

Ontogenetic Criteria to Distinguish Vertebral Types on the Debated Xenarthran Synsacrum

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ABSTRACT The presence of a synsacrum formed by the fusion of vertebrae that come into closed contact with the ilium and ischium is a feature that characterizes the clade Xenarthra. Nevertheless, the proper identity of each vertebral element that forms it is a matter of discussion. In this article, we provide ontogenetic information about skeletal ossification of the xenarthran synsacrum and define the position of the sacrocaudal limit within it. We analyzed the synsacrum of 25 specimens of nonadult and 101 adult armadillos and anteaters: *Dasypus hybridus*, *D. novemcinctus*, *Chaetophractus vellerosus*, *C. villosus*, *Tamandua tetradactyla*, and *Myrmecophaga tridactyla*. Two sets of vertebrae were identified: an anterior set, often attached to the iliac bones, in which transverse processes are originated mainly from an expansion of the base of the neural arches, and secondarily from a lateroventral ossification center. A posterior set is characterized by a series of vertebrae along which extra lateral ossifications (described here for the first time) are developed and form exclusively the transverse processes. Among armadillos, the sacrocaudal limit is set between the last vertebrae attached to the iliac bones and the first vertebrae that form the dorsal border of the sacroischial fenestra. In addition, anterior free caudals also showed extra lateral ossifications forming exclusively the transverse processes, supporting the notion that more posterior synsacrals are in fact caudal vertebrae that were incorporated to the synsacrum. In pilosans, the sacrocaudal limit is set between the first vertebrae that come into contact with the ischial bones and the immediately anterior one. However, the pattern of homologies is obscured by the low resolution in the ontogenetic sequence when compared to that of armadillos. *J. Morphol.* 276:494–502, 2015. © 2014 Wiley Periodicals, Inc.

KEY WORDS: armadillos; anteaters; skeletogenesis; lateral ossifications

INTRODUCTION

The contact between the iliac portion of the pelvic girdle and the axial skeleton through sacral vertebrae is a feature that characterizes most Tetrapoda. Within Amniota, this relationship has adopted different configurations. In some groups (e.g., most birds and several mammals like xenarthrans, the afrotherians *Orycteropus* and *Procavia*, the marsupial mole *Notoryctes*, and the flying fox

Pteropus), the sacrum fuses with the postsacral vertebrae, and sometimes even presacral, forming a synsacrum (Owen, 1866; Lessertisseur and Saban, 1968), establishing contact to the pelvic girdle (e.g., through syndesmosis, synchondrosis, or synostosis), primarily through the iliac bones and secondarily through the ischia.

The components of the synsacrum and its exact relation to the pelvic girdle can vary among groups, thus raising two questions: what is the precise identification of the sacral vertebrae, and when appropriate, which vertebral types are added to the sacrals from the caudal or lumbar regions, respectively. Different criteria were proposed to define sacral vertebrae: Williams (2011) proposed that sacral vertebrae are those that form sacral foramina, but that all posterior vertebrae that have partially fused centra, zygapophyses, or transverse processes, or articulate with the ilium, without sacral foramina, are considered lumbar vertebrae. Flower (1885) defined sacral vertebrae as those between the lumbar and caudal region that are ankylosed together in the adult state to form a single bone. Flower (1885) suggested a variant on this based on the identification in the human sacrum of ossification centers between the vertebrae and the ilium in the first sacrals, recommending that the term “sacral” should be restricted to this condition. Goodrich (1958)

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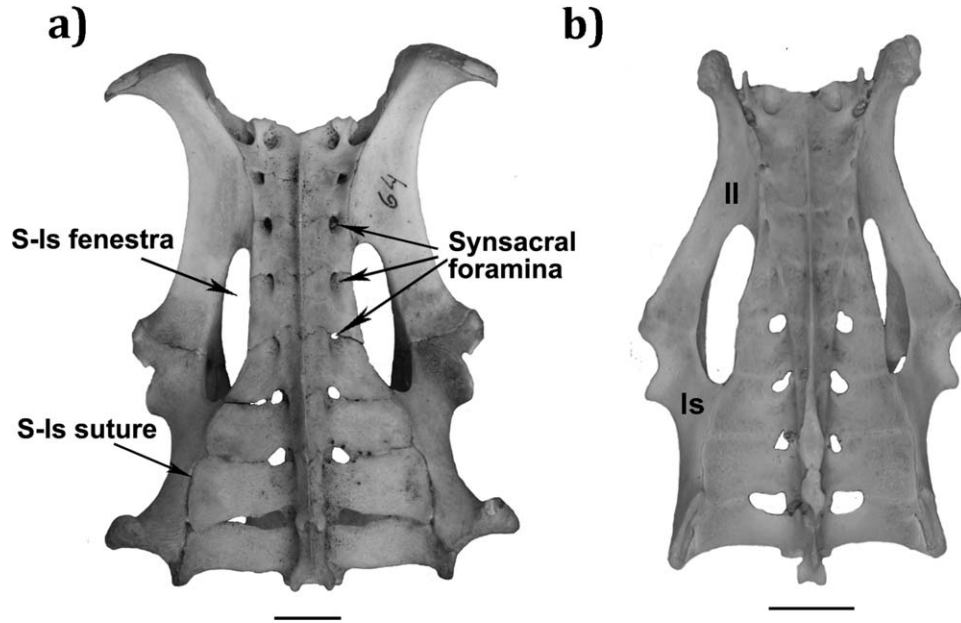


Fig. 1. Dorsal view of an adult synsacrum in Dasypodini and Euphractini. (a) *Dasypus hybridus* (MLP-1.I.03.70); (b) *Chaetophractus vellerosus* (AAC-69). References: **Il**, ilium; **Is**, ischium; **S-Is**, synsacroischial.

distinguished between lumbar and sacral vertebrae as follows: “The pelvic girdle becomes attached to the sacral vertebrae by means of stout, short, and 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.” Finally, Burke et al. (1995) defined sacral vertebrae as those united to the ilium by “transverse processes.”

The presence of vertebral types added from other regions is always associated with an extended synsacrum. A long synsacrum (formed by several vertebrae), strongly attached through syndrosis or synostosis to the iliac plus the ischiatic portions of the pelvic girdle, is restricted to a few group of mammals (Owen, 1866).

The eutherian clade Xenarthra (extant armadillos, sloths and anteaters, and all fossil lineages) shows a unique composite of traits in the axial skeleton, for example, the presence of accessory articulations on the posterior thoracic and all lumbar vertebrae called xenarthry (Rose and Emry, 1993; Gaudin, 1999), deviation in some genera from the conservative number of seven cervical vertebrae in mammals (Owen, 1866; Wetzel, 1985), and highly variable thoracolumbar vertebral number (Asher et al., 2011); the last two characters are shared with Afrotheria (Asher et al., 2009). In addition, all members of the clade show a long synsacrum, formed by the fusion of several vertebrae (Flower, 1885; Hoffstetter, 1958; Rose and Emry, 1993). The synsacrum contacts the ischium and forms a novel synsacroischial fenestra (Fig. 1).

The silky anteater *Cyclopes didactylus* is the only exception, although this is commonly considered a derived condition (Rose and Emry, 1993). However, there is no agreement regarding the identity of each vertebra (Flower, 1885; Hoffstetter, 1958; Engelman, 1978; Rose and Emry 1993; Narita and Kuratani, 2005). Are they all sacral, or have lumbar and/or caudal vertebrae been incorporated into the final assemblage? Misinterpretation of the elements that form each region of the column (cervical, thoracic, lumbar, sacral, and caudal) can lead to erroneous assumptions, including the possibility that these regions exhibit high intraspecific variability. In this respect, Asher et al. (2009, 2011) suggested that members of the clades Xenarthra and Afrotheria exhibited more intraspecific variation in vertebral counts than members of Laurasiatheria and Euarchontoglires.

There are different types of evolutionary change that can potentially lead to increase the vertebral number in the synsacrum, such as meristic changes (changes in column count), homeotic changes (changes in regionalization), and changes in module association (Raff, 1996; Polly et al., 2001; Buchholtz, 2007). The former are the result of changes in somitogenesis, and the subdivision of the presomitic mesoderm into a variable number of discrete units. Under this type of change, the increased vertebral number in the synsacrum would be achieved by multiplication of sacral vertebrae. Homeotic changes are the result of changes in expression domains of genes that specify the identity of different axial regions (e.g., the *Hox* family). In at least some instances, vertebral

TABLE 1. *Nonadult xenarthrans analyzed*

Taxa	Identification	Prenatal/ Postnatal	N° presacral vertebrae	N° synsacral vertebrae with extra lateral ossifications
<i>Dasypus hybridus</i>	AAC-143b	Pre	21	0
<i>D. hybridus</i>	AAC-191	Pre	21	3
<i>D. hybridus</i>	AAC-192	Pre	21	3
<i>D. hybridus</i>	AAC-193	Pre	21	3
<i>D. hybridus</i>	AAC-194	Pre	21	3
<i>D. hybridus</i>	AAC-195	Post	21	3
<i>D. hybridus</i>	AAC-196	Post	21	3
<i>Dasypus novemcinctus</i>	NMB-2853	Post	22	4
<i>Chaetophractus vellerosus</i>	AAC-146	Post	21	5
<i>C. vellerosus</i>	AAC-197	N/A	21	0
<i>C. vellerosus</i>	AAC-198	N/A	21	2
<i>C. villosus</i>	AAC-199	Pre	21	0
<i>C. villosus</i>	AAC-157	Pre	21	0
<i>C. villosus</i>	AAC-156	Pre	21	0
<i>C. villosus</i>	AAC-151	Pre	21	0
<i>C. villosus</i>	AAC-152	Pre	21	0
<i>C. villosus</i>	AAC-200	Post	21	0
<i>C. villosus</i>	AAC-148	Post	21	3
<i>C. villosus</i>	AAC-201	Post	21	2
<i>C. villosus</i>	AAC-202	Post	21	2
<i>C. villosus</i>	AAC-147	Post	21	3
<i>C. villosus</i>	AAC-203	Post	21	3
<i>Tamandua tetradactyla</i>	AAC-187	Post	27	0
<i>Myrmecophaga tridactyla</i>	USNM-20753	Post	25	1
<i>M. tridactyla</i>	USNM-49980	Post	24	1
<i>M. tridactyla</i>	MLP-1.VIII.95.1	Post	25	1
<i>M. tridactyla</i>	MNHN-1930-9	Post	25	1
<i>M. tridactyla</i>	USNM-252756	Post	25	1

N/A = information not available.

identities are set even before segmentation, and typically they augment one column series at the expense of another. The increased number of vertebrae in the synsacrum will lead to a decrease in number of the lumbar and/or caudal series.

Changes in module association would imply relaxed linkage between two modular units; a developmental constraint (or relaxation thereof) of one column series with respect to another can occur at any point of the ontogenetic trajectory (Raff, 1996; Polly et al., 2001). Under this assumption, an increased number of synsacral vertebrae are the result of coalesced elements from different anatomically distinct regions (e.g., sacral plus lumbar, plus caudal vertebrae, or both). Considering these issues, information about ontogeny could provide a developmental framework to distinguish elements that form each different region, similar to that proposed by Hautier et al. (2010) for cervical vertebrae in sloths. The aim of this contribution is to provide ontogenetic information about skeletal ossification of the xenarthran synsacrum to help address the questions regarding the position of the sacrocaudal limit in this developmentally complex structure.

MATERIAL AND METHODS

Institutions Abbreviation

Specimens housed at the following institutions contributed to our sample: Laboratório de Mamíferos Aquáticos, Universi-

dade Federal de Santa Catarina, Santa Catarina (UFSC); Museu de Ciências Naturais, Fundação Zoobotânica, Rio Grande do Sul (MCN); Smithsonian Institution National Museum of Natural History, Washington (USNM); Naturhistorisches Museum Basel, Basel (NMB), Muséum National d'Histoire Naturelle, Paris (MNHN); Museo de La Plata, Colección de Mastozoología and Dr. Carlini's Laboratory in the División Paleontología de Vertebrados, La Plata (MLP, AAC).

Nonadult Xenarthra

Information about skeletal ossification was gathered from 25 specimens which included fetuses, neonates, and young pups of four species of armadillos (Dasypodidae, Cingulata), *Dasypus hybridus* ($n = 7$), *Dasypus novemcinctus* ($n = 1$), *Chaetophractus vellerosus* ($n = 3$), and *Chaetophractus villosus* ($n = 11$), and two anteaters (Myrmecophagidae, Vermilingua, Pilosa), *Tamandua tetradactyla* ($n = 1$) and *Myrmecophaga tridactyla* ($n = 2$; Table 1). Although sloths were not included in the study, we compared our data with those obtained by Hautier et al. (2010 and supporting information) in which posteranial ossification of fetuses from *Bradypus* and *Choloepus* is provided. With the exception of *D. novemcinctus* and *M. tridactyla* specimens, all embryos, neonates, and early pups (hereafter nonadults) were cleared and double-stained following a modified protocol from Dingerkus and Uhler (1977) which included enzymatic clearing with trypsin, and double staining with alcian blue to show cartilage and alizarin red for bone (Wilson et al., 2010). Ossification centers were recorded with the earliest uptake of alizarin. Data on skeletal ossification for *D. novemcinctus* and *M. tridactyla* were obtained from dry skeletons of juveniles.

Adult Xenarthra

Vertebral counts of 101 adult synsacra were obtained from dry skeletons for the aforementioned species (Table 2):

TABLE 2. Adult taxa analyzed in this study

TAXA	Identification	<i>n</i>	Mode (<i>n</i>)	Lower limit (<i>n</i>)	Upper limit (<i>n</i>)
CINGULATA					
Dasypodidae					
Euphractinae					
<i>ChaetophRACTUS vellerosus</i>	AAC-69; AAC-134; AAC-160; AAC-161; AAC-162; AAC-163; AAC-164; AAC-165; AAC-166; AAC-167; AAC-168; AAC-169; AAC-170; AAC-171; MLP-16.V.00.7	15	8 (13)	7 (1)	9 (1)
<i>ChaetophRACTUS villosus</i>	AAC-10; AAC-28; AAC-47; AAC-49; AAC-98; AAC-99; AAC-100; AAC-102; AAC-103; AAC-104; AAC-106; AAC-107; AAC-108; AAC-109; AAC-114; AAC-115; AAC-118; AAC-119; AAC-120; AAC-121; AAC-122; AAC-123; AAC-124; AAC-126; AAC-128; AAC-130; AAC-172; AAC-173; MLP-1311; MLP-1992	30	8 (28)	7 (1)	9 (1)
Dasypodinae					
<i>Dasypus hybridus</i>	MLP-906; AAC-111; AAC-125; AAC-129; AAC-65; AAC-7; MLP-1.I.03.66; MLP-1.I.03.70; MLP-22.II.00.9; MLP-4.VIII.98.10; MLP-869; MLP-T24	12	8 (10)	7 (1)	9 (1)
<i>Dasypus novemcinctus</i>	MCN-2735; MCN-2836; MCN-2962; MCN-3489; MLP-1.I.03.72; MLP-1.I.03.76; MLP-1.I.03.77; MLP-2.III.00.14; MLP-2.X.02.1; UFSC-3099; UFSC-3362; UFSC-3391; UFSC-3677; UFSC-3989; UFSC-4763; UFSC-4770; UFSC-5264; UFSC-5265; UFSC-5266; UFSC-966	20	9 (17)	8 (3)	9 (17)
PILOSA					
Vermilingua					
Myrmecophagidae					
<i>Tamandua tetradactyla</i>	MCN-3277; MCN-3492; MNHN-1969-173; MNHN-1996-588; NMB-10420; UFSC-3042; UFSC-3387; UFSC-3672; UFSC-3789; UFSC-4040; UFSC-491; UFSC-4912; UFSC-679; UFSC-770; UFSC-771; UFSC-776; UFSC-838; UFSC-844	18	5 (15)	5 (15)	6 (3)
<i>Myrmecophaga tridactyla</i>	MCN-2654; MCN-2655; USNM-258580; MNHN-1883-545; USNM-220290; USNM-239008	6	5 (8)	—	—

n = number of specimen studied; the last three columns show information about the number of elements forming the synsacrum (mode, and lower and upper limits of the frequency distribution).

C. vellerosus (*n* = 15), *C. villosus* (*n* = 30), *D. hybridus* (*n* = 12), *D. novemcinctus* (*n* = 20), *T. tetradactyla* (*n* = 16), and *M. tridactyla* (*n* = 8). We considered adult specimens as those in which closure in any of the epiphyses of the long bones has already started. The identification criteria for the vertebral elements were based on the number of synsacral foramina and/or the presence of the sutures between consecutive vertebrae as shown in Figure 1. Incomplete synsacral foramina from the first and last vertebrae were considered as one complete foramen. Along the synsacrum of each specimen, vertebrae that contact the iliac bones were distinguished from those that have no contact with the pelvic girdle (those that form the dorsal border of the synsacroischial fenestra), and those fused to the ischiatic bones.

RESULTS

Cingulata

In *D. hybridus* (Dasypodinae) almost all adult specimens show eight elements forming the synsacrum (Table 2, Fig. 1a) while in *D. novemcinctus* it increases to nine. In both *D. hybridus* and *D. novemcinctus* the first two vertebrae are completely fused to the ilium through the transverse

processes; the third is partially fused to the ilium through its anterolateral margin. In *D. hybridus*, the next five vertebrae are arranged as follow: two vertebrae (sometimes one) are limiting the dorsal border of the synsacroischial fenestra, and the last three (or four) form a bony synsacroischial union, through the tip of its transverse processes. In *D. novemcinctus*, one vertebrae is incorporated posteriorly, increasing the number of postiliac vertebrae to six: two limiting the dorsal border of the synsacroischial fenestra, and four fused through the transverse processes to the ischia.

In nonadult specimens of *D. hybridus* and *D. novemcinctus*, the first three vertebrae of the synsacrum (those in contact with the ilium in the adult) show a single center of ossification for the vertebral body. Each half of the neural arch is developed from one ossification center that spreads dorsally, ultimately reaching its counterpart to form the neural apophysis, and laterally to form most of the transverse process that fuses to the ilium. Additionally, the first two synsacrals (the

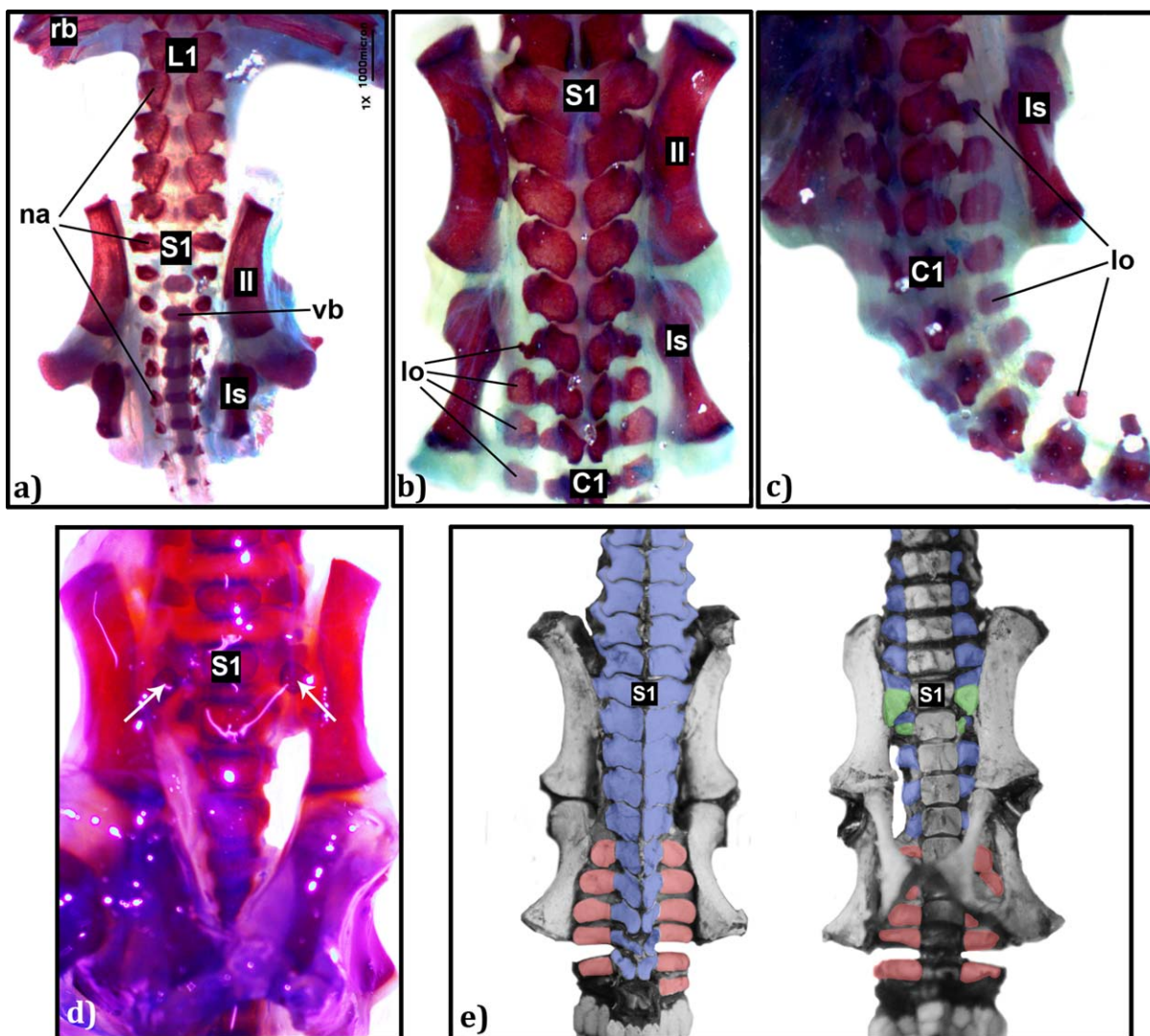


Fig. 2. Synsacrum in nonadults of *Dasypus hybridus* (a–d) and *D. novemcinctus* (e). (a) Dorsal view of an early foetus where the lateral ossifications are absent (AAC-143). (b) Dorsal view of a late foetus showing the posterior lateral ossifications in the synsacrum (AAC-194). (c) Transition between synsacrum and caudal regions showing lateral ossification in dorsal aspect (AAC-194). (d) Ventral view of the synsacrum showing ventral ossifications (with arrows) in the first synsacral (AAC-193). (e) Dorsal (left) and ventral (right) views of a juvenile in which lateral ossifications (red), neural arches (blue), and ventral ossifications (green) are highlighted. References: C1, first free caudal vertebra; II, ilium; Is, ischium; L1, first lumbar vertebra; lo, lateral ossifications; na, neural arches; rb, rib; S1, first synsacral vertebra; vb, vertebral body.

larger ones) show another ossification center ventral to the lateral expansions of the neural arches. The following two vertebrae (those limiting the dorsal border of the synsacroischial fenestra) show only the centers for the neural arches and the vertebral body, lacking the ventrals while the three most posterior (four in *D. novemcinctus*) showed an extra lateral ossification center at both sides of the vertebral body that build exclusively the transverse processes, as do most anterior free caudals (Fig. 2).

Most adult euphractines sampled here (*C. villosus* and *C. vellerosus*) have eight vertebrae forming the synsacrum, and low variability is observed (Table 2). They show a similar pattern than that

recorded in *D. hybridus*. The three most anterior vertebrae are strongly attached to the ilium; the following two show no contact with the pelvic girdle, and the rest are attached to the ischia (Fig. 1b).

The nonadults of *C. villosus* and *C. vellerosus* also have eight synsacral vertebrae, showing a similar pattern than that observed in *D. hybridus*: the first two with ventral ossifications contributing secondarily to the transverse processes, and posterior most vertebrae show extra lateral ossifications forming exclusively the transverse processes, the same as the adjacent free caudals. In addition, one young pup showed extra lateral ossifications not only along the vertebrae that contact the ischia

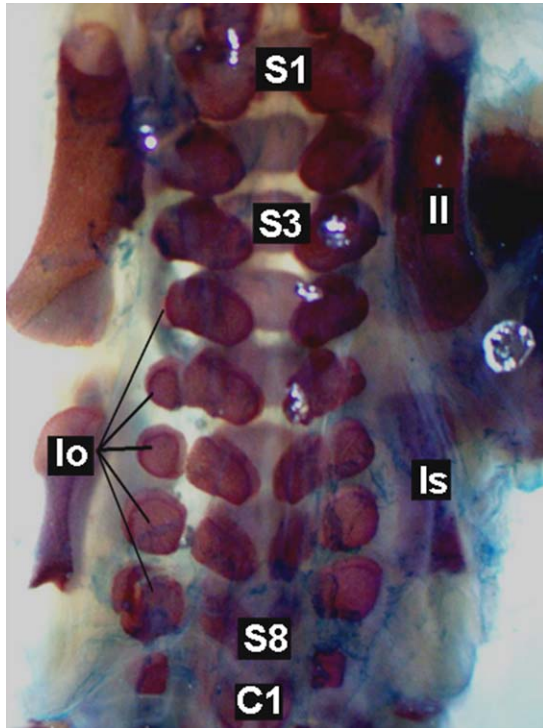


Fig. 3. Synsacrum in nonadult *C. vellerosus* (AAC-146). See references in Figure 2. This specimen shows lateral ossifications in all postiliac vertebrae.

but also in the vertebrae that form the dorsal border of the synsacroischial fenestra (five in total, Fig. 3). Nevertheless, these centers are relatively much smaller than those associated to the ischial bones, probably because in the adult state the transverse processes are reduced.

Pilosa

In *T. tetradactyla*, five elements generally form the adult synsacrum; the first two are completely fused to the ilium; the third vertebrae contacts the ilium through the tip of the anterior margin of the transverse processes; and the following two are variably attached to the ischium through the base of the transverse processes while its distal portions remain free (Fig. 4). In a few cases, a sixth element is added anteriorly, and the ilium is attached to four vertebrae.

The only neonate examined from *T. tetradactyla* does not show ventral ossifications in the first synsacrals, or extra lateral ossifications at the posteriormost synsacrum and free caudal level.

The adults of *M. triadactyla* also showed five synsacrals, and the relationship with the pelvic girdle is similar to that found in *T. tetradactyla* (Fig. 5). Although none of the adult specimens examined showed more than five synsacrals, we observed one nonadult with a sixth vertebra incorporated anteriorly as in *T. tetradactyla*. Ventral ossifications in the first synsacrals were not observed in the adult and nonadult specimens. One of the nonadult specimens analyzed (USNM-20753), showed a nodular bone at both sides of the fifth synsacral vertebrae that corresponds to the lateral ossification centers found in armadillos (Fig. 6a). Nevertheless, these nodular bones are not present, at this stage, in the anterior free caudal series. Other ontogenetically older specimens showed sutures that correspond to the fusion of the nodular bones and the neural arches, also at the level of the fifth synsacral vertebrae (Fig. 6b); in these specimens, the lateral bones form the transverse processes as in armadillos. The free

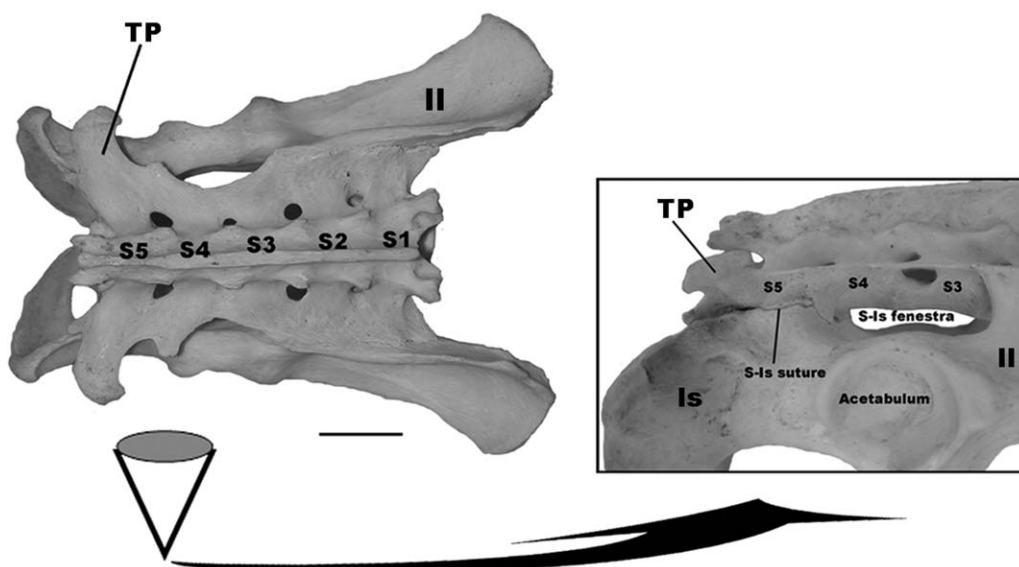


Fig. 4. Adult synsacrum in *Tamandua tetradactyla*. Dorsal (left) and lateral view (right). References: TP, transverse process. See above figures for other references.

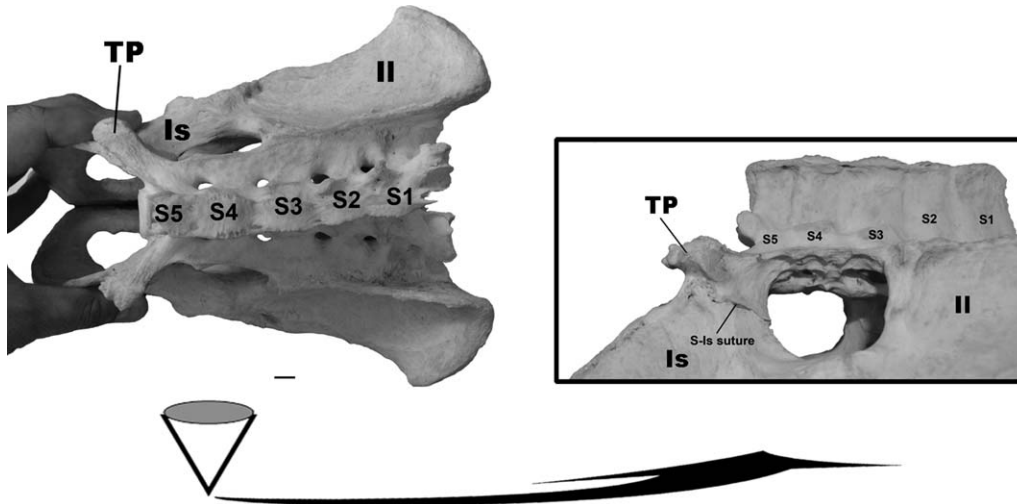


Fig. 5. Adult synsacrum in *Myrmecophaga tridactyla*. Dorsal (left) and lateral view (right). See above figures for references.

caudal series were conserved in only two specimens, and no traces of these sutures or nodular bones were recorded.

DISCUSSION

The skeletogenesis of the vertebral elements that form the synsacrum in xenarthrans shows different patterns that can help identify the sacro-caudal limit in the vertebral column. There are opposite interpretations about the type of vertebrae forming the xenarthran synsacrum. According to Flower (1885), the xenarthran synsacrum is formed by the fusion of true sacral vertebrae, and a number of pseudosacrals with widely expanded

transverse processes, which form the bony connection with the ischium (Flower, 1885; Engelman, 1978). Rose and Emry (1993) interpreted these pseudosacrals present in xenarthrans as anterior caudals, and they also suggested variable sacralization of the last lumbar, which is incorporated cranially to the synsacrum (see also Hoffstetter, 1958). More recently and contrarily to the classical view, Narita and Kuratani (2005, Table 1), considered all vertebrae forming the synsacrum in xenarthrans as sacral while in the rock hyrax (*Procapra capensis*, Hyracoidea), a species also with a large number of synsacral elements, the synsacrum was considered as formed by sacral and caudal vertebrae.

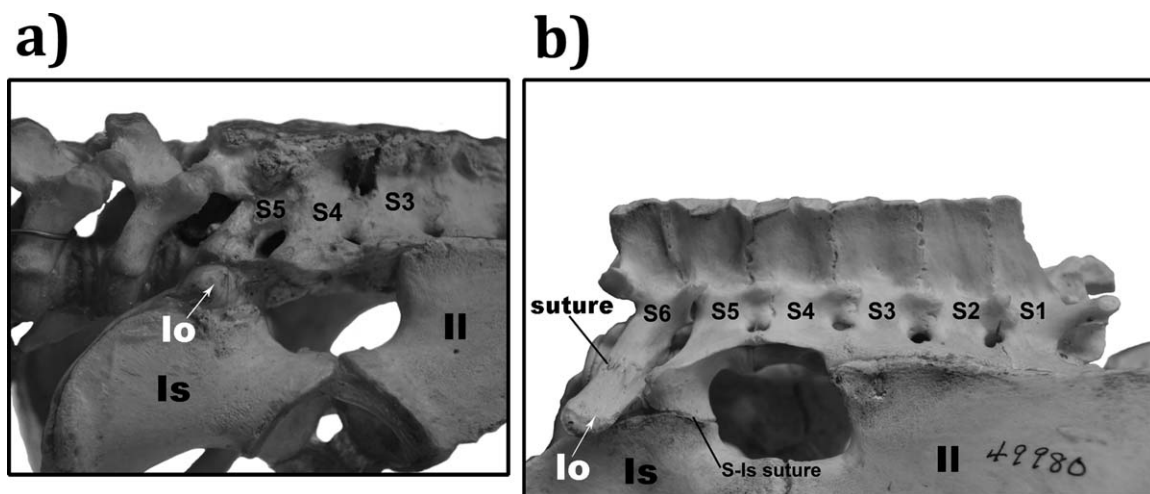


Fig. 6. Synsacrum in nonadults of *Myrmecophaga tridactyla*. (a) Lateral view of a young pup where the lateral ossifications form a separate nodular bone (USNM-20753). (b) Lateral view of a more mature pup where the lateral ossifications are incorporated to the vertebrae in the transverse processes (USNM-49980).

During skeletogenesis, the synsacrum of extant Cingulata (Dasypodidae) shows well-developed extra lateral ossifications in all vertebrae that come into contact with the ischium, and the same centers are visible at both sides of the first free caudals. These lateral ossifications form exclusively the transverse processes in the adults. In one specimen of *C. vellerosus*, these ossifications also appeared in the vertebrae that form the dorsal border of the synsacroischial fenestra, suggesting that all vertebral elements added posteriorly to the last vertebrae contacting the ilium should be considered caudal, and not only the ones fused to the ischium as suggested by Flower (1885), Engelman (1978), and Rose and Emry (1993). Within pilosans, the pattern is slightly different as shown by the nonadult specimens analyzed here. In anteaters, extra lateral bones are absent in the (fourth) synsacral adjacent to the last vertebrae in contact with the ilium. They are only present in the (fifth) most posterior synsacral, which is attached to the ischium and form the extended transverse processes. The scarce information derived from the free caudal series suggests absence of extra lateral ossification at this level. Ossification of the vertebral column in sloth fetuses of *Bradypus* and *Choloepus* was analyzed by Hautier et al. (2010), where no traces of lateral ossification were recorded at the synsacral level. Likewise, adult synsacral morphology was studied in a recent paper by Buchholtz and Stepien (2009) and suture lines between the transverse processes and the vertebral bodies of postiliac synsacrals were not mentioned. Nevertheless, juvenile stages are lacking in both studies. Increasing the number of specimens and stages of pilosans should help test whether extra lateral ossifications are present in the sloths synsacrals and in the anterior free caudals of myrmecophagids.

Among other eutherians, most studies on skeletal ossification of caudal and sacral series are poorly resolved. Nevertheless, the presence of lateral ossifications in the sacral and/or caudal series has been reported in some species in which ossification is known in detail. For example, Beyerlein et al. (1951) in a study on skeletal ossification of *Mesocricetus auratus* stated that "epiphyseal centers (on transverse processes) on sacral vertebra 4 and on caudals 1–5 may be vestiges of the tubercular centers of former ribs" (see also Table 1 in the article). Another detailed description has been given in the human posterior trunk, in which the synsacrum is formed by five vertebrae and the caudals are extremely reduced into a coccygeal region. Different from our observations, extra lateral ossifications are present in the first two or three sacrals, forming the transverse processes through which vertebrae come into contact with the iliac bones. Our observations suggest that in the sacrals the iliac contact is achieved by expan-

sion of the base of the neural arches primarily, and by ventral ossifications secondarily. Additionally, the most posterior vertebrae of the human synsacrum are ontogenetically similar to the first coccygeal, showing the same chondrification centers, and absence of lateral ossifications (Bardeen, 1905). The human and australopithecine pelvis is notable for its expanded width accompanied by wide sacral alae (Filler, 1994), features that have been related to their exclusive mode of upright locomotion (Lovejoy, 2005). Further studies should explore whether lateral ossifications in anterior caudals is a character restricted to Xenarthra or a more widespread feature among mammals.

CONCLUSIONS

A new ontogeny-based criterion to identify vertebral types in the xenarthran synsacrum is presented here. Most anterior caudal vertebrae show extra lateral ossifications forming exclusively the transverse processes, and they can be identified also along the most posterior region of the synsacrum. These vertebrae are not true sacrals. Alternatively, the transverse processes of the first two synsacrals (those completely fused to the iliac bones in adults) are formed by lateral expansions of the neural arches, and at least in armadillos, by a minor contribution of ventral ossifications.

Among armadillos the sacrocaudal limit can be established between the last vertebra in contact with the iliac bones and the first vertebra that form the dorsal border of the synsacroischial fenestra. In anteaters, the limit is apparently set at one vertebra more posteriorly, between the first vertebra in contact with the ischium and the next one. However, the pattern of homologies could be obscured, due to a lesser resolution in the skeletogenetic sequence than that presented in armadillos.

This clearly distinctive pattern of development shows that coalesced vertebrae from different regions form the synsacrum, and this fusion seems to occur at later stages in the ontogenetic trajectory as caudal vertebrae added to the synsacrum still conserved their unique extra lateral ossifications. In this regard, modular dissociation is the type of evolutionary change in agreement with the pattern found here, supporting the classical view of synsacrum formation (Flower, 1885; Rose and Emry, 1993).

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