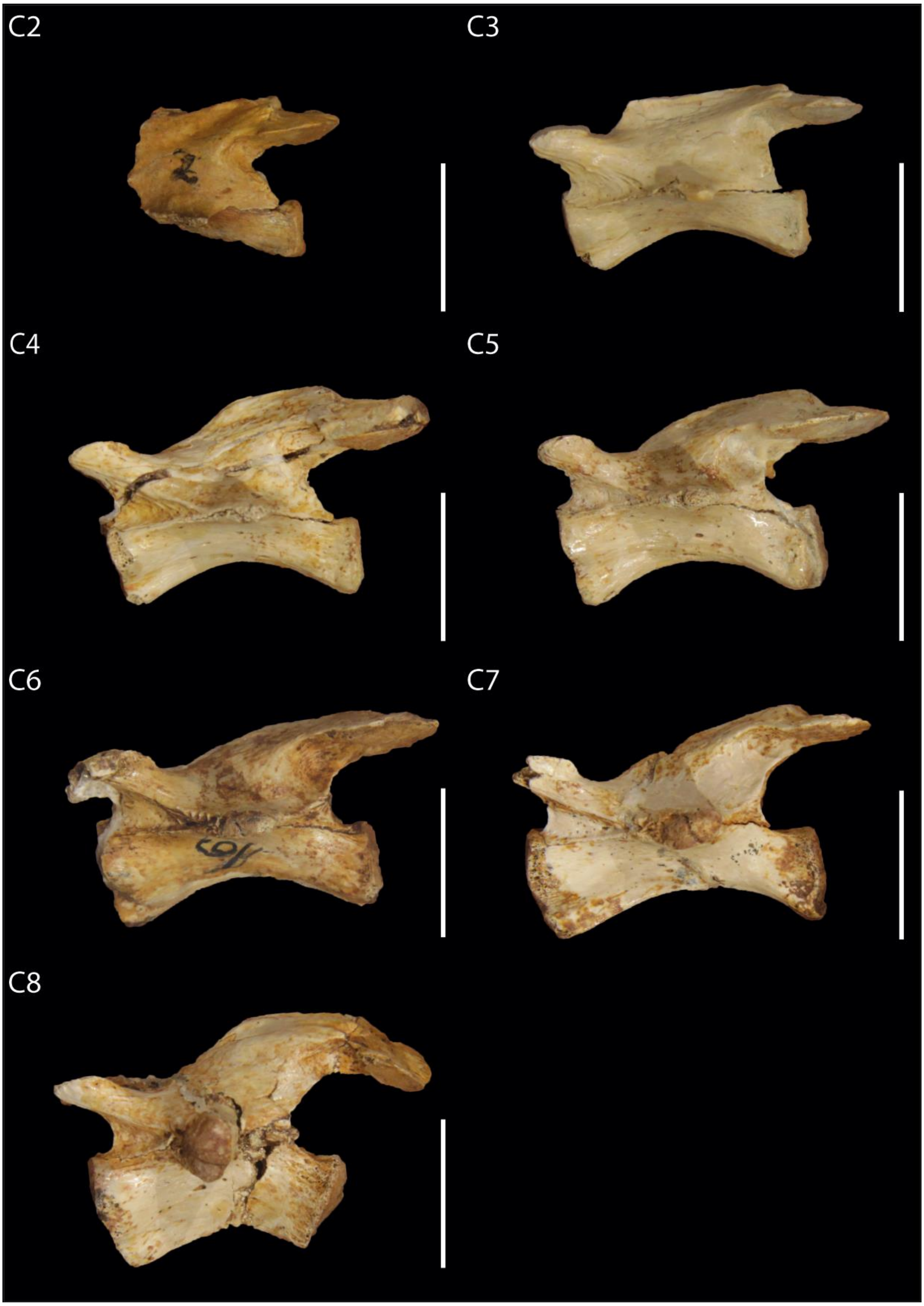

FIG11S: Lateral view of *E. essweini* (FR4922).

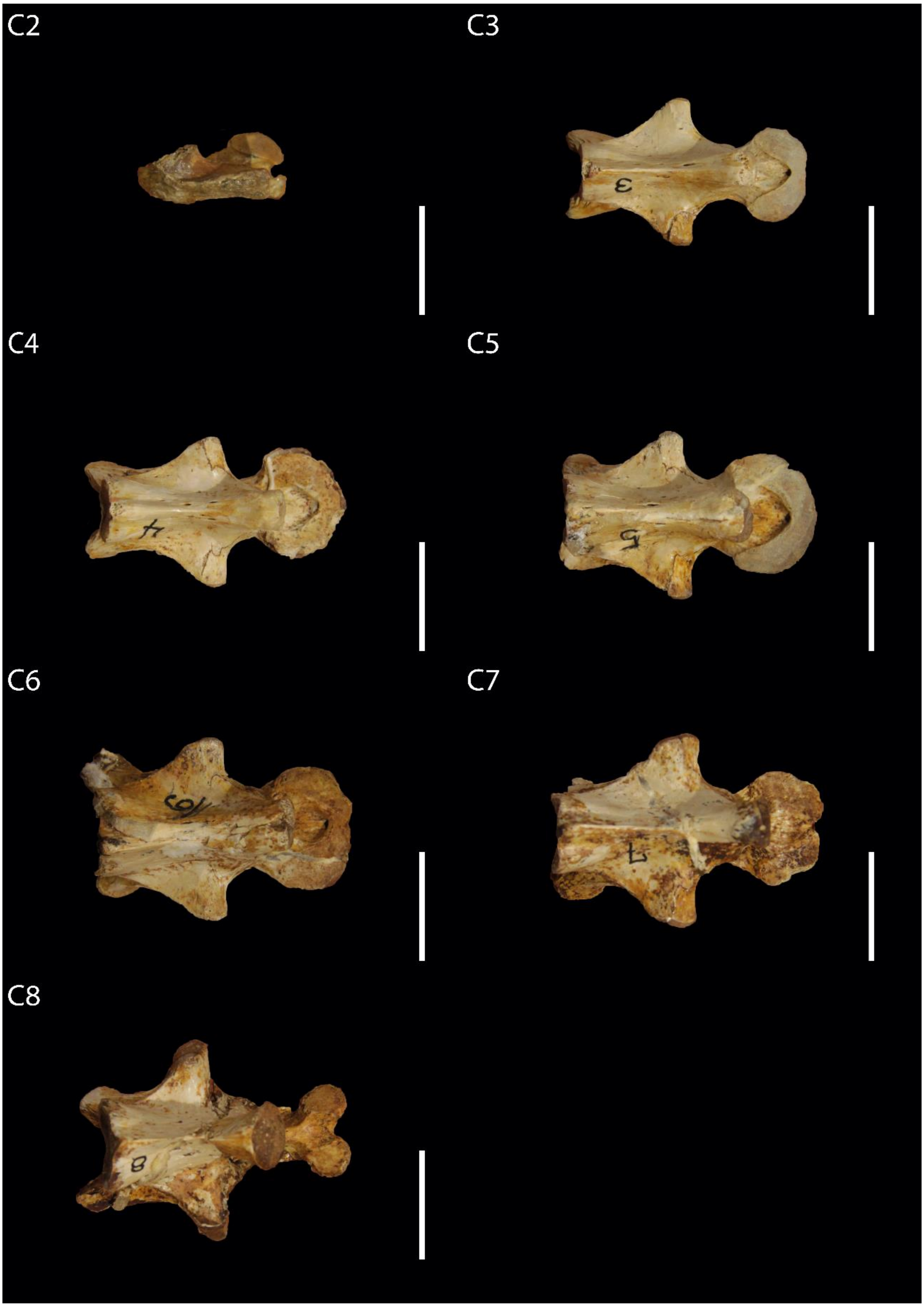

FIG12S: Ventral view of *E. essweini* (FR4922).

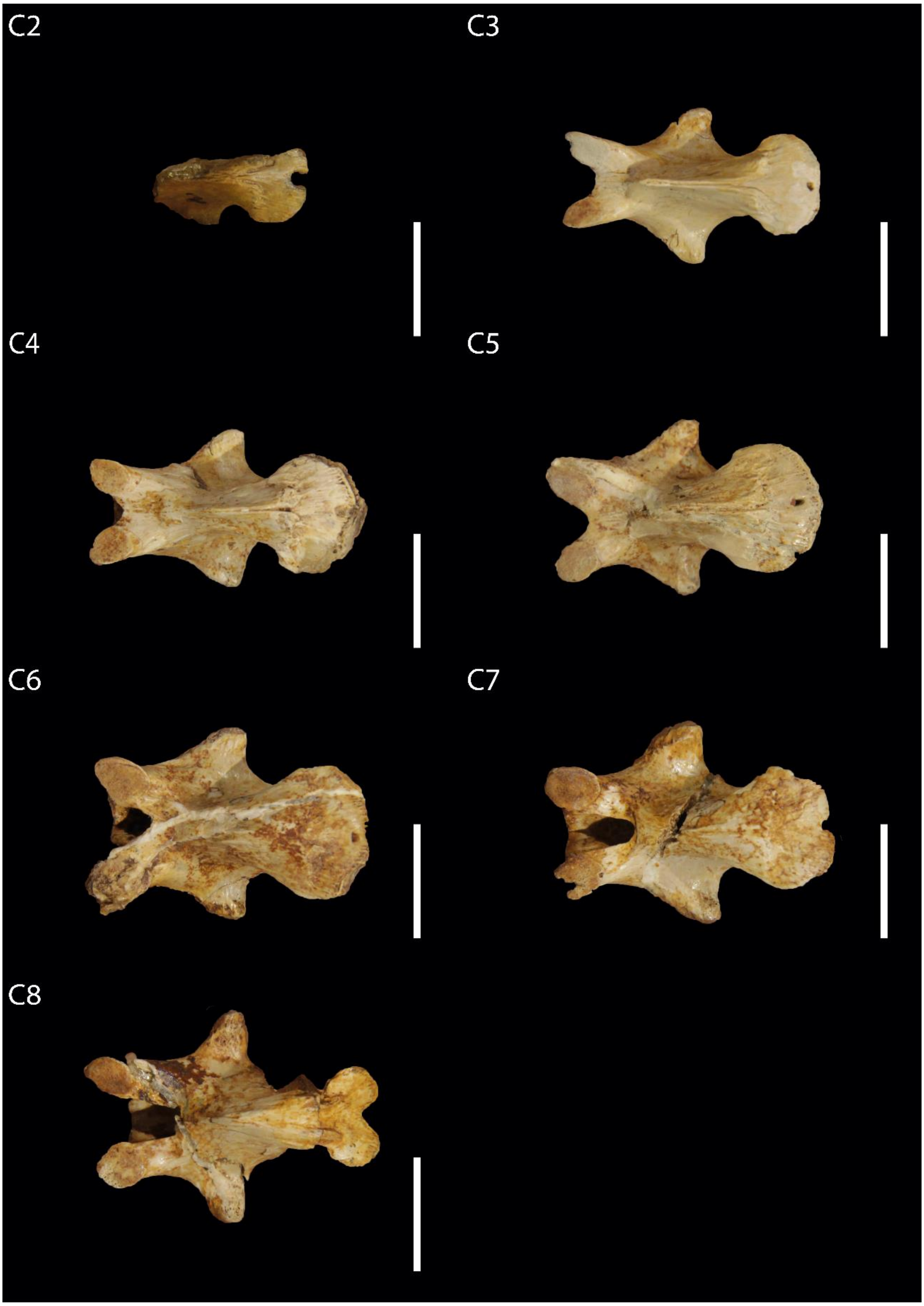

FIG13S: Dorsal view of *E. essweini* (FR4922).

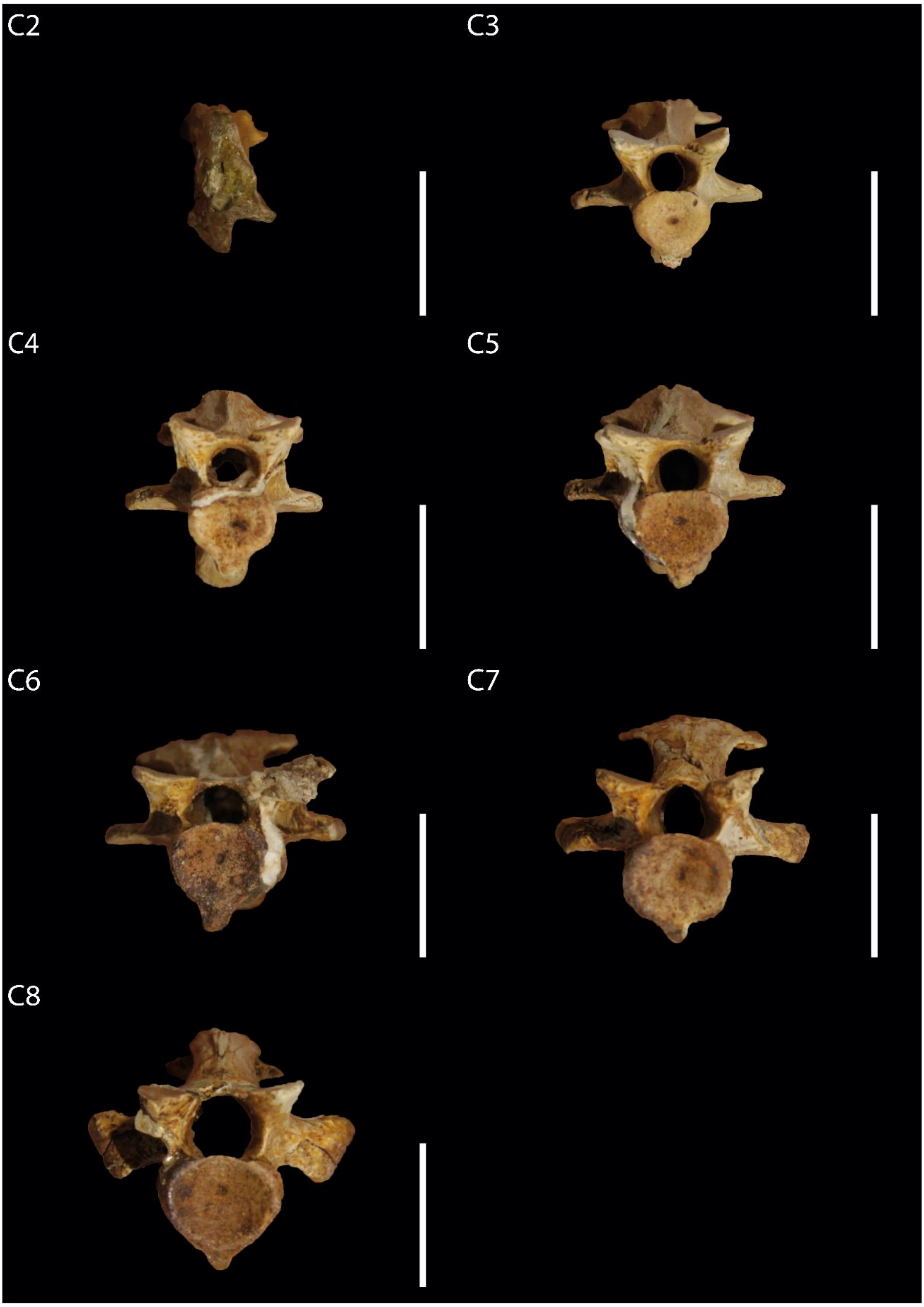

FIG14S: Cranial view of *E. essweini* (FR4922).

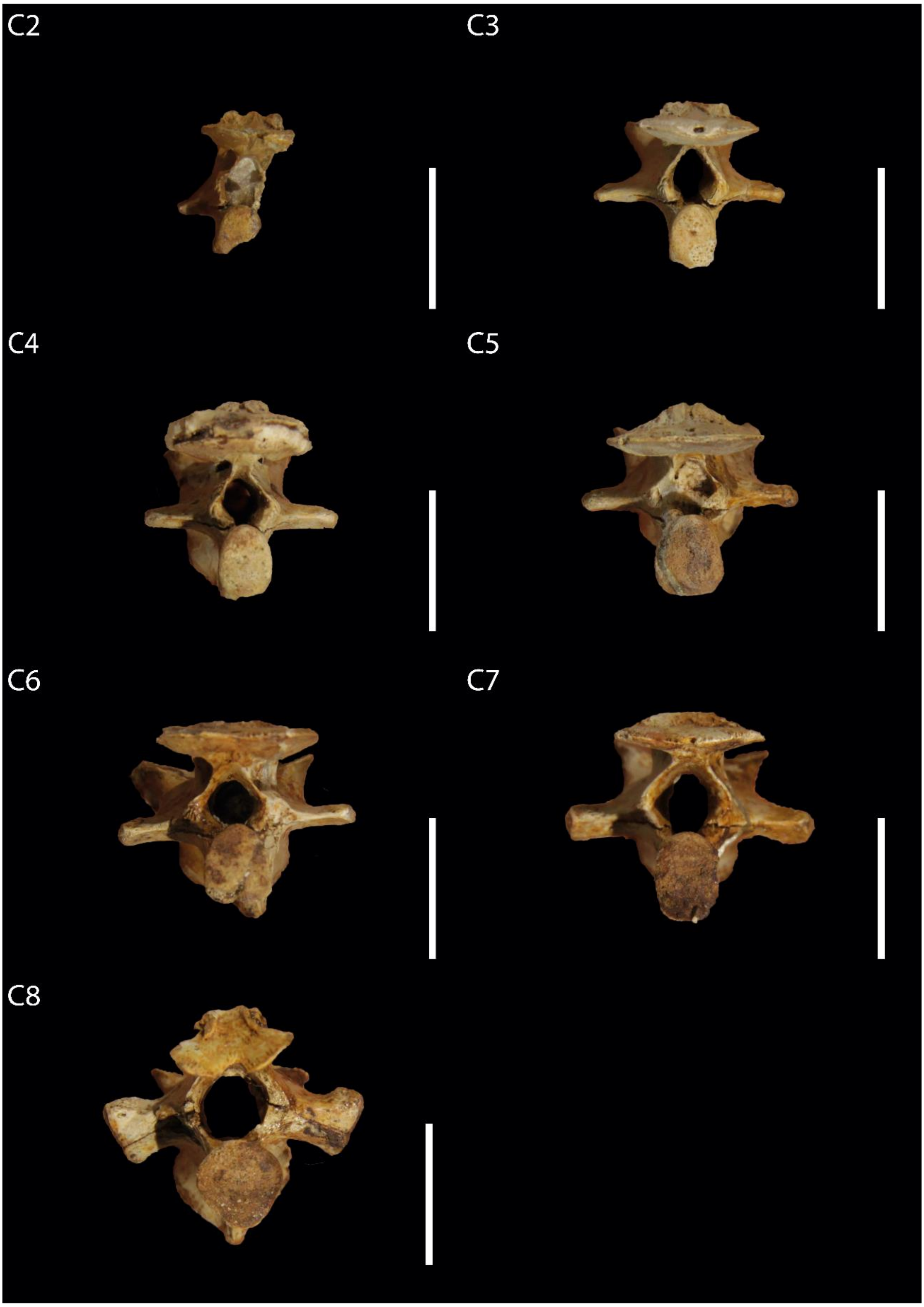

FIG15S: Caudal view of *E. essweini* (FR4922).

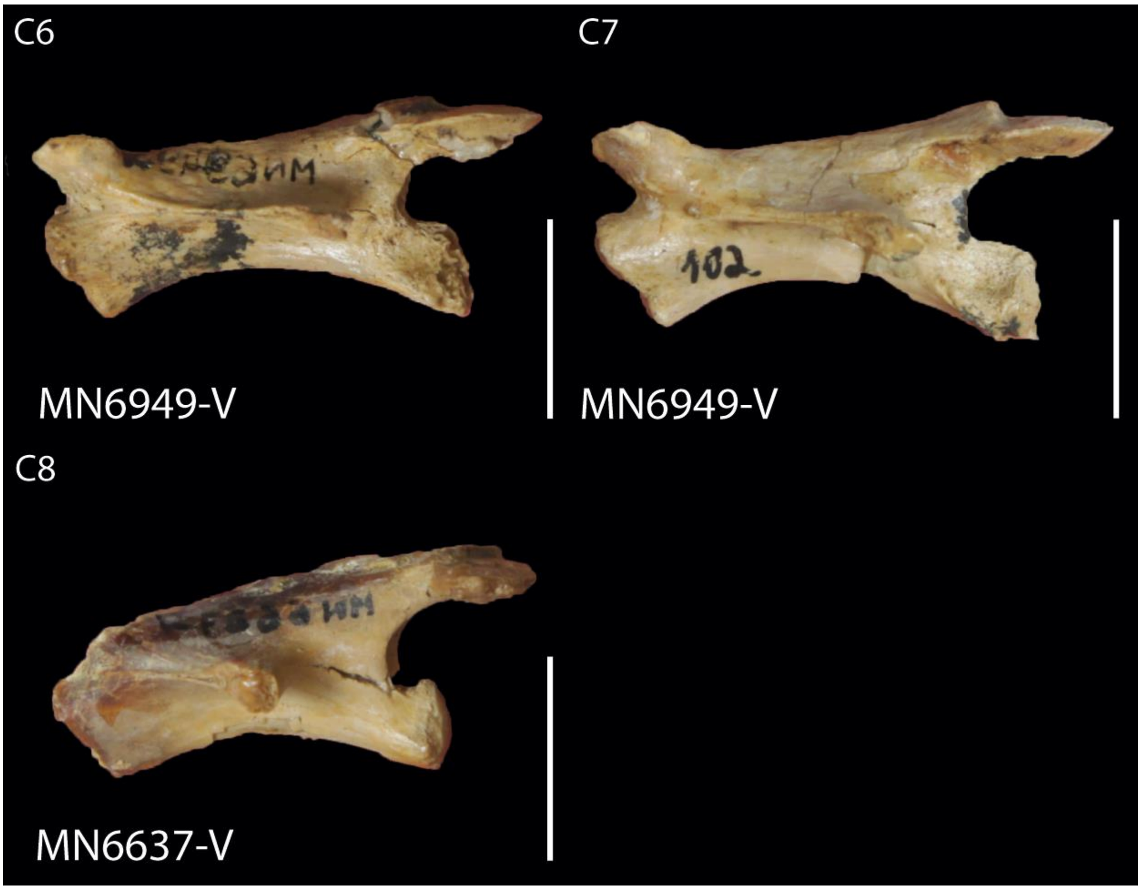

FIG16S: Lateral view of *A. barretoi*.

FIG17S: Ventral view of *A. barretoi*. (AMNH24453).

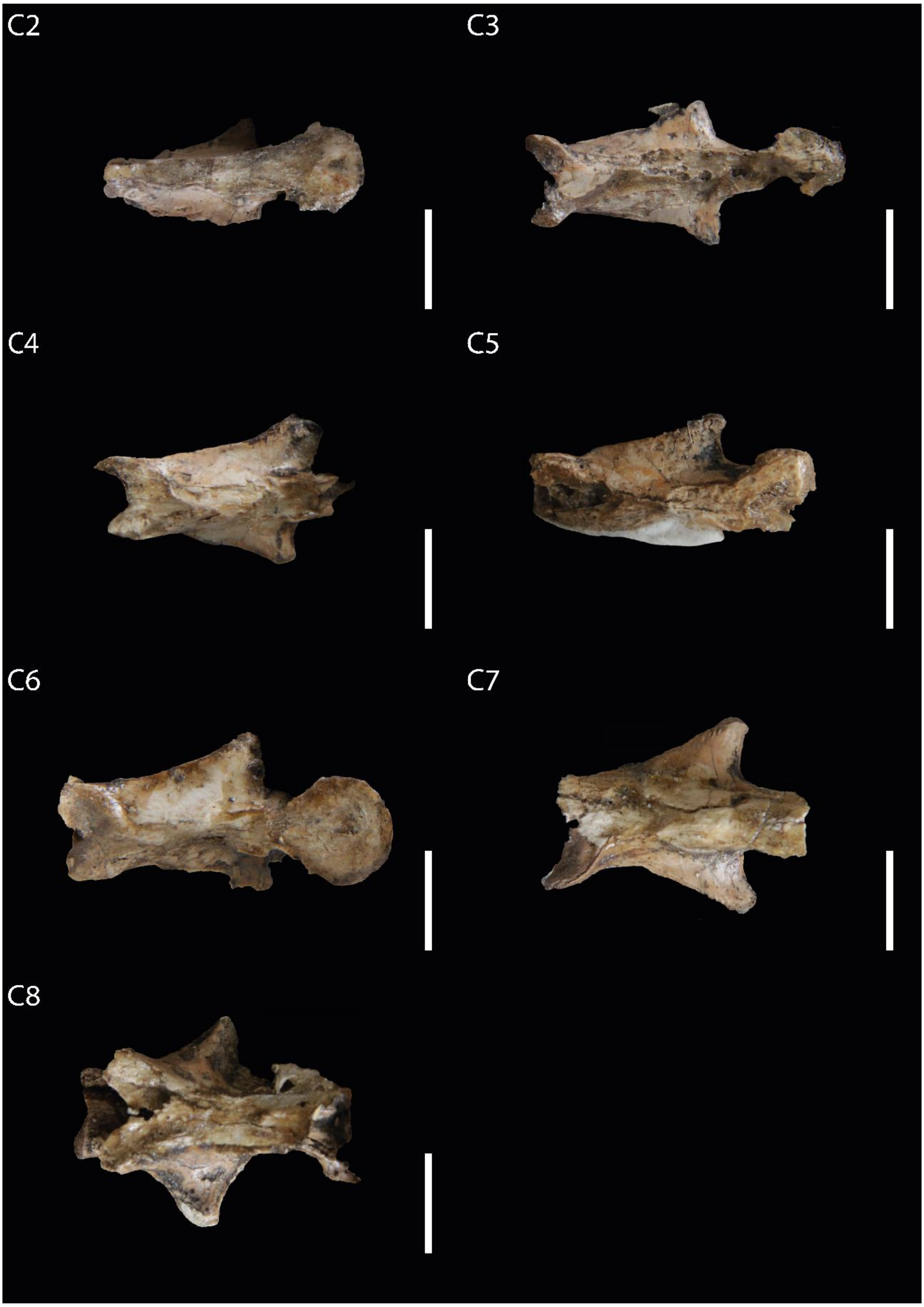

FIG18S: Dorsal view of *A. barretoi* (AMNH24454).

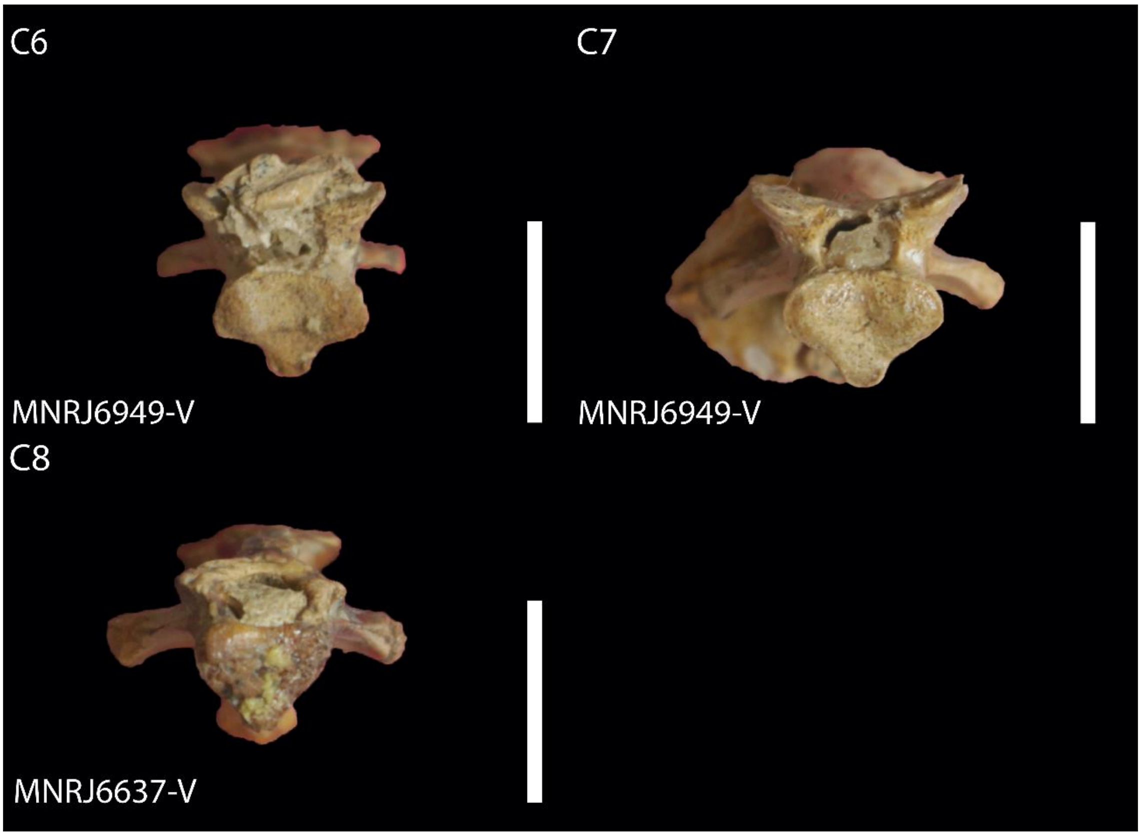

FIG19S: Cranial view of *A. barretoi*.

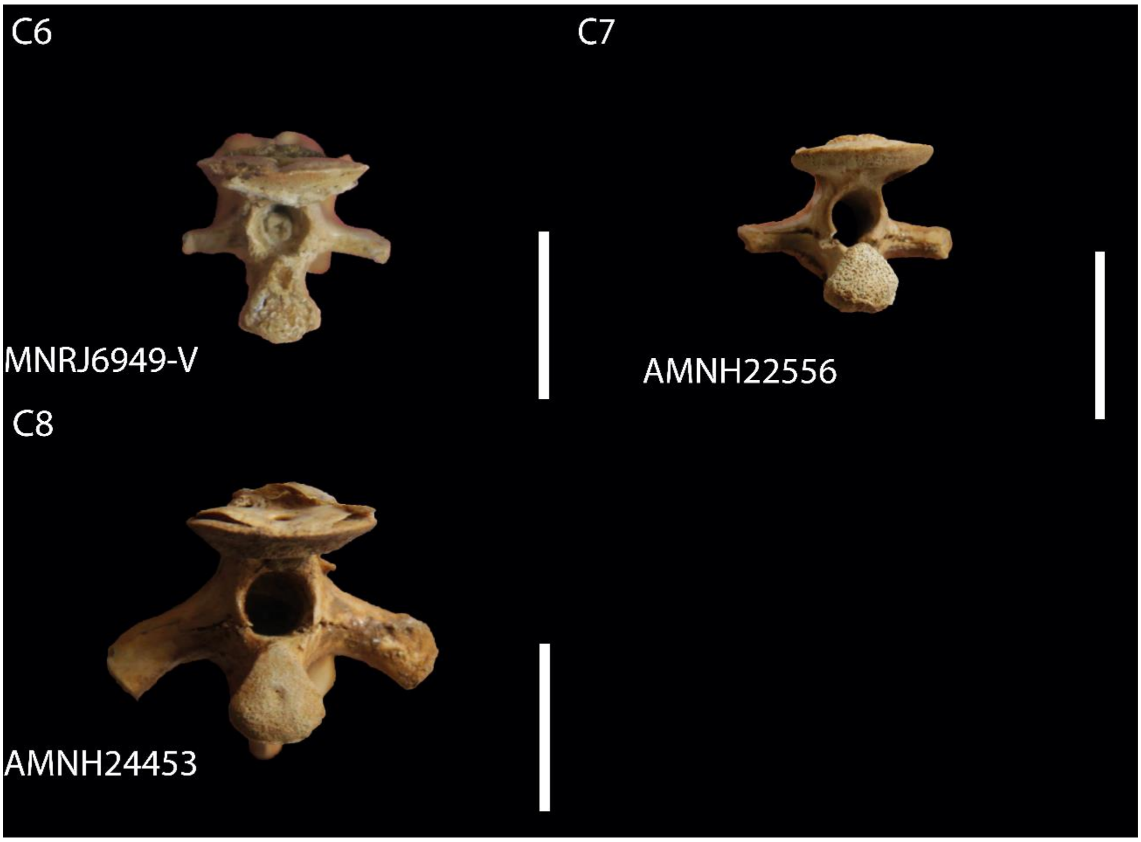

FIG20S: Caudal view of *A. barretoi*.

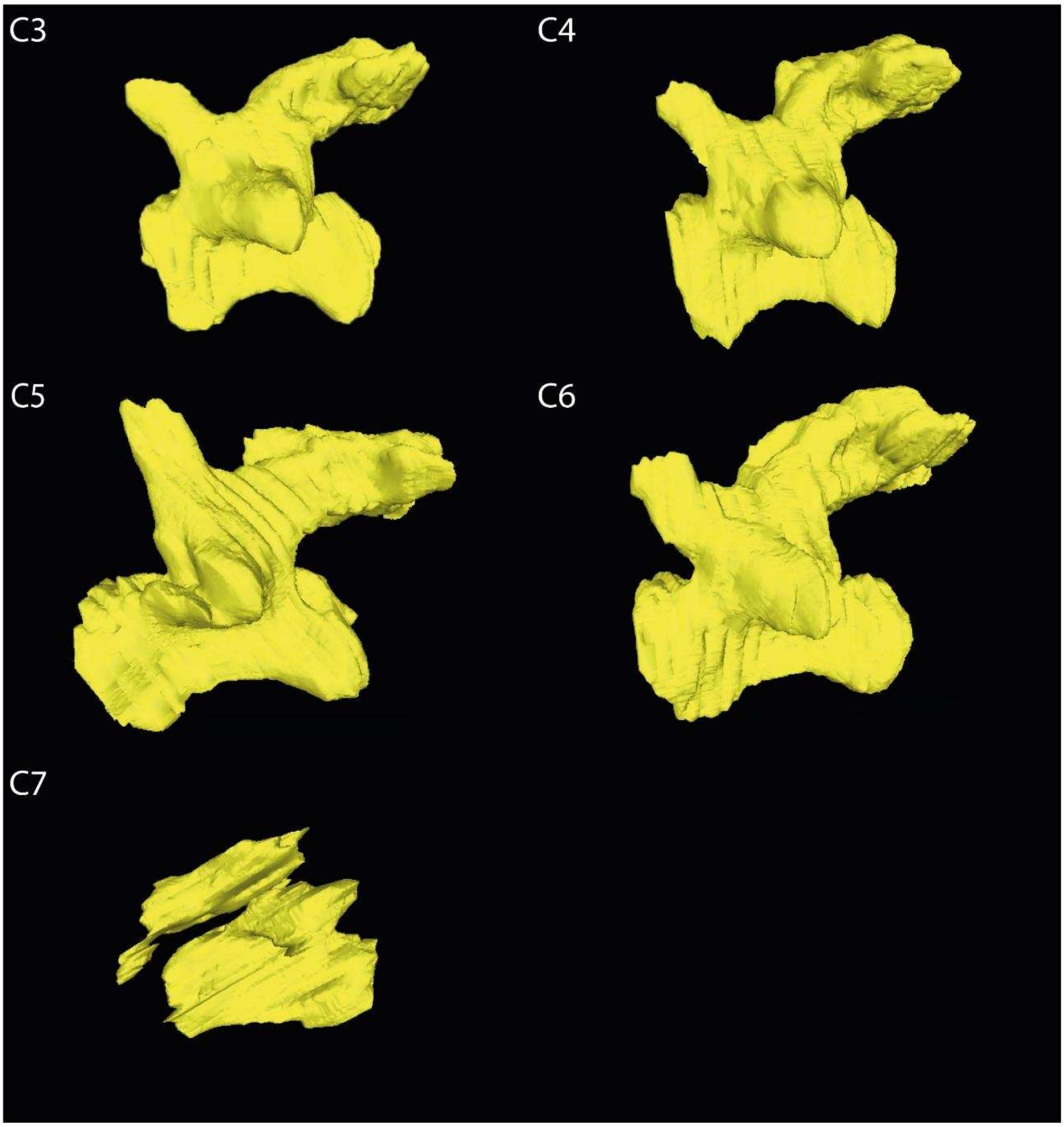

FIG21S: Lateral view of *C. placidoi* (BSPG1976-160).

Table 2: Presence (1) and Absence (0) of cervical laminae in Araripemydidae, Euraxemydidae and Bothremydidae.

	Araripemydidae						**Euraxemydidae**	**Bothremydidae**
	Araripemys barretoi						*Euraxemys essweini*	*Cearachelys placidoi*
Laminae	AMNH 22550	AMNH 22556	AMNH 24453	AMNH 24454	MN6637	MN6949	FR4922	BSPG1976-160
CRCAL	????11	????11	???111	1111111	???1??1	???11?	?111111	?1111??
CACAL	????11	????11	???111	1111111	???1??1	???11?	1111110	?0010??
PRAL	????11	????11	???111	???????	???1??1	???11?	?111111	?1111??
POAL	????00	????00	???000	???????	???0??0	???00?	000111?	?0000??
PRSL	???????	?????1?	???????	???????	???????	???00?	?111111	?1111??
SPOL	????00	????00	???000	???????	???0??0	???00?	?000001	?0000??
CPOL	????11	????11	???111	???????	???1??1	???11?	1111111	?1111??
CPRL	????11	????11	???111	???????	???1??1	???11?	?111111	?1111??
CAHL	????11	????11	???111	???????	???1??1	???11?	?111111	?11111?
CRHL	????00	????00	???000	???????	???0??0	???00?	?000000	?00000?
CRPHL	????01	?????1?	????10	???????	???0??0	????0??	?110000	?11111?
CAPHL	????00	????00	????00	???????	???0??0	???00?	?000000	?00000?

Table 3: Presence (1) and Absence (0) of cervical laminae in Pelomedusidae.

	Pelomedusidae							
	Pelomedusa			**Pelusios**				
	Pelomedusa subrufa			*Pelusios chapini*	*Pelusios gabonensis*	*Pelusios sinuatus*	*Pelusios subniger*	
Laminae	USNM40248	USNM63099	USNM222469	AMNH10065	AMNH10053	USNM42144	AMNH71188	USNM220896
CRCAL	?111111	?111111	1?11111	1111111	111111?	1111?11	1111111	1111111
CACAL	?111111	??????1	1??0111	1111111	111111?	1111?11	1111111	1111111
PRAL	?111111	?011111	0?11111	?111111	011111?	0111?11	0111111	0111111
POAL	?111111	??????1	0??000?	?111111	001??1?	0111?11	0011111	0001111
PRSL	?111011	?001011	0?01011	?101111	011101?	0111?11	0001001	0001011
SPOL	?000011	?000011	1?00011	?000011	100000?	1000?11	1000001	1000001
CPOL	?111111	?111111	1?11111	?111111	111111?	1011?11	1111111	1111111
CPRL	?111111	?111111	1?11111	?111111	111111?	1111?11	1111111	1111111
CAHL	?111111	?111111	1?11111	1111111	111111?	1111?11	1111111	1111111
CRHL	?000000	?000000	0?00000	1000000	110000?	1000?00	0000000	0000000
CRPHL	?111111	?111110	1?11111	1111111	111111?	1111?11	1111111	1111111
CAPHL	?000000	?000000	0?00000	0000001	000000?	0000?00	0000000	0000000

Table 4: Presence (1) and Absence (0) of cervical laminae in Podocnemididae

	Podocnemididae										
	Podocnemis										
	Podocnemis expansa			*Podocnemis unifilis*			*Podocnemis sextuberculata*		Podocnemis erythrocephala		
Laminae	AMNH46174	AMNH6597	AMNH46250	INPA10020	INPA10021	MZSP2708	INPA5402	INPA8936	INPA10261	INPA10266	INPA12413
CRCAL	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111
CACAL	1111110	1111110	1111110	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111
PRAL	0111111	0111111	0111111	0111111	0111111	0111111	0111111	1111111	0111111	0111111	0111111
POAL	0000000	0000000	0000000	0000000	0000000	0000000	0000000	0000000	0000000	0000000	0000000
PRSL	0111111	0111111	0111111	0111011	0111001	0111111	0101001	0111011	0111111	0111111	0111011
SPOL	1000001	1000001	1000011	1000001	1000001	1000011	1000011	1000011	1000000	1000001	1000001
CPOL	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111
CPRL	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111
CAHL	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111	1111111
CRHL	1000000	1000000	0000000	1000000	1000000	0000010	1000000	1110000	0110000	1100000	1100000
CRPHL	1111101	1111111	1111111	1111111	1111011	1111101	1111111	1110001	1111011	11?1110	0101011
CAPHL	0000001	0000011	0000011	0000001	0000001	0000001	0000001	0000011	0000001	00?0000	0000001

Table 5: Presence (1) and Absence (0) of cervical laminae in Podocnemididae

	Podocnemididae			
	Erymnochelys	**Peltocephalus**		
	Erymnochelys madagascariensis	Peltocephalus dumerilianus		
Laminae	AMNH63579	INPA21940	INPA22887	INPA25560
CRCAL	1111111	1111111	1111111	1111111
CACAL	1111111	1111110	1111111	1111111
PRAL	0111111	0111111	0111111	0111111
POAL	0000110	0000010	0000000	0000011
PRSL	0111011	0111111	0111111	0111111
SPOL	1000001	1000111	1000111	1000111
CPOL	1111111	1111111	1111111	1111111
CPRL	1111111	1111111	1111111	1111111
CAHL	1111111	1111111	1111111	1111111
CRHL	1000000	1100000	1110000	1110000
CRPHL	1111111	0001111	0001111	1100111
CAPHL	0000000	0000000	0000000	000000?