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ORIGINAL PAPER

Xenarthran Synsacrum Morphology and Evolution

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Abstract

Xenarthra is unique in having striking features in the axial skeleton, usually very different from the rest of the eutherian clades. Some of these features are widely spread among the members of the group (e.g., the presence of xenarthrales in most cingulates and all pilosans, and the synsacrum with sacroischial union to the pelvis in almost all xenarthrans) and others are restricted to some taxa (e.g., deviated number of cervical vertebrae in *Bradypus* and *Choloepus*). In this study, we aim to explore the great diversity of vertebral elements composing the xenarthran synsacrum within a phylogenetic framework. Vertebral counts of the adult synsacrum was obtained from almost all extant genera, with the exception of *Calyptophractus*, and several fossils. The modal number of vertebrae from the adult synsacrum was mapped onto a composite phylogeny of Xenarthra. The ancestral number of synsacrals for Xenarthra was recovered as ambiguous, although one of the optimizations recorded a number of six synsacrals, probably three iliac and three post-iliac vertebrae. The clade Cingulata is characterized by a high number of vertebrae forming the synsacrum (eight synsacrals), which is fused to the ischium through the tip of the transverse processes of the most posterior vertebrae. In pilosans, the ancestral number of synsacral vertebrae seems to be lower, probably formed by five or six vertebrae, and the union with the ischium is achieved through the base of the transverse processes of the most posterior vertebrae. Two exceptions stand out, one involving the extant suspensory sloths and *Megalocnus*, and the other involving a family of ground sloths, the Mylodontidae. A probable relationship of the synsacral number in the different taxa to the lifestyles is discussed.

Keywords Cingulata · Pilosa · Axial skeleton · Synsacrum · Morphology · Evolution

Introduction

The contact between the pelvic girdle and the axial skeleton through the sacral region is a feature that characterizes most Tetrapoda. In early stem tetrapods (e.g., *Acanthostega*, *Ichthyostega*), the sacral region (or sacrum) only included sacral vertebrae, which are those vertebrae that are in contact with the iliac bones (Coates 1996; Ahlberg et al. 2005; Carroll et al. 2005). Furthermore, sacral vertebrae are often defined by this relationship. For example, Burke et al. (1995) called sacral vertebrae those united to the ilium by transverse processes. In extant birds and some mammals (Owen 1866; Baumel and Witmer 1993; Rose and Emry 1993), the sacral region becomes more complex and with its complexity the definition of sacral region and sacral vertebrae drift apart, because the sacral region not only includes sacral vertebrae but also a variable number of presacral and postsacral elements. When presacral and/or postsacral vertebrae are fused to the sacrals the resultant structure is called synsacrum (McDonald 2003).

Nevertheless, when considering the literature in this regard, both concepts, sacral vertebrae and sacral region, seem to be synonymized, leading to multiple criteria to define the sacral region. For example, Flower (1885) called sacral vertebrae those between the lumbar and caudal region that are ankylosed together in the adult state to form a single bone

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(independently whether they are in contact with the iliac bones). Another variation proposed by Flower (1885) is based on a developmental criterion; in the human sacrum the most anterior sacrals, which would be true sacrals according to Flower, show ossification centers between the vertebrae and the ilium while the most posterior would be pseudo-sacral vertebrae incorporated from the caudal region. Goodrich (1958: 45) distinguished lumbar and sacral vertebrae as follows: "The pelvic girdle becomes attached to the sacral vertebrae by means of stout, short, sacral ribs. In Mammalia […] a few of the trunk vertebrae in front of the sacral may lose their ribs more or less completely and are then distinguished as lumbar from the more anterior thoracic vertebrae." More recently, Williams (2011) proposed another definition: sacral vertebrae are those that form sacral foramina; vertebrae that partially fused to the sacrum at the body, zygapophyses, or transverse processes, or articulate with the ilium but do not form sacral foramina, are considered lumbar vertebrae.

In extant mammals the number of vertebral elements forming the sacral region, here called synsacrals, were reported ranging from one (e.g., *Didelphis virginianus*) to 18 (some chiropterans) (Lessertisseur and Saban 1967; Rose and Emry 1993; Narita and Kuratani 2005), but the most common vertebral numbers for this region seem to be two to four.

The eutherian clade Xenarthra shows a striking number of traits in the axial skeleton, e.g., the presence of accessory articulations on the last thoracic and all lumbar vertebrae, deviation in some genera of the conservative number of seven cervical vertebrae in mammals, and highly variable thoracolumbar vertebral number, the last two characters being shared with Afrotheria (Asher et al. 2009). In addition, all members of the clade show a synsacrum, formed by the fusion of the sacrals and a non-defined number of postsacral vertebrae (also called pseudosacrals). Sometimes presacral vertebrae fuse anteriorly (Flower 1885; Rose and Emry 1993). The synsacrum comes into contact with the ischium and forms a novel sacroischial fenestra (Fig. 1). The silky anteater *Cyclopes didactylus* is the only exception, although this is commonly considered a derived condition (Rose and Emry 1993).

The number and identification of the synsacral elements within the different clades of Xenarthra have been reported through several papers and primarily in a descriptive fashion. The great diversity of vertebral elements composing the xenarthran synsacrum has never been studied within a phylogenetic framework, something that we aim to explore in this work.

Material and Methods

Institutions

Referred material in this work was obtained from the following institutions: MCN - Museu de Ciências Naturais, Fundaçao Zoobotânica, Porto Alegre, Brazil; MLP, AAC - División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; MNHN - Muséum national d'Histoire naturelle, Paris, France; NMB - Naturhistorisches Museum Basel, Basel, Switzerland; UFSC - Universidade Federal de Santa Catarina, Florianópolis, Brazil; USNM - National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Specimens

Vertebral counts of the adult synsacrum were obtained from 197 dry skeletons of almost all extant xenarthran genera, with the exception of *Calyptophractus*. Among cingulates (Table 1), we examined armadillos of Euphractinae (*Chaetophractus vellerosus*, *C. villosus*, *Euphractus sexcinctus*, *Zaedyus pichiy*, *Chlamyphorus truncatus*), Dasypodinae (*Dasypus hybridus* and *D. novemcinctus*), and Tolypeutinae (*Tolypeutes matacus*, *Cabassous chacoensis*, *C. unicinctus*, *C. centralis*, and *Priodontes maximus*) (Wilson and Reeder 2005). Within Pilosa (Table 2), the anteaters *Myrmecophaga tridactyla*, *Tamandua tetradactyla*, and *Cyclopes didactylus*, and the arboreal sloths *Choloepus hoffmanni*, *C. didactylus*, *Bradypus variegatus*, and *B. tridactylus* were examined. A few extinct taxa were also examined (*Lestodon trigonidens*, *Scelidotherium leptocephalum*, and *Glossotherium robustum*). In addition, complementary data were obtained from the literature, which included most fossil taxa considered in this study (Tables 1 and 2). Glyptodonts were not included in this study because of complete lack of fossil evidence of the region of interest in basal taxa and highly fused axial skeletons in more derived taxa. The basal pre-Miocene glyptatelines are known only from osteoderms (McKenna et al. 2006; Zurita et al. 2016), and more derived Miocene Propalaeohoplophorinae already show the characters of the rest of the Glyptodontidae, with rigid dorsal carapaces over an almost entirely fused vertebral column that forms bony tubes (e.g., great extension of fused vertebrae involving almost all the vertebra except the caudals and some of the neck) (Ameghino 1920).

The identification criterion of vertebral elements within the synsacrum was based on the number of sacral foramina and/or the presence of the sutures between consecutive vertebrae, as shown in Fig. 1. Incomplete sacral foramina from the first and last vertebrae were considered as one complete foramen. Within the synsacrum, we called iliac vertebrae those vertebrae that come into contact with the iliac bones. Those vertebrae anterior to the iliac vertebrae are called pre-iliac vertebrae, and those posterior to the iliac vertebrae are post-iliac vertebrae.

Character Mapping

The modal number of vertebral elements from the adult synsacrum was mapped onto a composite phylogeny of

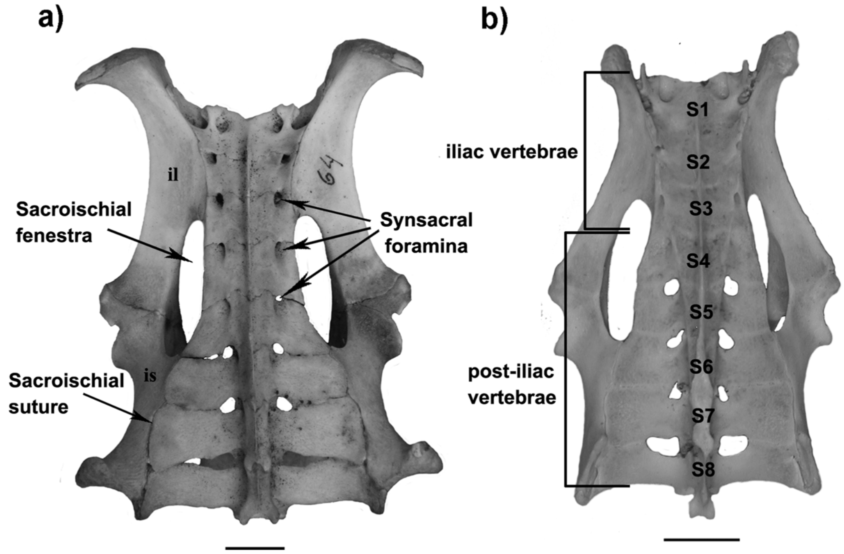


Fig. 1 Synsacrum skeleton in Dasypodinae and Euphractinae, dorsal view. **a** *Dasypus hybridus* (MLP-1.I.03.70); **b** *Chaetophractus vellerosus* (AAC-69). Abbreviations: il, ilium; is, ischium; S, synsacral vertebrae

Xenarthra obtained from recent publications (Gaudin 2004; Billet et al. 2011; Delsuc et al. 2016) by using the Parsimony Criterion for Ancestral State Reconstruction from MacClade 4 (Maddison and Maddison 2005). Intraspecific variation of synsacral vertebral number exists in most taxa analyzed. To circumvent this problem, the modal number of vertebrae was used as a convenient way of recording the most common pattern (Pilbeam 2004). In addition, the character mapping was optimized using ACCTRAN and DELTRAN in order to establish a range in ancestral states were the most parsimonious reconstructions were equivocal.

As only one specimen of *Cabassous centralis* and one of *C. chacoensis* were examined, we used the single number of synsacral vertebrae as the modal number. When considering some fossil xenarthrans, the number of synsacrals was reported on the basis of single specimen descriptions, so that number was considered as the modal number for the taxon.

Table 1 List of cingulates included in this study and number of synsacrals

Taxa	N	Source	Mode	Range (n)
Cingulata				
Dasypodidae				
Euphractinae				
Chaetophractus vellerosus	13	Present study	8	**7** (1) - **8** (12)
Chaetophractus villosus	28	Present study	8	**7** (1) - **8** (26) - **9** (1)
Euphractus sexcinctus	10	Present study	8	**7** (1) - **8** (8) - **9** (1)
Zaedyus pichiy	10	Present study	8	**7** (1) - **8** (8) - **9** (1)
Chlamyphorus truncatus	5	Present study	8	–
Dasypodinae				
†*Stegotherium tesselatum*	1	Scott 1903–1905	9	
Dasypus hybridus	10	Present study	8	**7** (1) - **8** (9)
Dasypus novemcinctus	27	Present study	9	**8** (4) - **9** (23)
Tolypeutinae				
Cabassous unicinctus	3	Present study	9	–
Cabassous centralis	1	Present study	9	–
Cabassous chacoensis	1	Present study	9	–
Priodontes maximus	4	Present study	12	**12** (3) - **13** (1)
Tolypeutes matacus	4	Present study	12	–

References: †, fossil taxa. N, number of specimens studied; n, number of specimens showing the number of synsacrals in the range of synsacral numbers

Table 2 List of pilosans included in this study and number of synsacrals

Taxa	N	Source	Mode	Range (n)
Pilosa				
Vermilingua				
Myrmecophagidae				
Tamandua tetradactyla	22	Present study	5	**5** (17) - **6** (5)
Myrmecophaga tridactyla	12	Present study	5	**5** (9) - **6** (3)
Cyclopes didactylus	8	Present study	5	**4** (2) **- 6** (1)
Tardigrada				
Bradypodidae				
Bradypus variegatus	8	Present study Buchholtz and Steppien 2009	6	**6** (5) - **7** (3)
Bradypus tridactylus	9	Present study	6	–
Mylodontidae				
†*Lestodon trigonidens*	1	Present study	8	–
†*Glossotherium robustum*	2	Present study Owen 1842	–	**8–11**
†*Scelidotherium leptocephalum*	1	Present study	7	–
†*Paramylodon harlani*	1	Stock 1925	9	–
Megatherioidea				
†*Schismotherium fractum*	1	Scott 1903–1905	5	–
†*Analcimorphus giganteus*	1	Scott 1903–1905	5	–
†*Hapalops longiceps*	1	Scott 1903–1905	6	–
†*Hapalops elongatus*	1	Scott 1903–1905	5	–
†*Hapalops rutimeyeri*	1	Scott 1903–1905	5	–
Megalonychidae				
†*Megalonyx jeffersonii*	1	McDonald 1977		
†*Megalocnus rodens*	1	Matthew and Paula-Couto 1959	8	–
Choloepus hoffmanni	11	Present study Buchholtz and Steppien 2009	8	**7** (4) - **8** (7)
Choloepus didactylus	11	Present study	7	**7** (7) - **8** (3) - **9** (1)
Megatheria				
Nothrotheriidae				
†*Nothrotheriops shastense*	1	Stock, 1925	5	–
Megatheriidae				
†*Thalassocnus litoralis*	2	Amson et al. 2015	–	**5–6**
†*Megatherium americanum*	1	Stock 1925	5	–

References: †, fossil taxa. N, number of specimens studied; n, number of specimens showing the number of synsacrals in the range of synsacral numbers

The topology of Cingulata follows Billet et al. (2011) and Delsuc et al. (2016), where *Dasypus* and *Stegotherium* are in a clade (Dasypodidae) basal to the rest of the cingulates. The rest of the armadillos are in the recently recognized clade Chlamyphoridae (Delsuc et al. 2016). The Euphractinae *Chaetophractus*, *Euphractus*, and *Zaedyus* are separated from *Chlamyphorus* plus Tolypeutinae (*Priodontes*, *Cabassous*, and *Toypeutes*). Within Euphractinae, the phylogenetic relationships of *Zaedyus pichiy*, *Chaetophractus villosus*, *C. vellerosus*, and *Euphractus sexcinctus* follow Delsuc et al. (2016), where *Chaetophractus vellerosus* is more closely related to *Z. pichiy* than to *Chaetophractus villosus*. The studied Pilosa are arranged according to the phylogenetic scheme proposed by Gaudin (2004) and Amson et al. (2017). The most basal dichotomy separates the anteaters *Myrmecophaga*, *Tamandua, and Cyclopes* (Vermilingua) from the sloths (Tardigrada). The genus *Bradypus* is the most basal within Tardigrada, followed by a dichotomy separating the Mylodontidae (*Scelidotherium*, *Paramylodon*, *Lestodon*, and *Glossotherium*) from the clade Megatherioidea. The genus *Schismotherium* is placed at the base of the Megatherioidea, followed by a dichotomy. In one group the genera *Hapalops* and *Analcimorphus* are in a pectinate position with respect to the Megalonychidae (*Megalonyx*, *Megalocnus*, and

Choloepus). The other group (Megatheria) dichotomizes into two clades, the Megatheriidae (*Megatherium* and *Thalassocnus*), and the Notrotheriidae (*Nothrotheriops*). For outgroup comparison we used the basal eutherian *Eomaia scansoria* from the Early Cretaceous of China (Ji et al. 2002), and three extant Afrotheria, *Orycteropus afer* (Rose and Emry 1993; Narita and Kuratani 2005), *Chrysochloris asiatica* (Leche 1883), and *Macroscelides proboscideus* (Leche 1883; Evans 1942). Most recent phylogenetic hypotheses place Afrotheria or Xenarthra alternatively as the most basal clade to the rest of Eutheria or both closely related into the Atlantogenata clade (Kriegs et al. 2006; Murphy et al. 2007; Asher et al. 2009; O'Leary et al. 2013; Foley et al. 2016). Character states were equally weighted and considered ordered.

An increased (or decreased) number of synsacrals might be due to a higher (or lower) number of either iliac, pre-iliac, or post-iliac vertebrae, or a combination of any of those. To evaluate the changes in vertebral composition of the synsacrum among different lineages, we also mapped the modal number of iliac, pre-iliac, and post-iliac vertebrae.

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Vertebral Formula of the Synsacrum

Extant Cingulata

In *Dasypus hybridus* (Dasypodinae, Dasypodidae) almost all adult specimens show eight elements (90%) forming the synsacrum (Fig. 1a), with the exception of one that showed seven (10%). The first two are completely fused to the ilium through their transverse processes; the third usually contacts the ilium through the anterior margin of the transverse processes. The rest are all post-iliac vertebrae arranged as follow: two (one in some specimens) limit the dorsal border of the sacroischial fenestra, and the consecutive three (or four) form a bony synsacroischial union, through the tip of their transverse processes. The synsacrum in *D. novemcinctus* was similar to that of *D. hybridus* but with the addition of one post-iliac vertebra, which contacts the ischial bones, nine synsacrals in total (85% of the specimens with nine synsacrals). Few specimens showed eight elements (15%) as in *D. hybridus* (see Table 1 and Online supplement).

Adult Euphractinae (Chlamyphoridae) sampled here (*Chaetophractus villosus*, *C. vellerosus*, *Zaedyus pichiy*, and *Euphractus sexcinctus*) have a mode of eight vertebrae forming the synsacrum, ranging from seven to nine synsacrals, and low variability is observed (Table 1). The arrangement of the synsacrals resembles that of *D. hybridus*, with the first three synsacrals fused to the iliac bones, the next two forming the dorsal border of the sacroischial fenestra, and the last three fused to the ischial bones through the tip of their transverse processes (Fig. 1b).

Among tolypeutines *Tolypeutes*, *Cabassous*, and *Priodontes*, the number of elements forming the synsacrum increases when compared to the rest of the Chlamyphoridae (Fig. 2). We examined five specimens of *Cabassous*, three *C. unicinctus*, one *C. chacoensis*, and one *C. centralis*, all with nine synsacrals (Fig. 2a, Table 1). Both *Tolypeutes* and *Priodontes* show more than nine vertebrae in the synsacrum. The former with 12 elements, three in contact with the iliac bones, and nine vertebrae posteriorly (Fig. 2b). The ischial bones are in contact with the tip of the transverse processes of the last five or six vertebrae. With respect to *Priodontes*, the three regions considered here (iliac, pre-iliac, and post-iliac) increased in number when compared to dasypodinae and euphractinae armadillos. We analyzed four specimens, three of which showed 12 synsacrals, and one 13 (with an extra pre-iliac vertebra). The iliac region ranged from four to five elements; the post-iliac showed seven elements; and up to two vertebrae were incorporated from the pre-iliac region (Online supplement). It is noteworthy that this taxon is the only armadillo with pre-iliac segments added to the synsacrum (Fig. 2c).

Fossil Cingulata

The synsacrum in *Stegotherium* is very much like that of *D. novemcinctus*, being composed of nine vertebrae (Scott 1903–1905). The first three are in contact with the ilium, while the three most posterior are fused to the ischium.

Extant Pilosa

In *Tamandua tetradactyla*, a modal number of five elements form the adult synsacrum, although a few specimens showed six vertebrae (Table 2). The first two are completely fused to the ilium, the third vertebra contacts the ilium through the tip of the anterior margin of the transverse processes, and the two most posterior contact the ischia through the base of the transverse processes while its distal portion remains free (Fig. 3a).

The giant anteater *Myrmecophaga tridactyla* showed five synsacrals (Fig. 3b) in most specimens, and three of twelve specimens showed six. The structure is somewhat similar to that of *T. tetradactyla*, although only the last vertebra fuses to the ischium, and the transverse processes are poorly developed.

The pygmy anteater *Cyclopes didactylus* lacks a sacroischial union in the pelvis. The modal synsacral number is five, ranging from four to six vertebrae. Although the modal number for pre-iliac, iliac, and post-

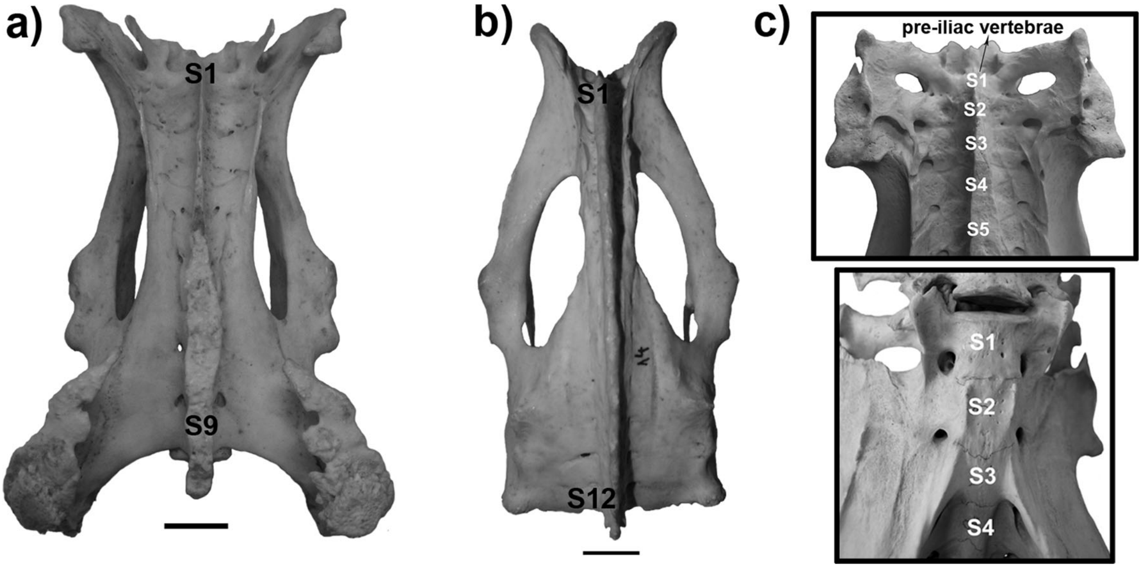


Fig. 2 Synsacrum in dorsal view of Tolypeutinae. **a** *Cabassous chacoensis* (AAC-60); **b** *Tolypeutes matacus* (AAC-14); **c** *Priodontes maximus* (USNM-299630), the box below in ventral view. Abbreviations: S, synsacral vertebrae

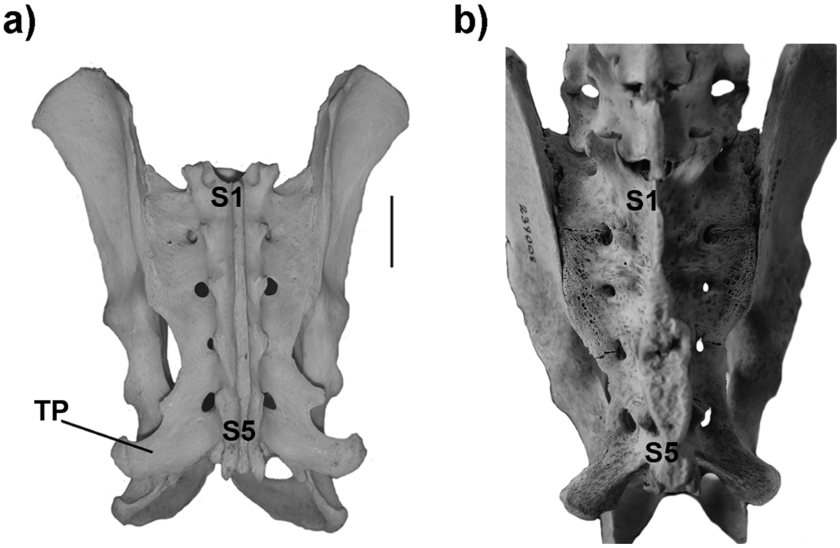
iliac are zero, three, and one, respectively, there is certain variability. In the eight specimen analyzed, the pre-iliac vertebrae ranged from zero to one, iliac from three to four, and post-iliac from zero to two.

Among extant sloths, six synsacral vertebrae characterize *Bradypus tridactylus* and *B. variegatus*, although three of eight specimens of *B. variegatus* showed seven synsacrals. When compared to vermilinguans, the increasing number of synsacrals is due to the addition of iliac vertebrae (four or five elements). Furthermore, *Choloepus didactylus* showed certain variation with seven (seven of 11 specimens), eight, or nine synsacrals, and the vertebral number in *C. hoffmanni* was seven (four of 11 specimens) or eight (seven of 11 specimens) (Table 2). In this species, four or five vertebrae are fused to the ilium, and the rest are added posteriorly. Contrary to the synsacrum of vermilinguans, the most posterior elements are fused to the ischium through the tip of the transverse processes in all extant sloths (Fig. 4).

Fossil Pilosa

Fossil "ground sloths" show certain variability in the number of synsacral vertebrae. Scott (1903-1905) proposed five to six synsacrals for *Hapalops* (*H. longiceps*, *H. elongatus*, and *H. rutimeyeri*), *Analcimorphus giganteus,* and *Schismotherium fractum*. The first three vertebrae usually contact the ilium,

Fig. 3 Adult synsacrum in dorsal view in anteaters (Vermilingua). **a** *Tamandua tetradactyla*; **b** *Myrmecophaga tridactyla*. Abbreviations: S, synsacral vertebrae; TP, transverse process



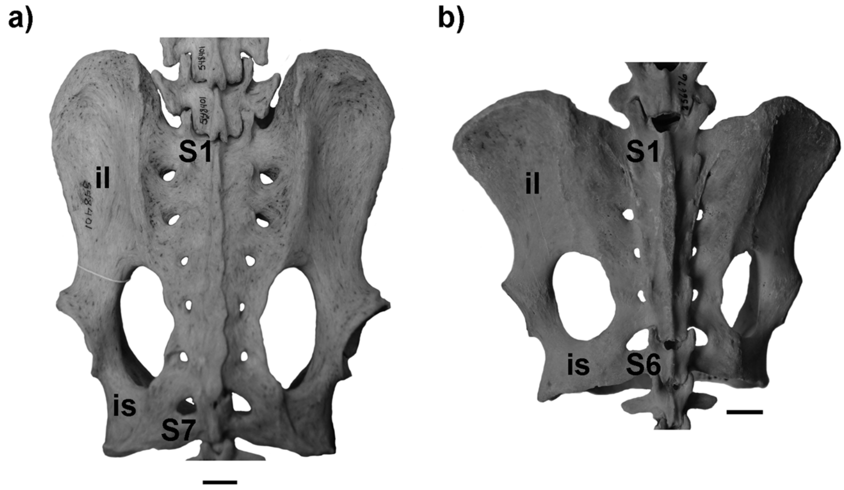


Fig. 4 Synsacrum in dorsal view in extant sloths (Tardigrada). **a** *Choloepus didactylus* (USNM-548401); **b** *Bradypus tridactylus* (USNM-256676). Abbreviations: il, ilium; is, ischium; S, synsacral vertebrae

and the last one or two are fused to the ischium. In the case where six vertebrae are present (e.g., *H. longiceps*, the largest species of the genus), the centrum of the last lumbar vertebra is free and only the neural arch is fused to the synsacrum, the next three are fused to the ilium, and the last two are fused to the ischium (Table 2 and Online Supplement). The genera *Megatherium* and *Nothrotheriops,* also present five synsacrals (Table 2). In *Glossotherium robustum* (Fig. 5) 11 synsacrals are reported in the synsacrum by Owen (1842), three vertebrae fused to the iliac bones, caudally one vertebra forms the dorsal border of the sacroischial fenestra, and three vertebrae are fused to the ischial bones. Four vertebrae are fused cranial to the iliac vertebrae. We also examined one specimen of *G. robustum* from the Museo de La Plata collection that showed a lesser number of synsacrals, three in contact with the ilium, three post-iliac, and two pre-iliac (eight synsacrals). The specimen of *Lestodon trigonidens* show eight synsacrals, five fused to the iliac bones, two posterior in contact with the ischial bones, and one anterior to the iliac vertebrae. The taxon *Scelidotherium leptocephalum* has seven vertebrae in the synsacrum, four fused to the ilium, two fused to the ischium, and one in between forming the dorsal border of the sacroischial fenestra. In addition to mylodontids, the taxon *Megalocnus rodens* (Megalonychidae) has eight synsacrals, five fused to the iliac bones, and three fused posteriorly (Matthew and Paula-Couto 1959: plates 18 and 19). The last two come into contact with the ischium through the tip of the transverse processes. The number of synsacrals in the megalonychid *Megalonyx jeffersoni* is lower than *Megalocnus rodens*, at five synsacrals (three iliac and two post-iliac vertebrae).

Character Mapping

In Fig. 6, the modal number of synsacral vertebrae mapped onto the selected phylogenetic topology is shown. The ancestral number of synsacrals inferred for Xenarthra is ambiguous (Fig. 6a), although an ancestral state of six synsacrals was

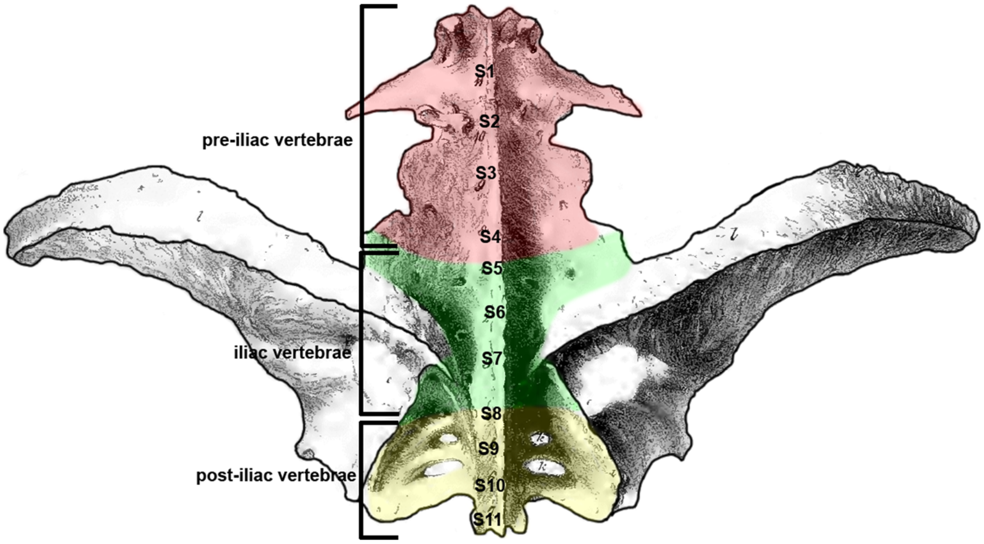


Fig. 5 Synsacrum in dorsal view in *Glossotherium robustum*. Modified from Owen (1842). References: red, pre-iliac synsacrals; green, iliac synsacrals; yellow, post-iliac synsacrals

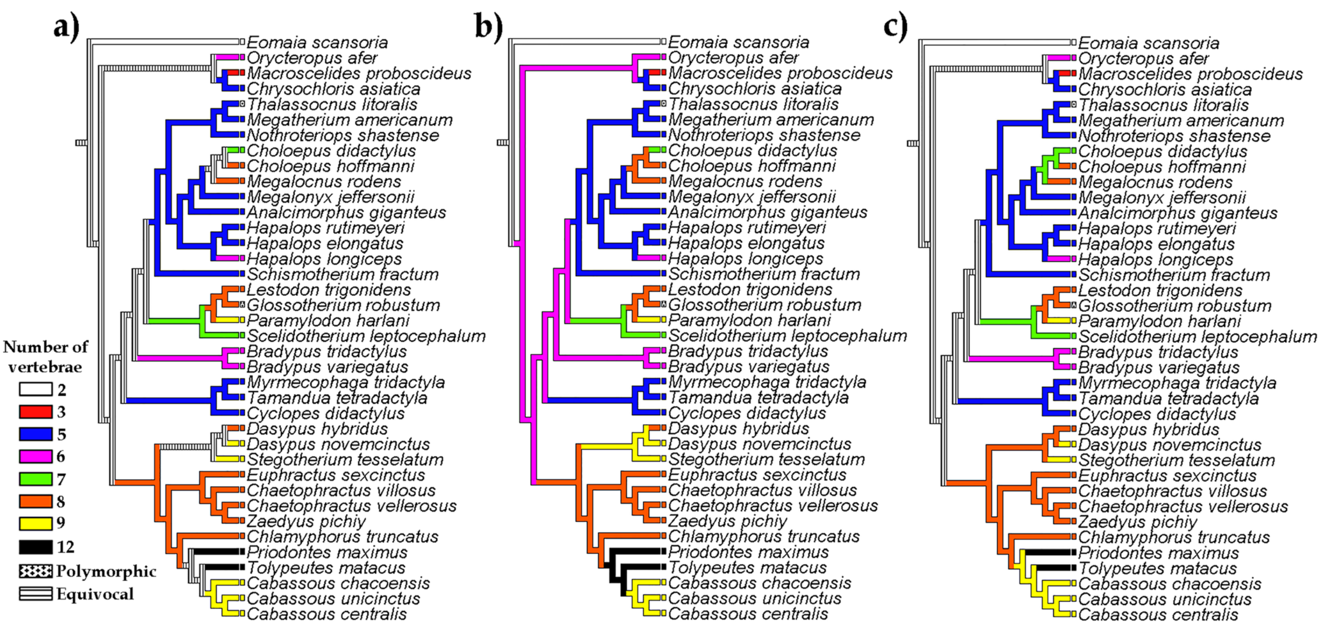


Fig. 6 Character mapping of the modal number of total synsacral vertebrae in Xenarthra and selected outgroups. Character states were equally weighted and considered ordered. **a** Most Parsimonious Reconstruction (MPR); **b** ACCTRAN optimization; **c** DELTRAN optimization. Color references indicate the number of synsacrals

obtained with ACCTRAN at this node (Fig. 6b). The mapping of the three regions separately (pre-iliac, iliac, and post-iliac) reported no pre-iliac vertebrae (Fig. 7), and ambiguous for the rest (ACCTRAN recovered three iliac vertebrae and three post-iliac). For Cingulata we recovered an ancestral number of eight vertebrae forming the synsacrum, three iliac and five post-iliac. ACCTRAN and DELTRAN optimizations (Fig. 6b, c) at the Dasypodidae node reported alternatively eight or nine synsacrals for the ancestor (three iliac and five or six post-iliac vertebrae). Changes in size between *Dasypus* species are somewhat coupled to changes in number, while most *D. novemcinctus* specimens show nine vertebrae, *D. hybridus*, a much smaller species, shows eight. The Chlamyphoridae showed the plesiomorphic condition for Cingulata, with eight synsacrals (three iliac and five post-iliac vertebrae). The phylogenetic scheme used here groups tolypeutines in a clade that

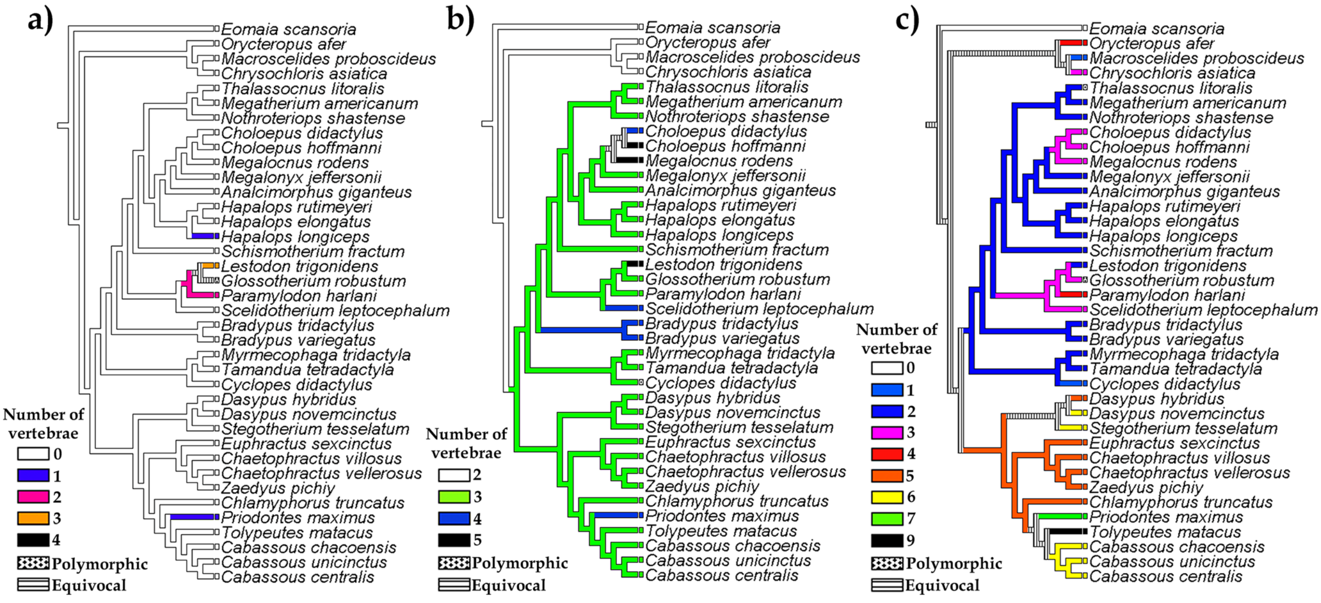


Fig. 7 Character mapping (MPRs) of the modal number of pre-iliac **a**, iliac **b**, and post-iliac **c** synsacrals in Xenarthra and selected outgroups. Character states were equally weighted and considered ordered. Color references indicate the number of synsacrals

is probably characterized by further increase of the synsacral vertebral number ranging from nine (according to DELTRAN optimization) to 12 (according to ACCTRAN) synsacral vertebrae.

The most parsimonious reconstruction of the ancestral synsacral number in Pilosa is ambiguous. Nevertheless, ACCTRAN optimization recovered a synsacral number of six vertebrae. In contrast, the character mapping of each region separately recovered three iliac and two postiliac vertebrae as the most parsimonious states in the ancestor (five in total). This incongruence may indicate that the ancestral number could be five or six synsacrals in Pilosa. Within Pilosa the sister group of sloths, the vermilinguans, showed five synsacrals (three iliac and two post-iliac). The species of *Bradypus*, the most basal Tardigrada, have six synsacrals, which seems to be the plesiomorphic condition for Pilosa if ACCTRAN optimization is considered (ambiguous in DELTRAN optimization). The ancestral condition for Megatherioidea is five synsacrals (three iliac and two post-iliac vertebrae). Two increases in the number of synsacrals are recorded in this clade: one within the genus *Hapalops,* one of the three species included is characterized by six synsacrals, *H. longiceps*, while the rest showed the plesiomorphic condition (five synsacrals); the other within the Megalonychidae, the clade *Megalocnus* + *Choloepus* showed an ancestral number that ranges between seven (recovered by DELTRAN) and eight (recovered by ACCTRAN) synsacrals. The members of the clade Mylodontidae show further increase in synsacral number (seven in the ancestor), and reach as much as 11 vertebrae as seen in *G. robustum*.

Discussion

There is clearly no unique arrangement of the synsacrum among xenarthrans. The clade Cingulata is characterized by a high number of elements forming the synsacrum (eight the ancestral condition), which is fused to the ischium through the tip of the transverse processes of the most posterior vertebrae. These transverse processes originate from independent ossification centers, similar to the condition observed in the following caudals (Galliari and Carlini 2015). Synsacral number ranges from seven to nine in all Dasypodinae and Euphractinae, with eight the most common number. These subfamilies group all generalized diggers of the clade and *Chlamyphorus* (sometimes put in its own family), a specialized digger that spends most of its lifetime in self-made tunnels.

On the other hand Tolypeutinae armadillos are characterized by a further increase in synsacrals. Here we recorded nine synsacrals for *Cabassous*; however, Wetzel (1980) reported a modal number of ten synsacrals, ranging from nine to 11. This suggests that the data obtained from the five specimens analyzed might underestimate the intra- and interspecific variability and probably would not be representative of all species of the genus. If Wetzel's specimens are taken into account, there is an important increase in number of synsacrals in this genus when compared with dasypodines and euphractines, similar to other tolypeutines. The present character mapping cannot conclude if the high number of synsacrals in *Priodontes* and *Tolypeutes* was acquired convergently or if it is ancestral for the clade and a reduction in number occurred in *Cabassous*. Nevertheless, the mapping of the regions of the synsacrum shows that the synsacrum of *Priodontes* is different from that of *Tolypeutes* because in the former the number of vertebrae increases in the three regions, while in the latter the pre-iliac and iliac regions show the ancestral number and the post-iliac region is much longer.

Cingulates cover a wide range of fossorial habits, from the least fossorial *Tolypeutes* (Attias et al. 2016), to the extremely fossorial pichiciego *Chlamyphorus* and the naked-tailed armadillo *Cabassous* (Nowak 1999; Vizcaíno et al. 1999; Vizcaíno and Milne 2002). The Euphractinae and the Dasypodinae are considered intermediates in their fossorial habits (Vizcaíno and Milne 2002). Armadillos are categorized as generalized scratch-diggers and show several postcranial specializations such as usually long acromion process of the shoulder girdle, large medial epicondyle of the humerus, large and long olecranon process of the ulna, tightly interlocking carpal bones, and robust claws, among other features (Hildebrand 1985; Vizcaíno et al. 1999). The large number of vertebrae forming the synsacrum has been related to this behavior by several authors arguing that mammals that dig with their forefeet usually brace with the hind feet and the forces involved converge on the pelvic girdle (Hildebrand 1985). The presence of the carapace in cingulates is considered as another factor influencing the strengthening of the pelvic girdle (Lessertisseur and Saban 1967). The genus *Tolypeutes* is considered as the least fossorial armadillo and the very long synsacrum could probably be also attributed to the bearing of a thick carapace.

In pilosans, although the ancestral number of synsacral vertebrae is not clear from this study, it seems to be lower than that observed in Cingulata, at least when considering the results from ACCTRAN optimizations. The synsacrum is probably formed by five or six vertebrae. The ancestral modal number of five synsacrals characterizes the vermilinguans. Nevertheless, the lowest limit in the range of variation for this trait is recorded in *Cyclopes*, which was the only species (of all xenarthran analyzed) where some specimens showed four synsacrals (Table 2). This condition (observed in few specimens) could be linked to the detachment of the ischial bones to the vertebral column, a condition similar to most mammals, and a more relaxed constraint in the fusion of post-iliac vertebrae. Fusion of post-iliac vertebrae always occur at least until the level of the ischio-sacral fusion in all other xenarthrans.

In *Bradypus*, the number of synsacral vertebrae increases to six when compared to vermilinguans, and the most posterior vertebrae fuse to the ischium through the tip of the transverse processes as in cingulates. In the megalonychid *Choloepus* (two-toed sloth), the condition is similar, but the number of synsacrals is greater (seven to eight synsacrals), with four or five iliac vertebrae, and three post-iliac. Both *Bradypus* and *Choloepus* showed a synsacrum with an increased number of iliac vertebrae, the former with four vertebrae, and the latter with four or five. The expansion of the iliac bones allows the addition of vertebrae into the sacral region. A series of recent papers lead by John Nyakatura focused on the analysis of kinematics on the quadrupedal suspensory locomotion of extant sloths (Nyakatura 2010, 2012; Nyakatura and Fischer 2010a, b, 2011). Although the studies were focused primarily on the pectoral girdle, forelimbs, and thoraco-lumbar spine, some conclusions were drawn for the pelvic girdle. According to Nyakatura (2010) the quadrupedal suspensory locomotion leads to hip extension due to gravity. In this regard, Nyakatura (2010: 146) stated: "The extensor moment evident in the hip is thus likely to be "permitted" by the excentric work of the hip flexor group (mainly *M. iliacus*, *M. psoas* major and *M. rectus femoris*) to prevent an uncontrolled extension of the hip due to gravity." Particularly the m. iliacus is a muscle that inserts on the iliac fossa, and occupies most of the internal surface of the iliac wing. An enlarged iliac bone allows the expansion of the surface for muscular attachment (e.g., m. iliacus). Although a longer iliac region of the synsacrum is shared by both arboreal sloths, this character is also present in the sister-taxon of *Choloepus*, the Antillean terrestrial sloth *Megalocnus*. This suggests that the character is not a convergence related to their suspensory habits but a character that appeared earlier in the evolution of megalonychids and probably became advantageous with the acquisition of suspensory postures.

In mylodontids, unlike tree sloths, the long synsacrum is achieved by the addition of vertebrae in all synsacral regions (pre-iliac, iliac, and post-iliac), reaching as much as 11 synsacrals in *G. robustum*. Many researchers emphasized that the limbs of mylodontids are well adapted for digging (Winge 1941; Aramayo 1988; Cuenca-Anaya 1995), not only to look for food but also to dig their own burrows (Vizcaíno et al. 2001). Furthermore, Vizcaíno et al. (2001) analogized the bipedal posture necessary to free the forelimbs to that adopted by the giant armadillo *Priodontes maximus*, which walks essentially on its hind limbs while maintaining the backbone roughly parallel to the ground, the forelimb flexed, and the hands, turned posteriorly, dragging along the ground (Frechkop 1949). Among armadillos analyzed the giant armadillo *Priodontes maximus* was the only one with increased synsacrals in the three regions, reaching as much as 13 synsacrals in some specimens. Despite these similarities between *Priodontes* and mylodontids, further studies should focus on biomechanical aspects that help elucidate functional significance of such a long synsacral region.

Conclusions

The number of synsacral vertebrae and the type of vertebrae within the synsacrum of Xenarthra show phylogenetic signal, and a limited range of character states characterizes several clades. The armored clade of Xenarthra, the Cingulata, is characterized by a long synsacrum (about eight synsacral vertebrae) that extends mainly by means of the addition of post-iliac vertebrae. Within this clade, a further increase occurred in Tolypeutinae armadillos were *Priodontes* reaches 13 synsacrals. The variability in the synsacrum within pilosans is probably a consequence of higher diversity in locomotor habits. Within the clade there are terrestrial taxa with quadrupedal locomotion; some of these taxa were proposed as capable of bipedal posture (e.g., *Paramylodon* and *Megatherium*), and others with some fossorial abilities (e.g., *Glossotherium* and *Scelidotherium*). In addition, the clade includes semiarboreal taxa like the anteater *Tamandua*, and several fossil sloths (*Hapalops*, *Schismotherium*, and *Analcimorphus*), fully arboreal (e.g., *Cyclopes*), fully arboreal and suspensory (e.g., *Choloepus* and *Bradypus*), and even with semi-aquatic and underwater fossorial habits like the genus *Thalassocnus* (White 1993; Muizon et al. 2004; McDonald 2007; Pujos et al. 2012; Amson et al. 2015).

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