

The vertebral column of *Chaetophractus villosus* (Desmarest, 1804) (Chlamyphoridae, Cingulata, Xenarthra): Anatomy and Thoracolumbar variation. Spinal cord relation

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Abstract. Mammals of the Xenarthra clade show a large number of unusual characters in the skeleton, mainly in the vertebral column. In spite of the importance of the knowledge on the axial skeleton in this group, there are no detailed studies on the morphology of the entire vertebral column. Here we performed a comprehensive study of the vertebral column of *Chaetophractus villosus* (Desmarest, 1804), a representative of Chlamyphoridae, in order to provide a more reliable comparative framework among armadillos. Morphological description was based on 44 adult postcranial axial skeletons. As a complement to the morphological descriptions of the skeleton we studied the paths followed by blood vessels and nerves in close relationship to the axial skeleton (using 13 fresh adult specimens, six females and seven males, part of the doctoral Thesis of one of the authors). Intraspecific variability in the thoracolumbar number in *C. villosus* was also evaluated. We identified certain variability in the position of the first vertebral pair that bears a xenarthral facet, ranging from T4-T5 to T6-T7, being T5-T6 and T6-T7 the most frequent positions. The second pair of xenarthrales is set near the thoracolumbar limit, and ranges between T9-T10 and T11-L1 (T10-T11 in most specimens). The variability in the total number of thoracolumbars in *C. villosus* falls within the range of most mammals and sets controversy about an important morphological feature that groups extant Xenarthra and Afrotheria into the southern placentals (Atlantogenata). In this regard, a more comprehensive study of this character is necessary to elucidate the patterns of distribution of this trait among xenarthrans.

Keywords. Armadillos; Vertebral morphology; Thoracolumbar number.

INTRODUCTION

Mammals of the Xenarthra clade show a large number of unusual characters in the skeleton such as the fusion of the transverse processes of caudal vertebrae to the ischium, the presence of a secondary scapular spine, the presence of dermal ossifications (osteoderms), and the reduction or simplification of the dentition (Engelmann, 1985). Also, among these skeletal features are those in the vertebral column that gave the clade the name Xenarthra Cope, 1889, due to their accessory apophyses (the xenarthrales) in the lumbar and posterior thoracic vertebrae. Xenarthrales are

present as one, two, or three pair of accessory articulations in the anterior and posterior faces of adjacent vertebrae.

Several hypotheses regarding the functional significance of the xenarthrales were proposed. Winge & Hoffstetter (see Gaudin & Biewener, 1992) suggested that xenarthrales are linked to a particular behavior observed in some extant armadillos that roll into an almost perfect ball when under attack. This rolling behavior would be possible due to friction movements between anapophyses, zygapophyses, and transverse processes. Nevertheless, only the extant genus *Tolypeutes* (Cingulata, Chlamyphoridae, Tolypeutinae) exhib-

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its such behavior as defense mechanism, which makes this hypothesis unlikely. Other authors have linked the development of xenarthrales to acquisition of fossorial habits in a common ancestor to the clade. According to Frechkop (see Gaudin & Biewener, 1992) the giant armadillo *Priodontes* can stand up in biped position, bearing the entire body weight on its hindlimbs while the trunk is horizontal with respect to the substrate. The accessory articulations would stiffen the vertebral column so the trunk can be supported by the hind limbs, freeing the forelimbs to dig. In this regard, Jenkins (1970) mentioned that in addition to stiffening the vertebral column for body weight support, the xenarthrales could also be important for transmitting forces to the pelvis and hindlimbs generated by the forelimbs during digging. Gaudin & Biewener (1992) performed biomechanical experimental studies using the vertebral column of *Dasyopus novemcinctus* and suggested, in agreement with Frechkop and Jenkins, that xenarthran facets are an adaptation of the group for digging. Furthermore, Oliver et al. (2016) suggested that xenarthrales not only stiffened the vertebral column but also stabilized the articulations, increasing the range of movements in dorso-ventral and lateral planes.

Another feature that characterizes Xenarthra when compared to the rest of extant mammals is the high variability in vertebral number of some regions of the vertebral column. In Table 1 are detailed some vertebral numbers according to different authors (Owen, 1868; Lessertisseur & Saban, 1967; Gaudin & Biewener, 1992; Narita & Kuratani, 2005; Galliari et al., 2010; Asher et al., 2011). In the cervical region, this clade includes members that deviate from the typical vertebral number of seven found in the rest of mammals. In extant arboreal sloths, the genus *Bradypus* shows eight to ten cervical vertebrae, while species of *Choloepus* show between five and seven cervicals, being six the most common number (Buchholtz & Stepien, 2009). Furthermore, from the study of few taxa of Xenarthra (*Dasyopus novemcinctus*, *Bradypus* spp., and *Choloepus hoffmanni*), Asher et al. (2011) proposed a character shared by Xenarthra and Afrotheria (e.g., elephants, aardvark, golden moles), a high intraspecific variability in the thoracolumbar vertebral number. Among others, this character supports the clade Atlantogenata (Xenarthra plus Afrotheria) and the hypothesis of the “southern placentals” (Asher et al., 2009, 2011).

Table 1. Number of vertebral elements in the vertebral column of Xenarthra, and other internal groups, according to different authors.

	Owen (1868)	Lessertisseur & Saban (1967)	Gaudin & Biewener (1992)	Narita & Kuratani (2005)	Galliari et al. (2010)
	<i>Dasyopus kappleri</i>	Dasyopodidae + Chlamyphoridae	<i>Dasyopus novemcinctus</i>	Xenarthra	Cingulata
Cervical	7	7	—	7-9	—
Thoracic	10	9-12	10	10-23	9-13
Lumbar	5	2-5	5	2-5	2-5
Sacral	8	8-13	—	5-9	—
Caudal	16	11-23	—	4-37	—

In spite of the importance of the knowledge on the axial skeleton in this group, there are no detailed studies on the morphology of the entire vertebral column. In this work, we aim to address this issue by studying the armadillo *Chaetophractus villosus* (Desmarest, 1804), with comparison on other cingulates. Some works have approached this matter through comparative studies of the xenarthran facets in cingulates (Gaudin, 1999) and its implications in biomechanics, or through the study of variability in the vertebral column. Nevertheless, most of these works focused on one species, *Dasyopus novemcinctus* (Gaudin & Biewener, 1992; Asher et al., 2011; Oliver et al., 2016). This armadillo was traditionally considered as a basal taxon of Cingulata (armadillos) and grouped into the Dasyopodinae (Dasyopodidae, Cingulata). Currently, the subfamily has been elevated to family status, and the rest of the extant armadillos were included in the family Chlamyphoridae (Delsuc et al., 2016). In this regard, a comprehensive study of the vertebral column of a representative of Chlamyphoridae, such as *Chaetophractus villosus*, could help address these issues in a more reliable comparative framework.

MATERIAL AND METHODS

Morphological description was based on 44 adult postcranial axial skeletons of *Chaetophractus villosus* housed on the Colección de Mastozoología and the Laboratorio de Morfología Evolutiva y Desarrollo from the Museo de La Plata (Table 2). All 44 specimens lacked caudal vertebrae, and a few lacked vertebrae from different regions. Nevertheless, data on caudal region was obtained from the unpublished doctoral Thesis dissertation of one of the authors (Aldana-Marcos, 1996: Chapter III). Traditional terminology for vertebral column regionalization was used: cervical region (C), thoracic region (T), lumbar region (L), sacral region (S), and caudal region (Cd) (Lessertisseur & Saban, 1967; Gray, 1977). Anatomical terminology of the vertebral column followed Gray (1977), Lessertisseur & Saban (1967), Gaudin & Biewener (1992), and Gaudin (1999).

Intraspecific variability in the thoracolumbar number in *C. villosus* (Table 3) was evaluated in 41 specimens, using the corrected coefficient of variation for the thoracolumbar (TL CV) (Asher et al., 2011). The CV represents the standard deviation of a data series expressed as a percentage of the mean and were calculated for thoracolumbar counts on *C. villosus* specimens ($CV = \text{stdev}(100)/\text{average}$). Following Asher et al. (2011), we also applied a correction term ($1 + (1/4n)$) for small sample size, where n is the sample size.

Results were compared to TLCV's obtained by Asher et al. (2011) for other mammalian clades.

As a complement to the morphological descriptions of the skeleton, we also focused on the study of the paths followed by vertebral artery and spinal nerves. We used the anatomical description of 13 fresh adult specimens, six females and seven males, that were part of the doctoral Thesis of one of the authors (Aldana-Marcos, 1996: Chapter III).

RESULTS

Vertebral Column Morphology

Cervical region

Comprises the first seven vertebrae (C1 to C7). The atlas (C1) is free and the axis (C2) fuses to a variable number of posterior cervical vertebrae (see Table 2 and

Table 2. Number of vertebral elements composing the different regions of the vertebral column of *Chaetophractus villosus*. References: C. Vb. = Cervical vertebrae (counting the mesocervical bone as one cervical); Meso. Vb. = Number of vertebrae fused into a mesocervical bone; T. Vb. = Thoracic vertebrae; L. Vb. = Lumbar vertebrae; S. Vb. = Sacral vertebrae.

ID Nº	C. Vb.	Meso. Vb.	T. Vb.	L. Vb.	S. Vb.
LMED-548	—	—	—	3	8
LMED-565	—	—	—	—	8
LMED-585	5	3	11	3	—
LMED-632	6	2	11	3	7
LMED-633	5	3	11	3	8
LMED-634	6	2	11	3	8
LMED-959	6	2	11	3	8
LMED-635	—	—	11	3	8
LMED-636	—	—	11	3	8
LMED-637	6	2	12	2	8
LMED-638	6	2	11	3	7
LMED-639	5	3	11	3	8
LMED-640	5	3	11	3	8
LMED-641	6	2	11	3	8
LMED-642	6	2	11	3	8
LMED-647	6	2	11	3	8
LMED-648	6	2	11	3	8
LMED-649	5	3	12	2	—
LMED-651	—	—	12	3	7
LMED-652	5	3	12	3	7
LMED-653	—	—	11	3	7
LMED-654	6	2	11	3	8
LMED-655	—	—	11	3	8
LMED-656	6	2	11	3	8
LMED-657	—	—	11	3	8
LMED-659	5	3	11	3	8
LMED-660	5	3	11	3	8
LMED-661	—	—	11	3	8
LMED-663	—	—	11	3	8
LMED-665	6	2	11	3	—
LMED-673	5	3	11	3	—
LMED-701	6	2	—	3	8
LMED-702	5	3	11	3	8
MLP 1214	—	—	11	3	—
MLP 15.X.98.03	5	3	11	3	—
MLP 785	6	2	11	3	—
MLP 795	6	2	11	3	—
MLP 819	6	2	11	4	—
MLP 821	5	3	11	3	—
MLP 831	5	3	11	3	—
MLP 855	5	3	11	3	—
MLP 860	6	2	11	3	—
MLP 918	6	2	11	3	—
MLP 922	6	2	11	3	—

description below). The vertebral canal is large, and the vertebral bodies are flattened and transversely wide.

The atlas (C1) is formed by two lateral masses linked by the dorsal and ventral arches. Each lateral mass shows a poorly developed transverse apophysis, and a flat surface (pseudopostzigapophysis) for the articular apophysis of the axis (Fig. 1A, B). The dorsal arch shows an eminence, the tubercle (a reduced neuropophysis), and posteriorly an articular surface that contacts the neuropophysis of the axis (Fig. 1B). At both lateral sides, the dorsal and ventral foramina of the first spinal nerve are observed (Fig. 2). The ventral arch is narrow, and bears the *fovea dentis* for the odontoid process of the axis (Fig. 1B). The anterior face of the atlas shows a pair of transverse foramina above the glenoid cavity (Fig. 1A), which relate to: a) the exit of the first spinal nerve that bifurcates inside the lateral masses and emerges into the previously described external nervous foramina, b) the vertebral arteries (Fig. 2).

The vertebral arteries branch from the aorta and penetrate into the vertebral column through the exit of the sixth cervical nerve (Fig. 2A). From the lateral mass of the sixth cervical vertebrae the artery takes a cranial direction inside the transverse canal that runs parallel to the vertebral canal in the lateral masses of the successive cervicals (Fig. 2B). In the atlas, the vertebral artery changes direction towards lateral and, after making a loop, splits into two branches (Fig. 2B). A small branch directs dorsally leaving the lateral mass through the dorsal foramen of the first spinal nerve, and connects with the external carotid. A larger branch returns internally and penetrates into the vertebral canal through the internal foramen of the atlas (internal exit of the first cervical nerve). Inside the vertebral canal, the artery forms a bulb (next to the first spinal ganglion), directs ventrally surrounding the Dura matter, and takes a cranial direction toward the medulla (Fig. 2B).

The axis (C2) is strongly fused to C3, and variably to C4, forming the mesocervical bone (Fig. 1C, D, E). When fusions are present between C3 and C4, they are observed between lateral masses of successive verte-

Table 3. Thoracolumbar Modified Coefficient of Variation calculated for *Chaetophractus villosus* and data on other mammals according to Asher et al. (2011). TL CV = $CV(1 + (1/4n))$.

	TL CV	n indiv	n species
Monotremata	2.557	34	2
Marsupialia	1.333	57	4
Atlantogenata	2.844	462	12
Boreoeutheria	1.673	1894	24
Xenarthra (except <i>C. villosus</i>)	3.340	119	4
<i>Chaetophractus villosus</i>	1.885	41	1
Afrotheria	2.596	343	8
Laurasiatheria	1.575	426	7
Euarchontoglires	1.713	1469	17
Lipotyphlan	1.435	165	4
Primates	2.780	732	7
Rodentia	0.710	237	8
Lagomorpha	1.989	499	2

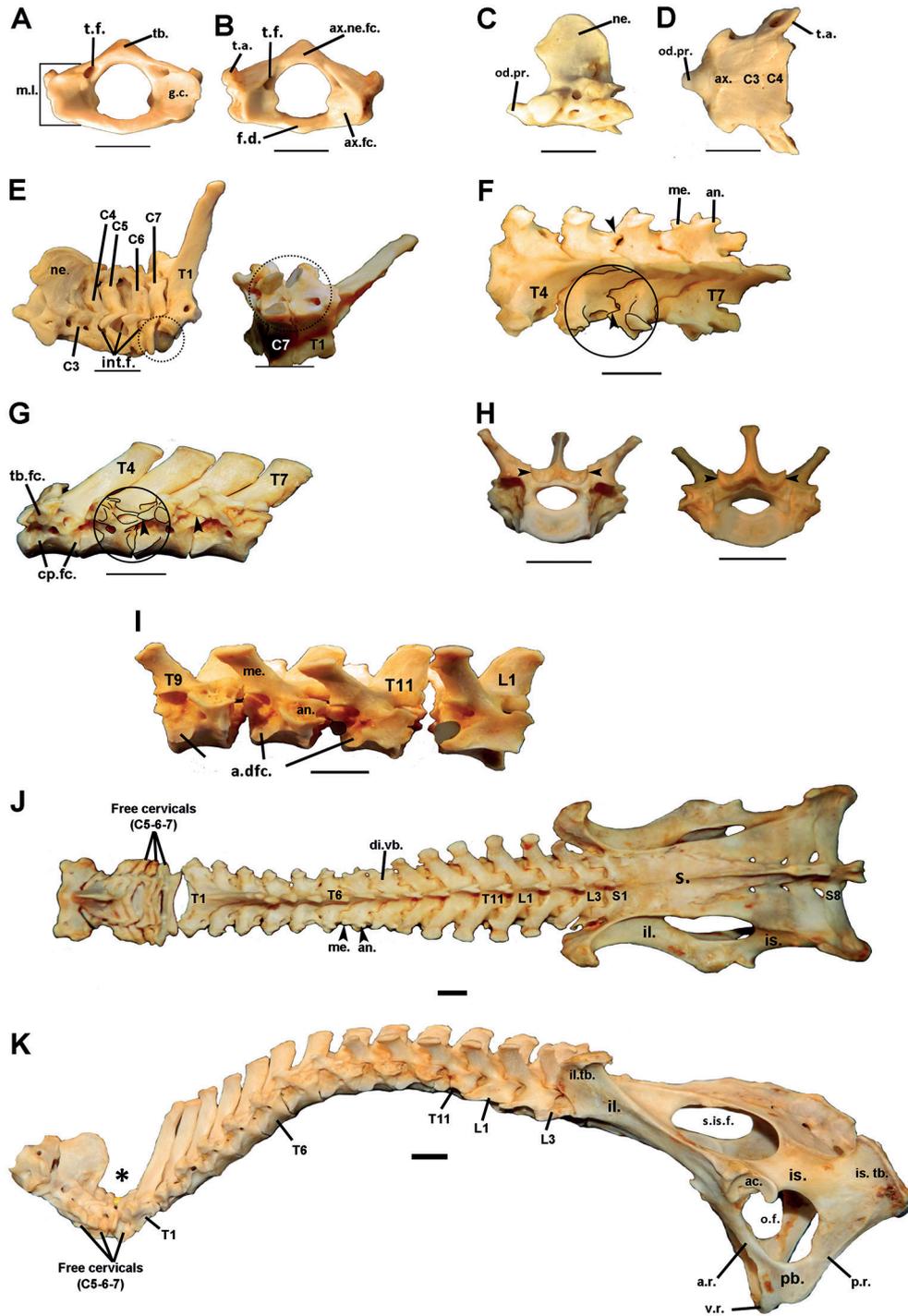


Figure 1. Major details in every region of the axial skeleton of *C. villosus*. (A-B) Anterior and posterior view of the atlas (C1), respectively. t.a. = transverse apophysis, ax.fc. = articular facet for the axis, ax.ne.fc. = articular facet for the neurapophysis of the axis, f.d. = *fovea dentis*, g.c. = glenoid cavity for the occipital bones, in lateral mass (l.m.), tb. = tuberosity, t.f. = transverse foramen. (C-D) Lateral and ventral view of the mesocervical bone (C2 + C3 + C4), respectively: od.pr. = odontoid process, ax. = axis, t.a. = transverse apophysis, ne. = neurapophysis. (E) left image: laterodorsal view of the axial region including the mesocervical bone, posterior free cervicals (C5-C7), and first thoracic vertebra (T1); right image: lateroventral view of the last free cervical (C7) and first thoracic vertebrae. ne. = neurapophysis, int.f. = intervertebral foramina, grey areas show the articular facets in C7 and T1 for the first rib. (F-G) dorsal and lateral views of the axial region between T4 and T7, respectively. Black arrowheads indicate the dorsal xenarthrales, me. = metapophysis, an. = anapophysis, tb.fc. = facet for the tubercle of the rib, cp.fc. = facet for the capitulum of the rib. The supplementary articulations (= xenarthrales) are clearly shown in the schematic drawing in the circular areas. (H) anterior (left) and posterior (right) view of T9 showing the pre- and postzygapophyses, respectively. Black arrowheads indicate the vertical component in both articular facets. (I) lateral view of the axial region between the last thoracics (T9-T11) and first lumbar (L1). Grey surfaces in T11 (also outlined in black) and L1 indicate the facets of the ventral xenarthrales. an. = anapophysis, a.dfc. = anterior demifacet for the capitulum of the rib, me. = metapophysis. (J-K) Dorsal and lateral views of the axial skeleton (with the exception of the caudal region) of a specimen that bears 11 thoracic and 3 lumbar vertebrae. ac. = Acetabulum, an. = anapophysis, a.r. = anterior ramus of the pubis, di.vb. = diaphragmatic vertebrae, il. = ilium, il.tb. = iliac tuberosity, is. = ischium, is.tb. = ischial tuberosity, me. = metapophysis, o.f. = obturator foramen, pb. = pubis, p.r. = posterior ramus of the pubis, S. = synsacral vertebrae, s.is.f. = sacroischial foramen, v.r. = ventral ramus of the pubis. * Dorsoventral curvature of the cervical vertebrae.

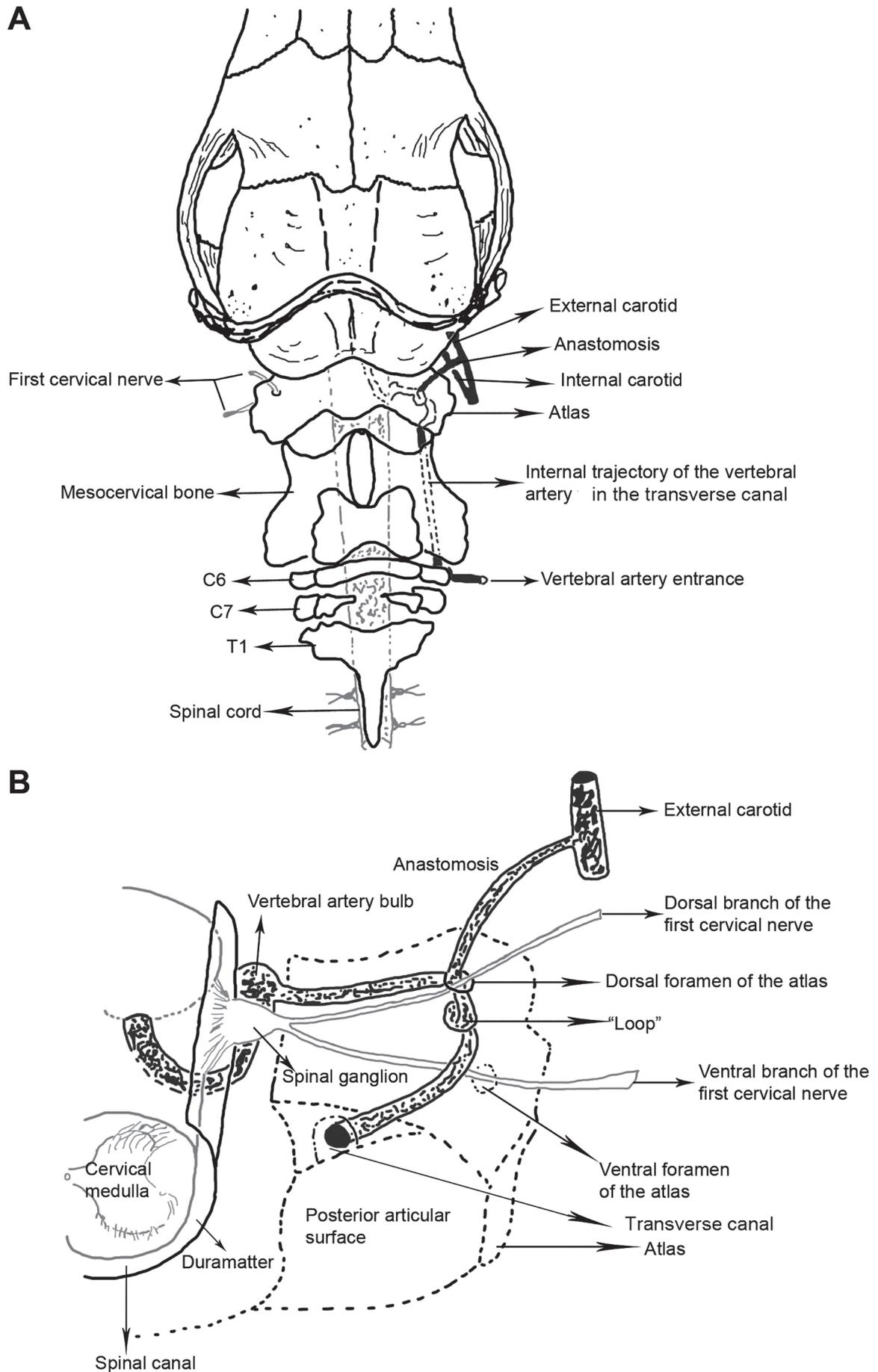


Figure 2. Trajectory of the vertebral artery and associated nerves in *C. villosus*. (A) Schematic drawing that shows the path of the vertebral artery along the cervical region in dorsal view. (B) Schematic drawing that shows the path of the vertebral artery within the lateral mass of the atlas in posterodorsal view.

brae, while the dorsal arch and vertebral body remain unfused (Fig. 1E). The neurapophysis of C2 is hypertrophied and articulates anteriorly with the dorsal arch of C1. Furthermore, it fuses with the neurapophysis of the following vertebrae that form the mesocervical bone (Fig. 1C, E). In the free cervicals the spinal nerves emerge through intervertebral foramina (Fig. 1E), in fused cervicals two foramina for the spinal nerves exist. The transverse apophyses and the lateral masses of the mesocervical bone surround the transverse canal of the vertebral artery (Fig. 2A).

In the dorsal arch of the free cervicals, the articulations between pre- and postzygapophyses are tangential, where prezygapophyses are more or less covered by the postzygapophyses, and the transverse apophyses show supplementary articulations (Fig. 1E). The dorsal arches lack neurapophysis, and sometimes the arches counterparts are not fused in the middle and the spinal dura matter is visible (Fig. 2A). The transverse process and the lateral mass of C7 bear articular facets for the first rib (Fig. 1E). The latter articulates with the vertebral column through three articular facets, two in C7, and a third one in the first thoracic vertebrae (T1).

This region shows a very pronounced dorsoventral curvature, convex ventrally, that spans until the first thoracic (Fig. 1J).

Thoracic region

Most specimens (approximately 90%) showed eleven thoracic vertebrae (T1 to T11), while few showed 12 (10%). The ribs articulate with the vertebrae through a tubercle that contacts an articular facet in the transverse process of the vertebrae, and a head that contacts an articular facet formed by two demifacets in the vertebral bodies of two adjacent vertebrae.

The first thoracic vertebrae (T1) showed a vertebral body similar in shape to C7 (Fig. 1E). The spinal nerve splits into two branches, emerging through intervertebral foramina. From T1 backwards, the neurapophyses take a posterodorsal direction, with T1 bearing the longest one. Along the anterior thoracic vertebrae each neurapophysis lean posteriorly over the adjacent one (Fig. 1F, G). At the base of each spinous process and facing posteriorly the postzygapophyses develop as two flat surfaces. The anterior face of the dorsal arch bears two flat depressions, the prezygapophyses, where the postzygapophyses of the preceding vertebrae articulate.

The region between T2 and T7 shows some modifications with respect to T1: the vertebral canal is smaller. The vertebral bodies gradually become more robust and isometric (Fig. 1G). The neurapophysis become gradually shorter. The transverse processes decrease in size caudally and are gradually modified to form the two pairs of supplementary articulations (= xenarthrales) that characterize these mammals (Gaudin, 1999).

The most dorsal xenarthran articulation (Figs. 1F, G) appears between T5 and T6 in most specimens (60%), and some variability is recorded (between T6-T7, 33%, and T4-T5, 7%).

The most ventral articulation appears near the thoraco-lumbar limit, between T9-T10 (13%), T10-T11 (70%), T11-T12 (3%), or T11-L1 (13%) (Fig. 1H). The diaphragmatic vertebra, which is the first vertebra in the series where the prezygapophyses show a vertical component, was T8 (87%) in most specimens (Fig. 1I), and some variability was recorded (T7, 10%, or T9, 3%). At this level of the vertebral column, several morphological changes become evident. Vertebrae increase in its transverse width, and spinous apophyses shorten even further. The pre- and postzygapophyses modified into a radial articulation where the postzygapophyses are laterally encased by the prezygapophyses of the following vertebra, due to the development of the vertical component mostly (Fig. 1H). The rib demifacets elongate dorsoventrally. Two new apophyses are developed, the metapophyses and anapophyses (Fig. 1F, I, J). The metapophyses appear poorly developed between the transverse processes and the prezygapophyses. The anapophyses develop between the transverse processes and the postzygapophyses. The vertebral canal is the smallest in diameter when compared to the rest of the column.

The vertebrae T10 and T11 show fully developed metapophyses of similar width to the neurapophysis. The metapophyses and anapophyses are intimately related to the formation of the xenarthran articulations. When fully developed, from T11 towards posteriorly in most specimens, these articulations have an articular cavity placed in the lateral mass, ventral to the metapophyses (the accessory prezygapophyses) (Fig. 1I). These accessory prezygapophyses are placed in the anterior part of the vertebrae and bear a dorsal articular surface, the dorsal xenarthran articulation, and a ventral one, the ventral xenarthran articulation (Fig. 1F, G, I). The dorsal and ventral xenarthran articulations of the accessory prezygapophyses articulate with the ventral and dorsal facets placed in the accessory postzygapophyses (fully developed anapophyses) of the preceding vertebrae.

The last thoracic vertebrae (T11 in most specimens) lacks the posterior demifacet for the head of the rib. From this vertebra, the spinal nerve emerges through a single intervertebral foramen. The articulation between prezygapophyses and postzygapophyses is radial.

Lumbar region

This region shows the largest vertebrae, great transverse width, large vertebral bodies, and longer metapophyses (Fig. 1I, J, K). The spinal nerves emerge through intervertebral foramina. The anapophyses protrude in posterior and lateral direction from the lateral masses, and accessory articulations are well developed. The vertebral canal is large and lodges the lumbar enlargement of the spinal cord. The number of lumbar vertebrae is variable between two and four, being three the most common number. The last lumbar articulates with the first sacral (S1) and shows, at both sides of the vertebral body, a laterally oriented facet that articulates with a zone where the S1 and the ilium are in contact. This facet is absent in other lumbar (Fig. 1K).

Sacral region

This region comprises all vertebrae that come into contact with the pelvic girdle. The vertebrae fused together to form a long synsacrum, which is attached to the iliac and ischial bones. In *C. villosus*, the number of synsacral vertebrae varies between seven and nine, being eight the most common number. The two or three most anterior vertebrae are fused to the iliac bones through their transverse processes, while the three or four most posterior do so to the ischial bones (Fig. 1J, K). In this manner, the sacral region and the pelvic girdle are firmly attached and form a single bone, the pelvis or pelvic region.

The dorsal face of the pelvic region forms the roof of the pelvic cavity and is slightly concave. Some specimens show the last lumbar vertebrae partially fused to the synsacrals, and a few lumbar features are retained, e.g., small metapophyses and neurapophysis (Fig. 3). Between the last free lumbar and the pelvis, the intervertebral articulations, both the zygapophyses and xenarthrales, are well developed. Synsacral foramina could be seen in the dorsal and ventral aspect of the pelvic girdle where the spinal nerves emerge (Fig. 3A). The lateral face of the pelvis is slightly convex, and triangle shaped (Fig. 1K). It shows the sacroischial foramen, the iliac and ischial tuberosities, which contact the carapace, the acetabulum, and the obturator foramen (Figs. 1J, K, 3A, B). The pubis forms the ventral part of the pelvis and is divided into a body, an anterior, a posterior, and a ventral ramus (Figs. 1K, 3A). The ventral ramus fuses with its contralateral and forms the pubic symphysis (Fig. 3A, B).

Caudal region

This region shows approximately 17 vertebrae. The transverse processes in first caudal (Cd1) are well developed (Fig. 3B), flat, and transversal to the sagittal plane, and the tips come into contact with the caudal osteoderms. The postzygapophyses articulate into a concavity of the prezygapophyses that face dorsally. A small neurapophysis emerges dorsally. The metapophyses extend slightly dorsolaterally and come into contact with the caudal osteoderms (Fig. 4). The zygapophyses are reduced and intervertebral articulation is only through the vertebral bodies. Ventral to the vertebral bodies a series of small hemal arches articulate between two consecutive vertebrae. Each hemal arch develops two ventrally oriented tuberosities, which are related to caudal osteoderms (Fig. 4). Posteriorly, most characteristics are gradually reduced, until the last caudals, where a cylindrical vertebral body represents the vertebrae. Posterior to the sacral bone, the vertebral canal shows internally the last nerve filaments of the *filum terminale*, which emerge through the intervertebral spaces. The vertebral canal disappears at Cd4.

Thoracolumbar vertebral intraspecific variation

The number of thoracolumbars (TL) recorded for this species varies between 14 and 15, combining 11T and 3L

(88%), 12T and 3L (5%), 12T and 2L (5%), or 11T and 4L (2%). Additionally, the modified CV (Asher *et al.*, 2011) for this species scored 1.885 (Table 3).

DISCUSSION

The axial skeleton of *Chaetophractus villosus* shows several features, which can be representative for the clade. The presence of a mesocervical bone is a feature that distinguishes Cingulata from Pilosa (McDonald, 2003). The number of vertebrae that the mesocervical bone incorporates is variable among cingulate species (e.g., in *D. novemcinctus* the mesocervical bone includes C2 to C4, in *D. hybridus* is C2 to C4 or C2 to C5, in *Priodontes maximus* C2 to C3, see Galliari *et al.*, 2010), but as a general rule the fusion always includes the axis and the next cervicals (Engelmann, 1985). Regarding *C. villosus*, between the axis and C3 the vertebrae are completely fused, while C4 do so partially, through its lateral apophyses. Nevertheless, the vertebrae C4 is completely immobilized to the rest of the mesocervical and constitute a functional unit. Other mammals with fossorial habits also possess mesocervical bones, e.g., *Talpa*, *Mesoscalops*, *Myospalax*, *Notoryctes*, and the fossils epiocotheriid palaeodonts (Rose & Emry, 1983; Rose *et al.*, 1991). Furthermore, Hildebrand (1985) hypothesized a possible use of the top of the head of armadillos to displace compact soil, for which a mesocervical bone for muscle neck attachment would be advantageous. However, this feature is also present in non-fossorial mammals, such as rodent members of Erethizontidae and Dinomyidae (Ray, 1958), cetaceans, and afrotherians from the order Sirenia (Howell, 1930). In the later, the fusion of cervicals is occasional and variable (Buchholtz *et al.*, 2007). Both in sirenians and cetaceans the cervical vertebrae fusion has been explained as adaptations to their aquatic lifestyles (Howell, 1930). Amongst armadillos, the genus *Tolypeutes* also shows mesocervical bones but their burrowing abilities are a matter of discussion (see Attias *et al.*, 2016, and bibliography therein).

The ventral arch of the atlas lacks a ventral tubercle, present in many mammals, and specially developed in ungulates and rodents (Lessertisseur & Saban, 1967). The lack of the ventral tubercle, and the multiple fusions between the anterior cervicals may indicate a limited dorsiflexion range of the neck.

The rib facets in the posterior half of the last cervical (C7) may suggest that this vertebra belongs to the thoracic region. Nevertheless, other features, as the highly reduced neural apophysis, and the vertebralarterial foramen, clearly indicate that C7 is the last cervical.

The distinction between the typical mammalian facets and the xenarthran facets is a matter of discussion among different authors, in part because of the high variability in the number and shape of the intervertebral articulations present in xenarthrans, and especially due to the lack of a comprehensive study. Among extant xenarthrans, *Priodontes* has six pairs of intervertebral articulations (Grassé, 1955). Other xenarthrans show

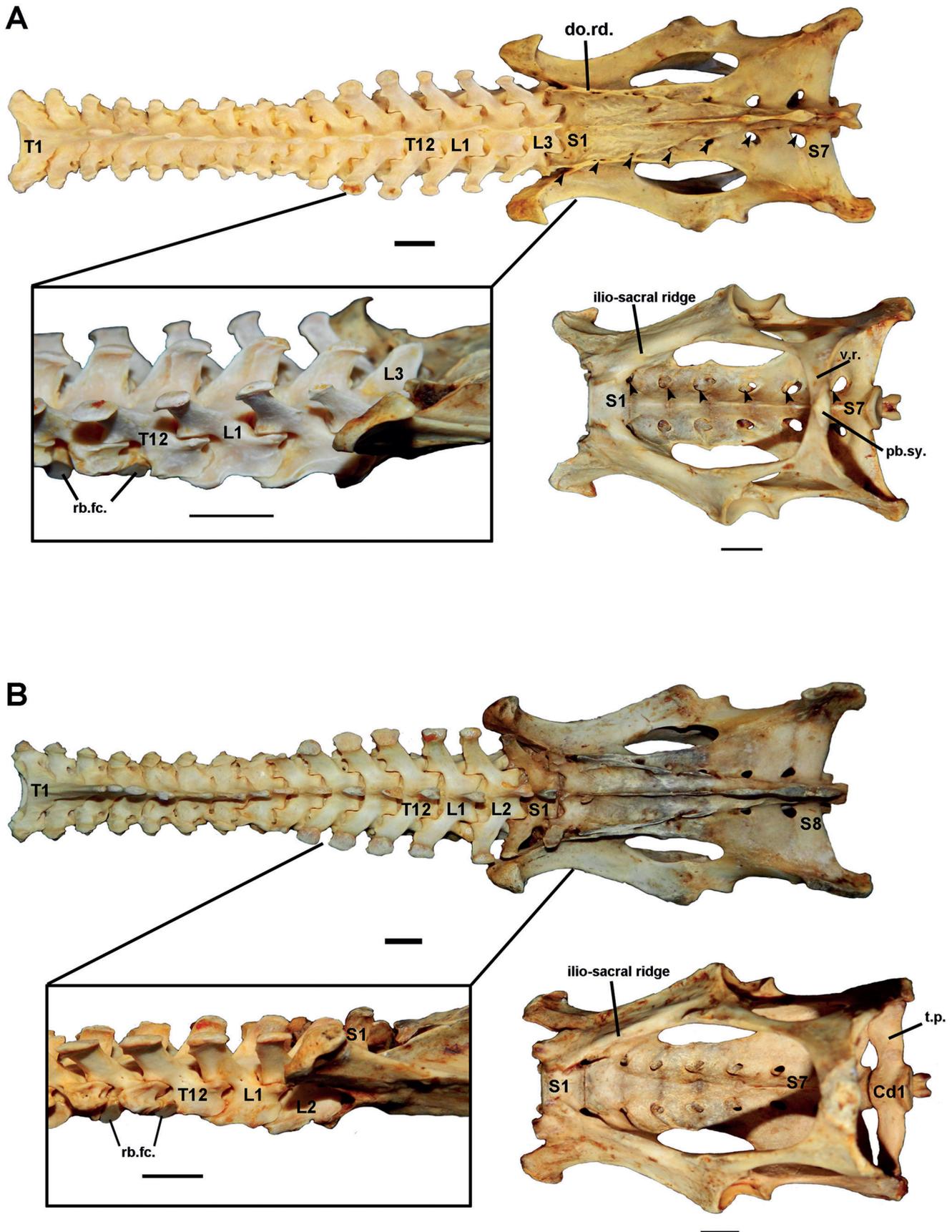


Figure 3. Axial skeleton in two specimens of *C. villosus* that deviate from the thoracolumbar count of 11T + 3L. (A) Specimen with 12T + 3L (LMED-652). Above, dorsal view of the thoracic, lumbar, and sacral regions. Below left, lateral view of the lumbosacral region. Below right, ventral view of the pelvis. Black arrowheads indicate the synsacral foramina, (B) Specimen 12T + 2L (LMED-637). Above, dorsal view of the thoracic, lumbar, and sacral regions. Below left, lateral view of the lumbosacral region. Below right, ventral view of the pelvis articulating with the first free caudal (Cd1). do.rd. = dorsal ridge; rb.fc. = rib facet, pb.sy. = pubic symphysis, v.r. = ventral ramus, t.p. = transverse process in first caudal (Cd1).

lower numbers, e.g., the extinct ground sloth *Haplopus* shows only two groups of intervertebral facets, one pair of zygapophysis (pre- and postzygapophysis), and one pair of complementary articulations (Scott, 1903-1905). According to Gaudin (1999), who studied the vertebral morphology of several xenarthrans, among the Euphractinae armadillos (e.g., *Zaedyus pichiy*, *C. villosus*, and *Euphractus sexcinctus*) the T6-T7 pair is the first pair of vertebrae that articulates through “extra” articulation facets. From this point backwards these “extra” articulations are present in the rest of the thoracics and lumbar. In this pair T6-T7 the xenarthral articulations are placed between the dorsal part of the anapophysis of T6, and the ventral part of the metapophysis of T7 (Gaudin, 1999). Nevertheless, Gaudin’s descriptions were based on two specimens of *Zaedyus pichiy*, highlighting the differences with *C. villosus* (three specimens) and *Euphractus sexcinctus* (one specimen). In our study, based on the analysis of 41 out of the 44 specimen studied, we identified certain variability in the position of the first vertebral pair that bears a xenarthral facet, ranging from T4-T5 to T6-T7, being T5-T6 and T6-T7 the most frequent positions. The appearance of the second pair of xenarthrales is set near the thoracolumbar limit, and ranges between T9-T10 and T11-L1, although in most specimens it occurs between T10 and T11 (72.4%).

The most posterior thoracics T10 and T11 (and T12 when present) show well-developed metapophyses, and low and wide neurapophyses, both with truncated ends. Several authors proposed that the morphology of these apophyses might be related to the support of the carapace (e.g., Flower, 1885; Hoffstetter, 1958).

According to Grassé (1955) and Lessertisseur & Saban (1967) some vertebrae from the sacral region undergo a more or less extended sacralization process, in which most posterior lumbar vertebrae are immobilized with the sacrals, and by hypertrophied transverse processes become attached to the anterior part of the iliac bones. Additionally, the most anterior caudals are also incorporated to the sacrals, extending this region and forming a synsacrum (Galliari & Carlini, 2015). In *C. villosus* the last lumbar is variably immobilized to the iliac bones and the synsacrum by the appearance (in some specimens) of an articular facet between the ilium alae and the lumbar apophyses (Fig. 1K). Nevertheless, although last lumbar vertebra may be immobilized, it is not necessarily fused to the synsacrum and maintains as a free structure.

The free caudal vertebrae show modifications in their apophyses to provide supporting points to the osteoderms of the caudal tube, and the presence of hemal arches are in relation to major blood vessels protection. Anatomico-histological analysis of the tail of all the armadillos showed that in this area is “the rete mirabile”, a site that makes blood collection easier, and allows the obtention of sterile blood samples, avoiding animal mortality, high-risk venipuncture sites, anesthetics and excessive stress (Luaces et al., 2011).

The Clade Atlantogenata was originally proposed by molecular data (Prasad et al., 2008) and currently other data sources such as embryological and morphologi-

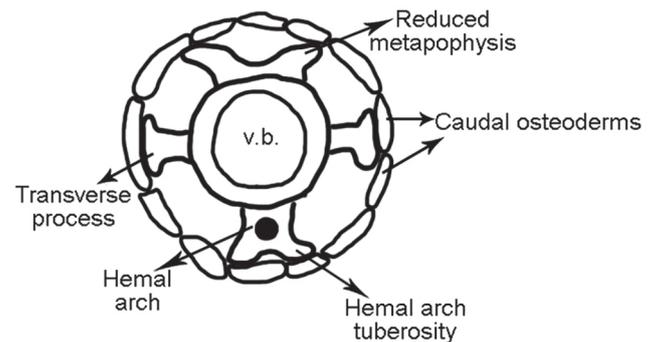


Figure 4. Schematic drawing of the anterior face of Cd5 and its relationship with the caudal osteoderms. v.b. = vertebral body.

cal data added support to this group. Asher et al. (2009, 2011) noted potentially different patterns of dental eruption and high levels of intraspecific variation in pre-sacral vertebral counts among atlantogenatans relative to boreoeutherians. Most afrotherians and some xenarthrans show late-erupting adult set of teeth (Asher & Lehmann, 2008; Ciancio et al., 2012) and more variation in vertebral formulae and anatomy than other mammals (Sánchez-Villagra et al., 2007; Buchholtz & Stepien, 2009; Asher et al., 2011). Additionally, Hautier et al. (2013) found a high level of variation in ossification sequence among southern placentals relative to northern placentals. Nevertheless, this variation is rarely in the same direction, which is inconsistent with the Atlantogenata hypothesis.

The variability in the total number of thoracolumbars in *C. villosus* falls within the range of most mammals. The variation coefficient in thoracolumbar number (CV) recorded for the 41 specimens was 1.885. According to Asher et al. (2009), an important morphological feature that groups extant Xenarthra and Afrotheria into the southern placentals is the high intraspecific vertebral variation, mainly the thoracolumbar number variation. Asher et al. (2009) argued that both groups (Xenarthra and Afrotheria) show species with the highest values of CV (i.e., the xenarthran *Dasybus novemcinctus*, CV = 4.65, and the afrotherian *Procavia capensis*, CV = 4.59). The other Xenarthra considered were only extant pilosans (*Bradypus variegatus*, *B. tridactylus*, *Choloepus hoffmanni*), and the average value for Xenarthra was CV = 3.34. Amongst Boreoeutheria (the rest of the extant placental mammals), the clade Rodentia includes taxa with the lowest CV values, recording species with no variation at all (CV = 0), and others with a range value spanning between 0.7 and 1.8. The rest of the Boreoeutheria analyzed by Asher et al. (2009) show values similar to *C. villosus*, with the exception of Primates (CV = 2.78) and *Sus scrofa* (CV = 3.58).

Both *Dasybus* and *Bradypus* are considered basal amongst armadillos and sloths, respectively (Gaudin, 2004; Gaudin & Wible, 2006; Billet et al., 2011; Delsuc et al., 2016). In this regard, a highly variable intraspecific number of thoracolumbars could be considered as a plesiomorphic character for Xenarthra. Nevertheless, a high variability of thoracolumbar number for the entire clade Xenarthra might be overestimated due to the low

number of species analyzed, and there might be a trend towards a reduction of this variation in some clades of armadillos (e.g., Euphractinae). In this sense, the inclusion of a greater number of extant and fossil taxa in future studies will help to elucidate if variation is really as high as previously hypothesized, or a common character to all Xenarthra, or only a species-specific trait.

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REFERENCES

- Aldana-Marcos, J.H. 1996. *Estudio experimental sobre dos peculiares estructuras del Armadillo Chaetophractus villosus: El núcleo de Onuf y la glándula de Harder*. Doctoral Thesis. Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina. 533 p.
- Asher, R.J. & Lehmann, T. 2008. Dental eruption in afrotherian mammals. *BMC Evolutionary Biology*, 6: 1-10.
- Asher, R.J.; Bennett, N. & Lehmann, T. 2009. The new framework for understanding placental mammal evolution. *BioEssays*, 31: 853-864.
- Asher, R.J.; Lin, K.H.; Kardjilov, N. & Hautier, L. 2011. Variability and constraint in the mammalian vertebral column. *Journal of Evolutionary Biology*, 24(5): 1080-1090.
- Attias, N.; Miranda, F.R.; Sena, L.M.M.; Tomas, W.M. & Mourão, G.M. 2016. Yes, they can! Three-banded armadillos *Tolypeutes* sp. (Cingulata: Dasypodidae) dig their own burrows. *Zoologia*, 33(4):1-8, e20160035. <https://www.scielo.br/j/zool/a/ZbhQHgdYgcppd3yy3GRtkCH/?format=pdf&lang=en>.
- Billet, G.; Hautier, L.; de Muizon, C. & Valentin, X. 2011. Oldest cingulate skulls provide congruence between morphological and molecular scenarios of armadillo evolution. *Proceedings of the Royal Society B*, 278(1719): 2791-2797.
- Buchholtz, E.A. & Stepien, C.C. 2009. Anatomical transformation in mammals: Developmental origin of aberrant cervical anatomy in tree sloths. *Evolution and Development*, 11(1): 69-79.
- Buchholtz, E.A.; Booth, A.C. & Webbink, K.E. 2007. Vertebral anatomy in the Florida Manatee, *Trichechus manatus latirostris*: A developmental and evolutionary analysis. *The Anatomical Record*, 290(6): 624-637.
- Ciancio, M.R.; Castro, M.C.; Galliari, F.C.; Carlini, A.A. & Asher, R.J. 2012. Evolutionary implications of dental eruption in *Dasypus* (Xenarthra). *Journal of Mammalian Evolution*, 19: 1-8.
- Delsuc, F.; Gibb, G.C.; Kuch, M.; Billet, G.; Hautier, L.; Southon, J. & Poinar, H.N. 2016. The phylogenetic affinities of the extinct glyptodonts. *Current Biology*, 26(4): R155-R156.
- Engelmann, G. 1985. The phylogeny of the Xenarthra. In: Montgomery, G.G. (Ed.). *The ecology and evolution of armadillos, sloths, and vermilinguas*. Washington, D.C., Smithsonian Institution Press. p. 51-64.
- Flower, W.H. 1885. *An introduction to the osteology of the mammalia*. London, Macmillan and Co. 383p.
- Galliari, F.C. & Carlini, A.A. 2015. Ontogenetic criteria to distinguish vertebral types on the debated Xenarthran Synsacrum. *Journal of Morphology*, 276: 494-502.
- Galliari, F.C.; Carlini, A.A. & Sánchez-Villagra, M.R. 2010. Evolution of the axial skeleton in armadillos (Mammalia, Dasypodidae). *Mammalian Biology*, 75(4): 326-333.
- Gaudin, T.J. 1999. The morphology of xenarthrous vertebrae (Mammalia: Xenarthra). *Fieldiana: Geology, New Series*, 41: 1-38.
- Gaudin, T.J. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society*, 140(2): 255-305.
- Gaudin, T.J. & Biewener, A.A. 1992. The functional morphology of xenarthrous vertebrae in the armadillo *Dasypus novemcinctus* (Mammalia, Xenarthra). *Journal of Morphology*, 214: 63-81.
- Gaudin, T.J. & Wible, J.R. 2006. Chapter 6: The phylogeny of living and extinct armadillos (Mammalia, Xenarthra, Cingulata): a craniodental analysis. In: Carrano, M.T.; Gaudin, T.J.; Blob, R.W. & Wible, J.R. (Eds.). *Amniote paleobiology: perspectives on the evolution of mammals, birds and reptiles*. Chicago, University of Chicago Press, 153-198p.
- Grassé, P.P. 1955. *Traité de Zoologie: anatomie, systématique, biologie. mammifères*. Paris, Masson et Cie.
- Gray, H. 1977. Osteology – The skeleton. In: Pick, T.P. & Howden, R. (Eds.). *Anatomy, descriptive and surgical*. New York, Gramercy Books. p. 33-216.
- Hautier, L.; Bennett, N.C.; Viljoen, H.; Howard, L.; Milinkovitch, M.C.; Tzika, A.C.; Goswami, A. & Asher, R.J. 2013. Patterns of ossification in southern versus northern placental mammals. *Evolution*, 67(7): 1994-2010.
- Hildebrand, M. 1985. Digging of quadrupeds. In: Hildebrand, M.; Bramble, D.M.; Liem, K.F. & Wake, D.B. (Eds.). *Functional vertebrate morphology*. Cambridge, Belknap Press. p. 89-109.
- Hoffstetter, R. 1958. Xenarthra. In: Piveteau, J. (Ed.). *Traité de paléontologie: Mammifères*. Paris, Masson. v. 6, p. 535-636.
- Howell, A.B. 1930. *Aquatic mammals: their adaptations to life in the water*. Springfield, Charles C. Thomas, 341 pp.
- Jenkins, F.A. 1970. Anatomy and function of expanded ribs in certain edentates and primates. *Journal of Mammalogy*, 51(2): 288-301.
- Lessertisseur, J. & Saban, R. 1967. Squelette Axial. In: Grasse, P.P. (Ed.). *Traité de Zoologie. Mammifères, teguments, squelette*. Paris, Masson. v. 16, fasc. 1. p. 584-708.
- Luaces, J.P.; Rossi, L.F.; Aldana-Marcos, H.J. & Merani, M.S. 2011. The rete mirabile of the tail, an effective site for sampling sterile blood from armadillos (Dasypodidae, Xenarthra). *Italian Journal of Zoology*, 78(1): 63-69.
- McDonald, H.G. 2003. Xenarthran skeletal anatomy: primitive or derived? (Mammalia, Xenarthra). *Senckenbergiana biologica*, 83(1): 5-17.
- Narita, Y. & Kuratani, S. 2005. Evolution of the vertebral formulae in mammals: A perspective on developmental constraints. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 304(2): 91-106.
- Oliver, J.D.; Jones, K.E.; Hautier, L.; Loughry, W.J. & Pierce, S.E. 2016. Vertebral bending mechanics and xenarthrous morphology in the nine-banded

- armadillo (*Dasyus novemcinctus*). *The Journal of Experimental Biology*, 219(19): 2991-3002.
- Owen, R. 1868. *On the anatomy of vertebrates. V.3, mammals*. London, Longmans, Green, and Co. 612p.
- Prasad, A.B.; Allard, M.W.; NISC Comparative Sequencing Program & Green, E.D. 2008. *Molecular Biology and Evolution*, 25(9): 1795-1808.
- Ray, C.E. 1958. Fusion of cervical vertebrae in the Erethizontidae and Dinomyidae. *Breviora*, 97:1-11.
- Rose, K.D. & Emry, R.J. 1983. Extraordinary fossorial adaptations in the oligocene palaeodonts *Epoicotherium* and *Xenocranium* (Mammalia). *Journal of Morphology*, 175(1): 33-56.
- Rose, K.D.; Krishtalka, L. & Stucky, R.K. 1991. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 11. Palaeodonts (Mammalia). *Annals of the Carnegie Museum*, 60: 63-82.
- Sánchez-Villagra, M.R.; Narita, Y. & Kuratani, S. 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. *Systematic Biodiversity*, 5: 1-7.
- Scott, W. 1903-1905. Volume V: Mammalia of the Santa Cruz Beds: I. Edentata. In: Hatcher, J.B. (Ed.). *Reports of the Princeton University Expeditions to Patagonia, 1896-1899*. New Jersey, The University of Princeton. 364 p., 63 figs.