ORIGINAL INVESTIGATION

Evolution of the axial skeleton in armadillos (Mammalia, Dasypodidae)

Fernando C. Galliari[a], Alfredo A. Carlini[a,b], Marcelo R. Sánchez-Villagra[b],*

[a]*Departamento Científico de Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata, La Plata, Argentina*
[b]*Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland*

Abstract

Intraspecific and interspecific variation in cervical, thoracic, and lumbar region of the vertebral column of Dasypodidae were examined in a phylogenetic framework. The number of vertebrae for each region were recorded for 86 specimens and metric data for each vertebra (centrum length, high, and width) were recorded for 72 specimens, including eight of the nine living genera. The number of vertebrae and degree of fusion between them were used to define four characters which were plotted on two alternative phylogenies of Dasypodidae. The ratio between centrum height and width is similar across all taxa analyzed except for *Chlamyphorus,* which exhibits a deviation in the last two lumbars. *Tolypeutes matacus* is unique among the taxa examined in having a second co-osified bone called postcervical bone, which is a fusion of the seventh cervical and first thoracic vertebrae. The thoraco-lumbar numbers of dasypodids are reduced when compared with other xenarthrans and are more diverse than those of some other mammalian clades of similar geological age and higher ecomorphological diversity. Changes in size are somewhat coupled with changes in the number of body segments. Independent of the phylogenetic framework taken, changes in size are accompanied with small changes in numbers of thoracolumbar vertebrae within each genus. There are functional and phylogenetic correlates for changes in number of thoraco-lumbar vertebrae in dasypodids.

Introduction

The adult morphology of the vertebral column is an excellent proxy for embryological and molecular aspects of evolution, as the number of vertebrae is directly coupled with the number of somites; and the limits between regions of the vertebral column are coupled with boundaries in Hox gene expression domains (Burke et al. 1995; Richardson et al. 1998).

Different groups of vertebrates are known to posses distinct patterns of variation in vertebral count (Narita and Kuratani 2005). For example, it is well-known that mammals have a very stable number of cervical vertebrae, and pleiotropic effects of mutations leading to changes in this region are hypothesized to be coupled with this exceptional degree of conservatism when compared with any other group of tetrapods (Galis 1999). Certain changes in vertebral numbers are reportedly diagnostic of certain clades (Müller et al. 2008), such as an increase in thoraco-lumbar numbers in afrotherian mammals (Sánchez-Villagra et al. 2007) or less a reduction in the precaudal series count in trichechids (Buchholtz et al. 2007).

Among mammals, the xenarthran vertebral column is of particular interest for several reasons. The unique

*Corresponding author.
E-mail address: m.sanchez@pim.uzh.ch (M.R. Sánchez-Villagra).

Table 1. Body size range and degree of fossoriality in dasypodids.

Taxon	Weight range (Kg)	Head-body length (mm)	Tail length (mm)	Total length (mm)	Degree of fossoriality
Zaedyus pichiy	1.25 - 2.35	277	124,8	401,8	Intermediate
Chlamyphorus truncatus	0.27 - 0.35	98,4	31,2	129,6	Very high
Calyptophractus retusus	–	75 - 140	35	–	Very high
Euphractus sexcinctus	3.00 - 6.50	395,7	220,2	616,4	Intermediate
Chaetophractus villosus	1.00 - 3.65	291,1	145,6	436,7	Intermediate
Chaetophractus vellerosus	0.26 - 1.33	–	–	376	Intermediate
Dasypus novemcinctus	2.00 - 6.50	–	–	645,7	Intermediate
Dasypus hybridus	1.09 - 2.04	–	–	459,5	Intermediate
Tolypeutes matacus	1.00 - 1.15	250,7	63,7	–	Low
Priodontes maximus	18.70 - 32.30	–	–	895,5	Intermediate
Cabassous tatouay	3.40 - 6.40	457,8	179	–	Very high
Cabassous chacoensis	–	300-306	90-96	–	No information

Data from Wetzel (1980), Redford and Eisenberg (1992), and Nowak (1999).

morphology of some articulations in the thoraco-lumbar region is the basis of the name 'Xenarthra' and a diagnostic feature to the clade (Gaudin 1999). The living sloths are among the very few mammals with a number of cervical vertebrae different than seven (Starck 1995; Buchholtz and Stepien 2009).

One of the three morphologically distinct living clades of xenarthrans are armadillos, the Dasypodidae. With a total of 9 living genera and 21 species (Gardner 2005), they exhibit a wide range of body size and degree of fossoriality (Table 1).

We examined the intraspecific and interspecific variability in the vertebral column of Dasypodidae and discuss these data in a phylogenetic and evolutionary framework.

Material and methods

We examined 86 adult and young adult specimens, recording vertebral counts for all of them and metric data for 72, distributed in 11 species (Table 2), and thus sampling eight of the nine living genera of Dasypodidae. *Calyptophractus* is the only one not included in this study. The materials are from the collections of the Museo de La Plata (MLP) and the Museo Argentino de Ciencias Naturales (MACN). Some specimens are from the personal collection of Alfredo A. Carlini (AAC) at the MLP.

Age classes were established according to the degree of fusion of the epiphysis from the vertebral centrum and the distal epiphysis of the femur as follows: adults, with both epiphyses of the vertebrae fused to the centrum and the distal epiphysis of the femur fused to the diaphysis; young adults, with vertebral epiphyses fused and distal epiphysis of the femur not completely fused; juveniles, with both vertebral and femur epiphysis unfused. The latter were not included in this study.

Only one specimen of *Cabassous tatouay* and one of *C. chacoensis* were examined and these data were supplemented with those obtained from a revision of the genus (Wetzel 1980). Because of access to mounted skeletons only, we were not able to collect metric data for *Priodontes maximus*. Skeletons that lacked the cervical region or few vertebrae of any region were used only if the position of the rest of the vertebrae could be identified. The only measured skeleton of *Euphractus sexcinctus* lacked the atlas hence the first vertebra was not taken into account in the analysis.

We examined the cervical, thoracic, and lumbar regions (Flower 1885) of the vertebral column. Sacral vertebrae are those attached to the pelvic girdle (or fused posteriorly to these vertebrae) and were not included in this study.

The variation in the number and fusions in some regions was used to define the four characters listed below, which were plotted onto two alternative phylogenies of the taxa examined.

Character 1: Fusion of cervical vertebrae: 0, fusion of second and third vertebrae; 1, fusion of second-fourth vertebrae; 2, fusion of second-fifth vertebrae.

Character 2: Postcervical bone (PC): 0, absent; 1, present.

Character 3: Number of thoracic vertebrae (TV): 0, nine; 1, ten; 2, eleven; 3, twelve; 4, thirteen.

Character 4: Number of lumbar vertebrae (LV): 0, two; 1, three; 2, four; 3, five.

Character 5: Number of thoracolumbar vertebrae (TLV): 0, thirteen; 1, fourteen; 2, fifteen; 3, sixteen.

Table 2. Dasypodids examined in this work.

Taxon	Identification number
Chaetophractus villosus	AAC-098, AAC-099, AAC-100, AAC-101, AAC-102, AAC-103, AAC-104, AAC-105, AAC-106, AAC-107, AAC-108, AAC-109, AAC-114, AAC-115, AAC-116, AAC-118, AAC-119, AAC-119, AAC-120, AAC-121, AAC-122, AAC-123, AAC-124, AAC-126, AAC-127, AAC-128, AAC-130, AAC-132, MLP-1214, MLP-819, MLP-795, MLP-15.X.98.03, MLP-821, MLP-855, MLP-918, MLP-785, MLP-922, MLP-831, MLP-860.
Chaetophractus vellerosus	AAC-134, MLP-18.XI.99.09, MLP-22.III.99.08, MLP-30.XII.02.69, MLP-30.XII.02.41.
Zedyus pichiy	AAC-110, AAC-112, AAC-113, AAC-117, AAC-131, MLP-9.XII.02.10, MLP-1210, MLP-1209, MLP-889, MLP-767, AAC-033, AAC-034, AAC-035, MACN-3.35.
Euphractus sexcinctus	MLP-1180, MACN-13.77.
Chlamyphorus truncatus	AAC-002, AAC-005, AAC-027.
Dasypus hybridus	AAC-111, AAC-125, AAC-129, AAC-133, MLP-5.IX.97.03, MLP-4.VIII.98.10, MLP-22.II.00.9, MLP-869, MLP-1211.
Dasypus novemcinctus	MLP-2.III.00.14, MLP-1215, MACN-17.105.
Tolypeutes matacus	MLP-13.XII.02.06, MLP-11.III.99.01, MLP-8.X.02.16, MLP-1217, AAC-013, AAC-014, MACN-29.908, MACN-17.112.
Cabassous tatouay	MLP-1183.
Cabassous chacoensis	AAC-060.
Priodontes maximus	MLP-S/N, MLP-1218.

The two phylogenetic topologies taken as a framework are Gaudin and Wible (2006, p. 160, Fig. 6.1), based on a parsimony analysis of a comprehensive examination of 163 discrete cranio-dental characters and Delsuc et al. (2002, p. 1662, Fig. 3) based on a maximum likelihood analysis of data from the ADRA2B, BRCA1, and VWF genes. *Chlamyphorus truncatus* was not included in the analyses of Gaudin and Wible or Delsuc et al. The genus *Chlamyphorus* as used by Gaudin and Wible corresponds to a specimen of *Chlamyphorus retusus*, which following Gardner (2005) actually pertains to *Calyptophractus retusus*. The phylogeny of Gaudin and Wible (2006) differs from that of Delsuc et al. (2002) in the following aspects: First, in the hypothesis of Gaudin and Wible (2006) *Tolypeutes* is near the middle of a pectinate pattern and more derived than *Priodontes* and *Cabassous*, Delsuc et al. (2002) suggested instead that *Tolypeutes* is the sister-group of a *Priodontes/Cabassous* clade. Second, Gaudin and Wible (2006) presented *Euphractus* in a trichotomy with *Chaetophractus* and *Zaedyus/Calyptophractus*, whereas Delsuc et al. (2002) hypothesized that *Euphractus* is the sister-group of *Zaedyus*.

Characters were mapped onto the two phylogenetic topologies with Mesquite 2.5 (Maddison and Maddison 2008) and maximum parsimony criterion was assumed because it is the most common methodology used when the data source is morphological. Character 5 listed above is obviously not independent from characters 3
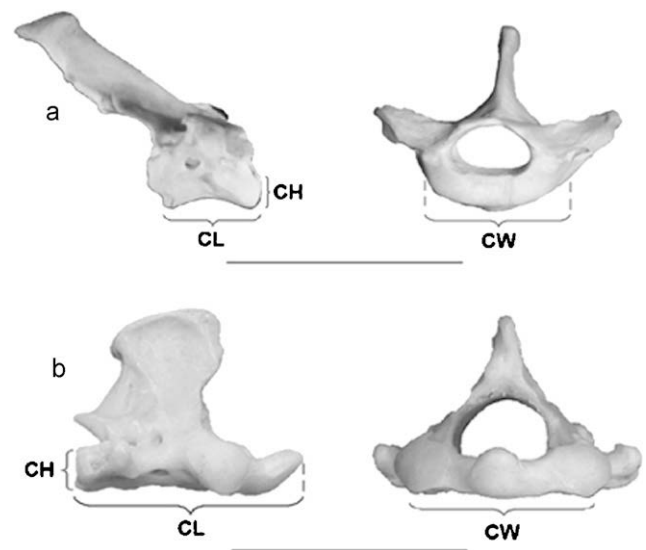

Fig. 1. Measurements taken from each presacral vertebrae of Dasypodids. (a) Measures taken for vertebrae from thoracic and lumbar regions. (b) Measures for vertebrae from cervical region. Abbreviations: CL = Centrum length; CH = Centrum height; CW = Centrum width.

and 4, but it is useful to visualize the global changes in this region in dasypodid phylogeny. The character list we provide here is not expected to be uncritically incorporated in its totality in data matrices for phylogenetic analyses.

Three measurements were taken for each presacral vertebra examined (Fig. 1) using a caliper and recorded to the nearest 0.05 mm: centrum length (CL, measured ventrally), width (CW, measured ventrally) and height (CH, measured anteriorly except in cervical vertebrae that were measured posteriorly as shown in Fig. 1a and b respectively). In the case of the fused cervical vertebrae (and a fusion between the last cervical and first thoracic recorded in three specimens of *Tolypeutes matacus*), we report for CL an average length for each vertebra based on a division of the total of the fused structure by the number of elements. Vertebrae in which measurements could not be taken were recorded as an average dimension between the immediately preceding and following vertebrae. For the others two measurements

(CH and CW) the length recorded in the fused structure was the same for each conforming element.

Results

Fig. 2 summarizes the ranges in vertebral numbers in the taxa examined on the two alternative phylogenetic topologies considered, which also illustrate the hypothesized ancestral and terminal states in the characters examined. Although *Chlamyphorus* was not included in the phylogenetic analysis, the TV ranges between 11 and 12, the LV between 2 and 3, and the TLV are 14 in all specimens examined.
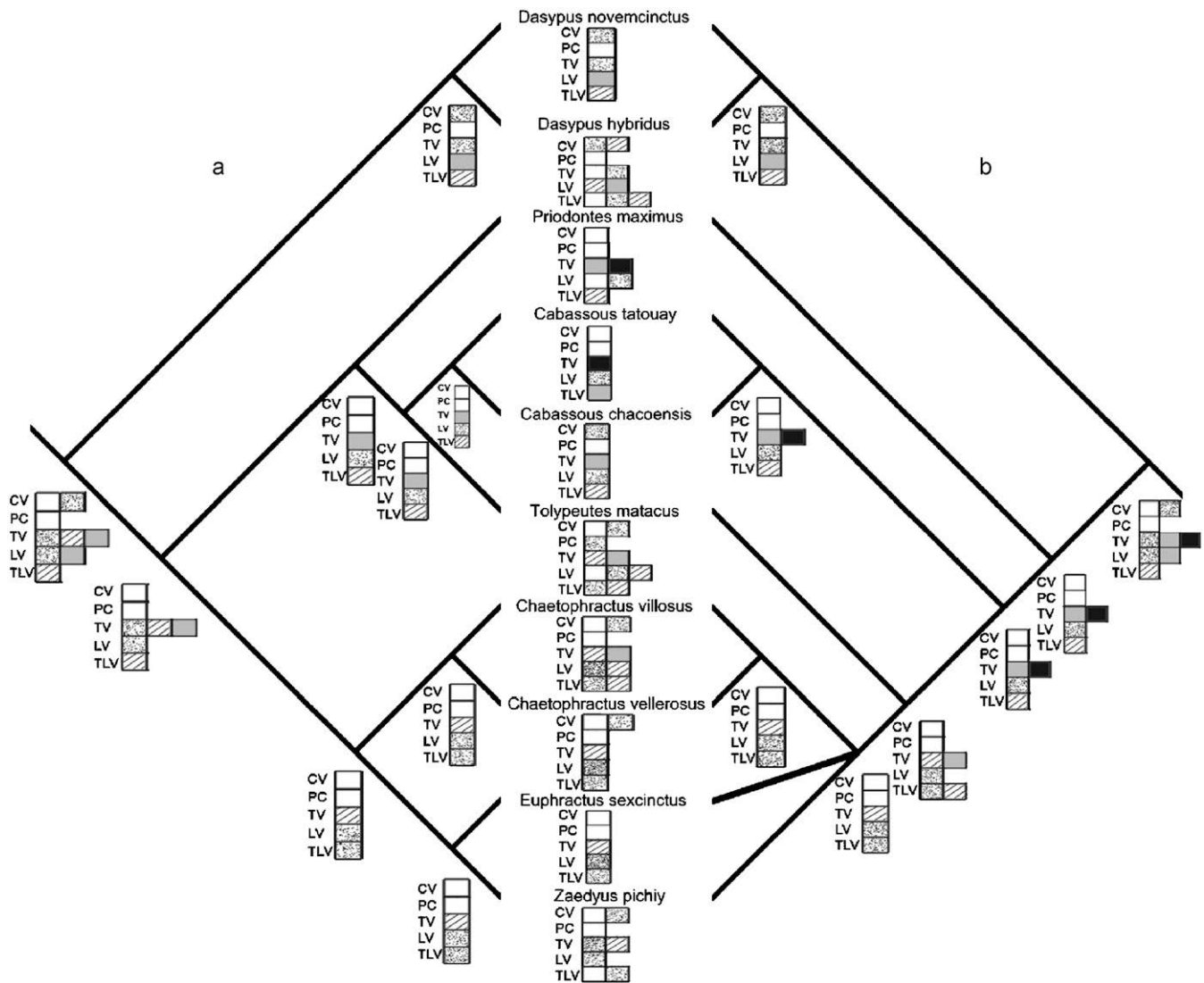

Fig. 2. Two alternatives phylogenies on which characters were plotted. (a) Delsuc et al. (2002); (b) Gaudin and Wible (2006). Characters: CV = number of fusioned cervical vertebrae; PC = postcervical bone; TV = number of thoracic vertebrae; LV = number of lumbar vertebrae; TLV = number of thoracolumbar vertebrae. States: White = 0; Dotted = 1; Diagonal stripes = 2; Grey = 3; Black = 4. States references in text. Notice that more than one box for each character denotes a polymorphic condition for that species or node.
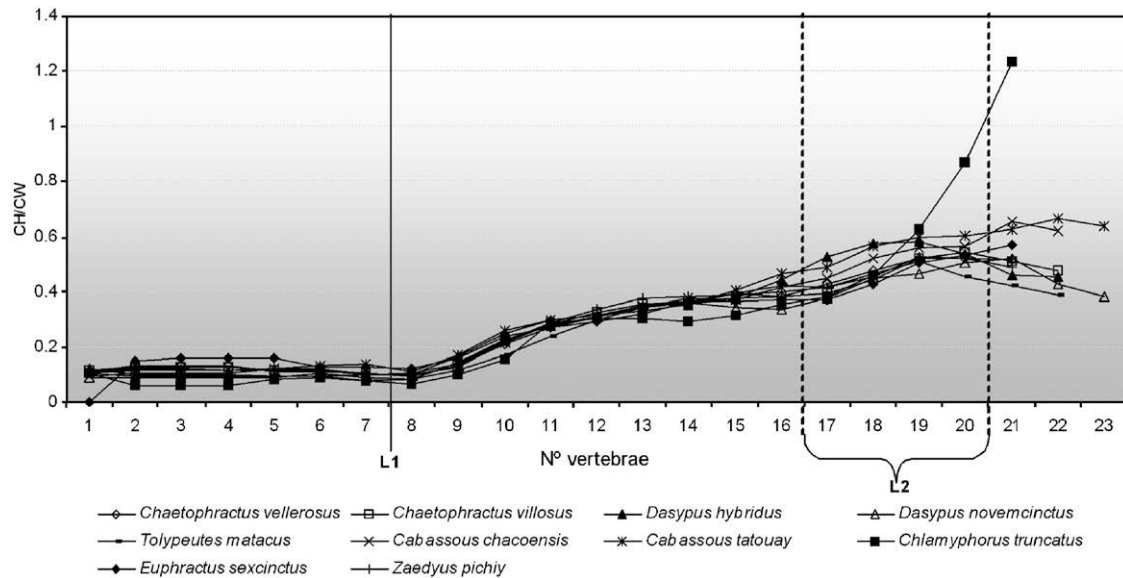
Fig. 3. Ratio between centrum width (CW) and centrum heigth (CH) of the presacral vertebrae for several Dasypodids. Abbreviations: L1 = limit between cervical and thoracic region; L2 = range limit between thoracic and lumbar region showing a highly variable position of this limit.

The ratio between height and width of the pre-sacral vertebrae best captures the morphometric variation we recorded here. This is illustrated in Fig. 3 for seven genera and ten species. The same general relations are found across all species with just one outlier in the lumbar region. In *Chlamyphorus* the last two lumbar vertebrae have a much larger ratio, even above one in the last lumbar, a unique condition among the armadillos examined.

As shown in Fig. 4a, *Chlamyphorus* is the only armadillo examined in which the pelvic shield has a vertical orientation with respect to the vertebral column. The pelvic girdle is highly fused with this shield by several ischial bony extensions called fulcra (Atkinson 1870). This might be influencing the change in proportions between height and width of the lumbar vertebrae centrum.

Discussion

There is variation in the presacral region of dasypodids which is coupled with phylogenetic and functional changes in the group. The thoraco-lumbar numbers of dasypodids are more diverse than those of some other mammalian clades of similar geological age and higher ecomorphological diversity. Living carnivores, for example, almost always have 20 thoracolumbar vertebrae (Sánchez-Villagra et al. 2007). Whatever constraints are associated with this conservatism in carnivores (functional, developmental, etc.), this is much less evident in dasypodids. On the other hand, in the cervical region the

number of elements remains constant among the different taxa examined but with a diverse scheme of fusion between the second vertebrae and the three that follow (Figs. 4 and 5a), forming a co-ossified bone (Rose and Emry 1993) called mesocervical bone (Scillato-Yané 1982). As shown in Fig. 4b and 5b, *Tolypeutes matacus* is unique among the taxa examined in having a second co-ossified bone called postcervical bone, which is a fusion of the seventh cervical and first thoracic vertebrae, thus confirming what was reported by Scillato-Yané (1982).

Some species exhibit more polymorphisms than others, as is the case of *Dasypus hybridus* when compared with *D. novemcinctus*. Some states in that polymorphic condition are unique, as in characters 1 and 3. Some of the alternative methods of coding polymorphic states in character analyses (Wiens 2000) would result in the identification of an autapomorphy in some taxa, such as *Dasypus novemcinctus* in those two characters.

The number of vertebrae in armoured clades of tetrapods is less than that of their respective sister-groups (Müller et al. 2008). Turtles for example, have invariably 10 dorsal vertebrae. An extinct group of pararreptiles, the placodonts, are also characterised by reduction in the number of dorsal vertebrae from around 20 in basal forms to 15–12 in armoured species. The same is found in dasypodids (Fig. 4) when compared to anteaters and sloths. The number of thoraco-lumbar vertebrae in the other two groups of Xenarthrans, Folivora and Vermilingua, is much larger than in armadillos, as exemplified by the following taxa: *Choloepus*: 28 (Asher and Lehmann 2008), *Scelidother-*
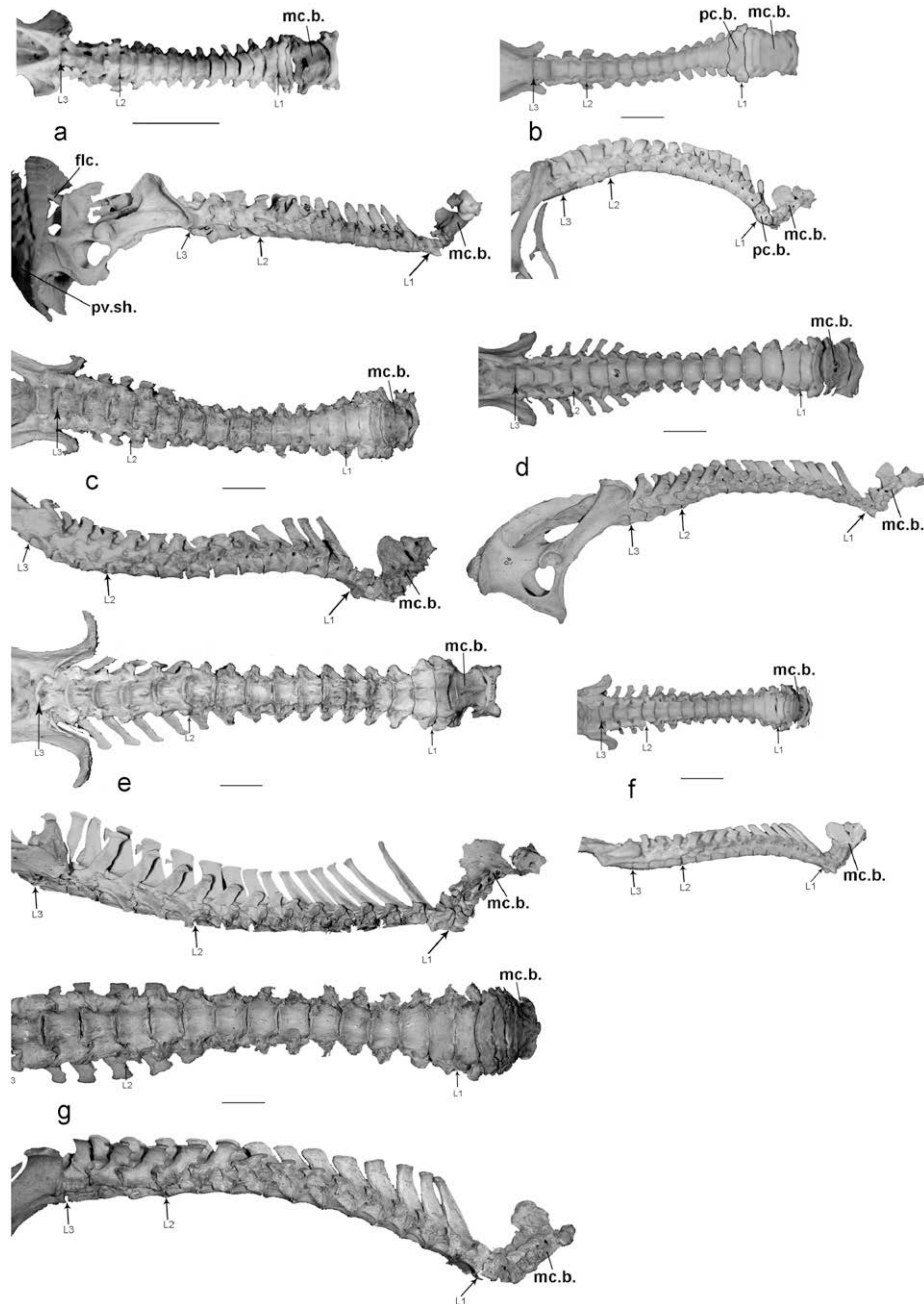
Fig. 4. Axial skeleton in dasypodids showing cervical, thoracic, and lumbar region. (a) *Chlampyphorus* (b) *Tolypeutes* (c) *Chaetophractus* (d) *Cabassous* (e) *Dasypus* (f) *Zaedyus* (g) *Euphractus*. Ventral view above each letter and lateral view below them. Scale bar = 20 mm. Abbreviations: flc. = ischial fulcra; L1 = limit between cervical and thoracic region; L2 = limit between thoracic and lumbar region; L3 = limit between lumbar and sacral region; mc.b. = mesocervical bone; pc.b. = postcervical bone; pv.sh. = pelvic shield.

ium leptocephala: 20, *Thalassocnus natans*: 19, *Megatherium americanum*: 19 (Sánchez-Villagra et al. 2007), *Myrmecophaga trydactyla*: 18, *Tamandua tetradactyla*: 19–20 (Jenkins 1970). A total of 19 thoraco-lumbar or more vertebrae appears to be the plesiomorphic condition for Theria and for the sister group of xenarthrans (Sánchez-Villagra et al. 2007), so there is no doubt that dasypodids have experienced a reduction in number.

However, the presence of co-ossified bones in the neck is associated with digging habits (Rose and Emry 1993, and bibliography therein).

Considering the fossil record of dasypodids, we notice that the number of lumbar vertebrae found in *Dasypus* is congruent with that found in *Stegotherium*. Those genera are hypothesized to be sister groups by Gaudin and Wible (2006). The number found in the euphrac-
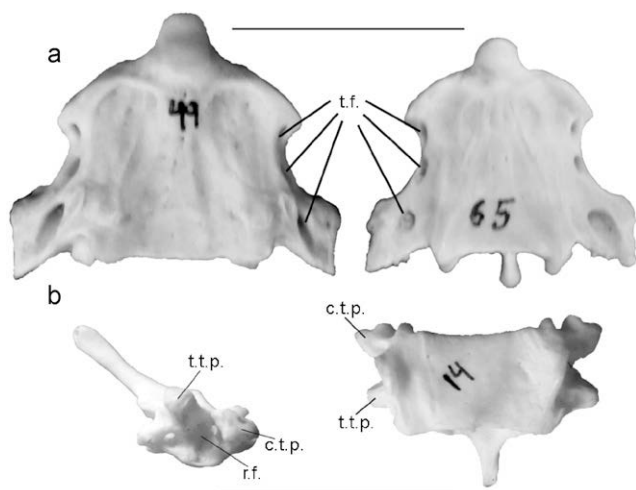
Fig. 5. Cervical fusion in Dasypodids. (a) Mesocervical bone in *Chaetophractus* (left) and *Dasypus* (right). The arrangement of the transverse foramina indicates the segmentary origin of this structure. (b) Postcervical bone in *Tolypeutes*. The bone has two transverse processes on each side, one from the cervical and another from the thoracic vertebrae. Scale bar = 20 mm. Abbreviations: c.t.p. = cervical transverse process; r.f. = first rib facet; t.f. = transverse foramina; t.t.p. = thoracic transverse process.

tines *Chaetophractus, Euphractus* and *Zaedyus* are more similar to those of the fossil genus *Proeutatus* (Scott 1903–1905). This fossil is in a clade sister to the euphractines according to Gaudin and Wible (2006). A pattern also supporting the hypothesized position of these fossils is found for the thoracolumbar vertebrae, where *Stegotherium* has 15 TLV, similar to *Dasypus*, and *Proeutatus* has 14 TLV, similar to euphractines. This way there appears to be a reduction tendency in number of thoracolumbar vertebrae, in concordance with a more rigid carapace found in euphractines respect to dasypodines since the divergence of these two groups. This seems to support the fact that euphractines are more derived than dasypodines as it has already been suggested by Carlini et al. (2009) when examining the external ornamentation of the osteoderms in some Oligocene daypodids, and Krmpotic et al. (2009) based on an internal analysis of the osteoderms of some recent and fossil dasypodids.

The vertebral characters examined show more congruence with the phylogenetic tree of Gaudin and Wible (2006; see also Carlini and Scillato-Yané 1995), which is also true when one considers information from the fossil record. *Tolypeutes* posseses a combination of state characters from both the rest of tolypeutines and also from the euphractines, so a closer relationship with *Priodontes/Cabassous* clade is less well-supported than its pectinate position hypothesized by Gaudin and Wible (2006). The clade *Chaetophractus/Euphractus/Zaedyus* is well justified by all characters but a closer relationship

between *Zaedyus* and *Euphractus* with respect to *Chaetophractus* cannot be resolved with the characters given.

Asher and Lehmann (2008) suggested that the relatively late eruption of the permanent dentition is a diagnostic feature of afrotherian mammals, which also show an increase of vertebral counts and absence of clavicle. These authors pointed out the similarity of this suite of evolutionary changes with a human genetic pathology called cleidocranial dysplasia (CCD), suggesting a potentially shared developmental basis for the evolution of these features. Dasypodids are characterized by derived dental features, such as the lack of enamel in adults (Starck 1995), but we are not aware of a special pattern or retarded dental eruption in this group (Martin 1916). Neither of these features which characterise afrotherians and the CCD condition are present in xenarthrans, as the clavicle is generally not reduced in this group (Starck 1995) and the number of thoracolumbar vertebrae is less than 19. This is relevant, as xenarthrans are depicted as sister-group of afrotherians in many recent comprehensive treatments of placental phylogeny (Springer and Murphy 2007).

When examining vertebral numbers, the extent of increase in somatic growth or segmentation has been of interest (Head and Polly 2007). In their review of amniote vertebral counts, Müller et al. (2008) concluded that there are no universal principles guiding the patterns of somitogenesis and that different kinds of constraints evolved independently within the different clades. In dasypodids, changes in size are somewhat coupled with changes in the number of body segments. Independent of the phylogenetic framework taken, changes in size are accompanied with small changes in ranges of thoracolumbar vertebrae within each genus (Fig. 2).

Acknowledgements

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