The Morphology of Xenarthrous Vertebrae (Mammalia: Xenarthra)

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# Table of Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>1</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>LIST OF ABBREVIATIONS</td>
<td>4</td>
</tr>
<tr>
<td>DESCRIPTIVE ANATOMY</td>
<td>4</td>
</tr>
<tr>
<td>Cingulata</td>
<td>4</td>
</tr>
<tr>
<td>Euphracta (esp. Zaedyus pichiy)</td>
<td>4</td>
</tr>
<tr>
<td>Tolyypeutes matuscus</td>
<td>13</td>
</tr>
<tr>
<td>Other Cingulates</td>
<td>15</td>
</tr>
<tr>
<td>Vermilingua</td>
<td>17</td>
</tr>
<tr>
<td>Tamandua mexicana</td>
<td>17</td>
</tr>
<tr>
<td>Other Vermilinguas</td>
<td>19</td>
</tr>
<tr>
<td>Tardigrada</td>
<td>19</td>
</tr>
<tr>
<td>Bradypus variegatus</td>
<td>19</td>
</tr>
<tr>
<td>Hapalops</td>
<td>21</td>
</tr>
<tr>
<td>Other Tardigrada</td>
<td>24</td>
</tr>
<tr>
<td>CONCLUSIONS</td>
<td>26</td>
</tr>
<tr>
<td>Morphological Summary</td>
<td>26</td>
</tr>
<tr>
<td>Phylogeny and Evolution of Xenarthra Vertebræ</td>
<td>27</td>
</tr>
<tr>
<td>Relationship of Xenarthra to Early Cenozoic Fossil Taxa</td>
<td>30</td>
</tr>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>33</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>33</td>
</tr>
<tr>
<td>APPENDIX: SUMMARY OF MORPHOLOGICAL DATA</td>
<td>36</td>
</tr>
</tbody>
</table>

## List of Illustrations

1. *Mephitis mephitis*, thoracic and lumbar vertebrae in anterior, posterior, and left lateral views  
2. *Zaedyus pichiy, Tamandua mexicana*, and *Bradypus variegatus*, thoracic and lumbar vertebrae in dorsal view  
3. *Zaedyus pichiy, Tamandua mexicana*, and *Bradypus variegatus*, thoracic and lumbar vertebrae in anterior and posterior view  
4. *Zaedyus pichiy*, stereophotographs of thoracic and lumbar vertebrae in right lateral view  
5. *Tolyypeutes matuscus* (juvenile), thoracic and lumbar vertebrae in left lateral view  
6. *Tolyypeutes matuscus* (juvenile), sacral vertebrae in dorsal, ventral, and right lateral views  
7. *Priodontes maximus*, first lumbar vertebra in anterior view  
8. *Tamandua mexicana*, stereophotographs of posterior thoracic vertebrae in right lateral view  
9. *Bradypus variegatus*, stereophotographs of thoracic and lumbar vertebrae in right lateral view  
10. *Hapalops* sp., posterior thoracic vertebrae in dorsal view  
11. *Hapalops* sp., posterior thoracic vertebrae in left lateral view  
12. *Protherotherium typicum*, isolated mid-thoracic vertebra in dorsal view  
13. Diagrammatic representation of typical xenarthran intervertebral facets in anterior and posterior view  
14. Distribution of vertebral character states on a phylogeny of the Xenarthra

## List of Tables

1. Ratio of maximum width to anteroposterior length of anterior zygaphysical facets in anterior thoracic vertebrae of *Xenarthra*  

iii
The Morphology of Xenarthrous Vertebrae
(Mammalia: Xenathra)

Timothy J. Gaudin

Abstract

The presence of supplementary intervertebral articulations termed "xenarthrales" in the posterior dorsal vertebrae has been considered perhaps the most important diagnostic feature of the mammalian order Xenarthra. Xenarthrales are poorly understood, however, and substantial confusion exists in the literature over which facets are supplementary and which are not. Furthermore, much of the variation that exists in these joints, both within taxa and among the various xenarthran lineages, has gone unnoticed. Finally, the structural evolution of these facets has been inadequately treated. The goal of the present study is to describe the morphology of xenarthrous vertebrae in juvenile and adult extant xenarthrans and in extinct xenarthrans, to develop a model for the structural evolution of the supernumerary joints, and to use this information to assess the affinities of several enigmatic groups of early Cenozoic taxa (Palaeocondonta, Ernanodon, and Eurotamaudia) with purported ties to the Xenarthra. Vertebral morphology is described in detail for two armadillo species, one species of anteater, and one extant and one extinct species of sloth, with brief comments on other xenarthran taxa. The results suggest that all xenarthrans are characterized by two sets of zygapophyseal facets in the post-diaphragmatic vertebrae, one medial and one lateral to the metapophysis. In addition, the Xenarthra is characterized primitively by a pair of xenarthrous facets on each side of the vertebra between the dorsal surface of the anapophysis and the ventral surface of the metapophysis of the succeeding vertebra. Other xenarthrous joints evolve within various xenarthran lineages. It is suggested that the supplementary facets developed initially in the diaphragmatic region of the vertebral column by means of a progressive widening of the zygapophyseal facets in the thoracic vertebrae and an increase in size of the metapophysis, which subdivided the zygapophyseal facets into medial and lateral facets. Hypertrophy of the anapophyses and their contact with the metapophyses led to the formation of true xenarthrous facets.

A review of vertebral morphology in the Palaeocondonta, Ernanodon, and Eurotamaudia revealed few resemblances to undoubtedly xenarthrans beyond hypertrophy of the metapophyses and anapophyses—characteristics known to occur in many different groups of mammals. No supplementary intervertebral articulations could be documented unequivocally in any of these taxa. Thus, on the basis of vertebral morphology there is little evidence that would suggest a close phylogenetic relationship between true xenarthrans and palaeocondonts, Ernanodon, or Eurotamaudia.

Introduction

The single most important osteological characteristic of Xenarthra is the presence of accessory articular processes or anapophyses, which articulate ventral to the metapophyses, or between them and the transverse processes, of the following vertebrae (Rose & Emry, 1993, p. 87).

The distinctive nature of the vertebral column in the mammalian order Xenarthra was recognized in the earliest osteological descriptions of the group (e.g., Cuvier, 1836a). In most mammals successive vertebrae are joined not only by an intervertebral disc, but also by a single pair of synovial joints carried on more or less distinct ar-
Fig. 1. _Mephitis mephitis_, UCM 521: thoracic and lumbar vertebrae shown in anterior, posterior and left lateral views (proceeding left to right). A, T4; B, L3. Scale bar = 1 cm. Abbreviations: ap, anapophysis; az, anterior zygapophyseal facet; dp, diapophysis; la, lamina; mp, metapophysis; ns, neural spine; pe, pedicel; pz, posterior zygapophyseal facet; rf, rib facet; sn, notch for emergence of spinal nerve; tp, transverse process; vc, vertebral centrum.

A peculiar processes of the neural arches termed zygapophyses (Fig. 1). In addition to the typical zygapophyseal articulations, all xenarthrans possess one or more pairs of supplementary intervertebral articulations that are usually present between all lumbar and a variable number of posterior thoracic vertebrae. The supernumerary articulations termed “xenarthral,” are well developed in xenarthrans that span a wide range of locomotory habits, including a subterranean armadillo (*Chlamyphorus*), fossorial armadillos and anteaters (*e.g.*, *Dasypus, Euphractus, Myrmecophaga*), arboreal climbing anteaters (*Tamandua, Cyclopes*), and semiarboreal (*e.g.*, *Hapalops, White*, 1993a,b) to fully terrestrial (*e.g.*, *Mylodon, Megatherium*) extinct ground sloths. Xenarthral are present in the oldest well-known fossil xenarthran skeleton, the Casamayoran armadillo *Utaetus* (*Simpson*, 1948). The supplementary joints are strongly reduced only in the suspensory tree sloths, and they are absent only in the glyptodonts; in the latter the dorsal portions of the backbone are fused into a bony tube used to support the massive carapace of the animals (*Hoffstetter*, 1958; *Gillette & Ray*, 1981).

Because of the peculiar and complex nature of these xenarthrurous articulations, their almost universal presence among living and fossil xenarthrans, and the near universal absence of similar supplementary intervertebral joints in other mammals (but see *Scutisorex*: *Lessertisseur & Saban*, 1967; *Kingdon*, 1984; *Cullinane & Aleper*, 1998; *Cullinane et al.*, 1998), the presence or absence of xenarthral has been used as a “litmus test” for determining phylogenetic relatedness to the Xerarthra. The pangolins and aardvuarks were originally included with xenarthrans under the taxonomic grouping Edentata, but they were subsequently removed to separate orders largely because they lacked xenarthral (*Weber*, 1904; see *Hoffstetter*, 1982, and *Glass*, 1985, for history of edentate classification). Several enigmatic groups of early Cenozoic mammals have been linked to the Xerarthra on the basis of “incipient” development of xenarthral. These include the Palaeonodonta (Simpson, 1931), a group known from Paleocene to Oligocene deposits of North America and Europe, and *Eranodon* (*Ding*, 1987), a Late Paleocene genus from China. Both *Eranodon* and the palaeonodont *Metacheirmys* have enlarged anapophyses in the posterior dorsal vertebrae. Similarly enlarged anapophyses can be found, however, in groups of mammals, dents (*Rose & Emry* are not necessary true xenarthrous articules *Messel* fauna of G true xenarthrous articulately unqualified to verify the vertebral articulation *Emry*, 1993; *Szalay* and his colleagues琅 *Wys*, 1986; *Novacek* taxonomic grouping lines, palaeonodonts, mon superordinal *α* morphological study phylogeny. Their *w* that the phylogeneti may be overemphasized.

Part of the difficult genetic significance of the xenarthral early Cenozoic taxa thra, lies in the fact articulations among not well understood.

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1 Curiously, the join poraneous edition of *mens fossiles*, where, *Myrmecophaga* are dievrie, 1836b, p. 208).

2 *Glass* (1985) cites term. I can find no me copy of Gill's mammal classification is incom a discussion of family a list of genera for an eluding the Bruta (= dentata). Vertebral mo ordinal level descripti
found, however, among a number of unrelated groups of mammals, e.g., felids and geomyid rodents (Rose & Emery, 1993). Hence such processes are not necessarily structural antecedents of true xenarthrous articulations. The purported Middle Eocene antcestor Eurotornia, from the Messel fauna of Germany, allegedly possessed true xenarthrous articulations (Storch, 1981). Unfortunately, several subsequent authors have been unable to verify the presence of accessory intervertebral articulations in this taxon (Rose & Emery, 1993; Szalay & Schrenk, 1994). Novacek and his colleagues (Novacek, 1986; Novacek & Wyss, 1986; Novacek et al., 1988) resurrected the taxonomic grouping Edentata, including pangolins, palaeoanodonts, and xenarthans, in a common supraordinal cohort based on the results of morphological studies of eutherian interordinal phylogeny. Their work has led them to suggest that the phylogenetic significance of xenarthrans may be overemphasized.

Part of the difficulty in determining the phylogenetic significance of xenarthrans, and in identifying xenarthrans or incipient xenarthrans in early Cenozoic taxa potentially allied to Xenarthra, lies in the fact that the morphology of these articulations among ungrouped xenarthrans is not well understood.

As stated above, the presence of accessory intervertebral articulations in xenarthrans has been noted since the early nineteenth century. Cuvier (1836a) wrote the first brief description of such joints. They were not formally named, however, until Gill (1886, p. 66) coined the term “xenarthral” (Gk., xenos = “strange,” arthron = “joint”) in order to distinguish xenarthran vertebrae from normal, “normarthral” vertebrae. Simpson (1931, 1948) used the adjective “xenarthral” to refer to these accessory joints. This adjective is the one most commonly used in the recent literature (e.g., Emry, 1970; McKenna, 1975; Engelmann, 1985; Vaughn, 1986; Rose & Emery, 1993). The joints have also been referred to by the noun “xenarthrales” (e.g., Frechkopf, 1949; Grassé, 1955; Hoffstetter, 1958; Deblase & Martin, 1981; Storch 1981), and the condition of possessing such joints has been termed “xenarty” (e.g., Lessertisseur & Saban, 1967; Hoffstetter, 1982; Novacek & Wyss, 1986). The first detailed morphological description of xenarthrian intervertebral articulations (Owen, 1851a) preceded Gill’s work by some 20 years. Owen described the morphology of the supplementary intervertebral articulations in at least two extant species from each of the three major xenarthran suborders, the Cingulata (armadillos), Vermilingua (Neotropical anteaters), and Tardigrada (sloths). Moreover, Owen described regional variation in the morphology of the extra intervertebral joints along the backbone of individual species. Owen (1851a) began each description with the anteriormost xenarthrous vertebra and then described how the morphology of the facets changed as one moved posteriorly along the spine.

Flower’s (1885) description was similar but much briefer than Owen’s. He described the morphology of the xenarthran articulations along the whole length of the vertebral column, but only in the vermillugian Myrmecophaga (Flower, 1885). He also briefly summarized the form of the xenarthran facets in the sloth genus Bradypus. Interestingly, Flower differed from Owen in deciding which facets to designate as the normal zygopophyseal facets and which to designate as supplementary. Owen (1851a) consistently recognized the medialmost pair of intervertebral facets, those lying medial to the metamorphoses, as the normal zygopophyseal facets. Flower (1885, figs. 22–24) designated a set of facets lying lateral to the metamorphoses as the homologues of the typical mammalian zygopophyses.

As noted by Rose and Emery (1993), the confusion over which set of facets constitutes supplementary articulations and which are the normal zygopophyseal facets has persisted to the present. The designation of a lateral facet as the zygopophyseal facet by Flower is followed by Grassé (1955) and Vaughn (1986). Owen’s (1851a) identification of the zygopophyses as lying more medially.

1 Curiously, the joints are not described in a contemporary edition of Cuvier’s Recherches sur les ossements fossiles, where, e.g., the vertebrae of the antcestor Myrmecophaga are described as “unremarkable” (Cuvier, 1836b, p. 208).

1 Glass (1885) cites Gill (1872) as the source of the term. I can find no mention of the term, however, in my copy of Gill’s mammalian classification. Indeed, Gill’s classification is incomplete, because it contains neither a discussion of family and subfamily characteristics nor a list of genera for any of the Inedcabilia, a group including the Bruta (= Xenarthra + Pholidota + Tubulidentata). Vertebral morphology is not mentioned in the ordinal level description of Bruta.
ground sloth genera from other North American museums. The descriptions provided below, however, will focus on five representative taxa: the extant armadillos *Tayassu* and *Tolypeutes*, the extinct anteater *Tamandua*, the extinct sloth *Bradypus*, and the extinct sloth *Hapalops*. Unlike the study reported by Owen (1851a), the present analysis also incorporates ontogenetic data from juvenile specimens, as well as paleontological information unavailable to Owen. Based on this descriptive information as well as on functional (Gaudin & Biewener, 1992; Gaudin, 1993; Gaudin & Fortin, unpubl. data) and phylogenetic (Engelmann, 1978, 1985; Gaudin, 1993, 1995) information garnered from other sources, a scenario is postulated for the structural evolution of xenarthrous intervertebral facets. Finally, this scenario is used to evaluate the phylogenetic affinity of several extinct early Cenozoic taxa with purported ties to Xenerthra.

**List of Abbreviations**

The following abbreviations will be utilized throughout the text: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; L1, L2, L3 ... first lumbar vertebra, second lumbar vertebra, third lumbar vertebra, respectively, etc.; S1, S2, ... first sacral vertebra, second sacral vertebra, etc.; T1, T2, ... first thoracic vertebra, second thoracic vertebra, etc.; UTCM, University of Tennessee at Chattanooga Natural History Museum, Chattanooga.

**Descriptive Anatomy**

**Cingulata**

**Euphracta** (esp. *Zaedyus pichiy*)

The vertebral columns of six euphractan armadillos (*sensu* Engelmann, 1985) were examined, two from the species *Zaedyus pichiy* (FMNH 23809, 104817), three from *Chaetophractus villosus* (FMNH 60467, 122623, 134611), and one from *Euphractus sexcinctus* (FMNH 152051). The description below is based primarily upon Z. *pichiy* (Figs. 2A, 3A, 4A-D). It should be noted at the outset that vertebrae are bilaterally symmetrical structures. Nearly all of

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**Fig. 2.** Thoracic ar T8, L1, L2, Proceeding from right to left. C, D, bars = 1 cm. Abbreviations: Z. pichiy: zantheartous facett; D, apophysal facet; px, process.
her North American provided below, how representative taxa: the Erd Tolyepites, the extant sloth Bradypalaeoplos. Unlike the 1a, the present anatomic data from juv.paleontological in. Based on this det. as on functional Gaudin, 1993; Gauld phylogenetic (Enn., 1993, 1995) infor.unable sources, a scenario is evolution of xenar.Finally, this scenario phylogenetic affinity of c taxa with purported

ions will be utilized American Museum of FMNH, Field Museum; L1, L2, L3... first lumbar vertebra, third, etc.; S1, S2, ... sacral vertebra, etc.; ebra, second thoracic uesty of Tennessee at y Museum, Chatta-

octhera, the vertebral facets, foramina, and processes described in this paper are paired, with the midline neural spine constituting the single major exception. In order to simplify the descriptions and avoid confusion, however, each vertebra is described unilaterally, with the implicit assumption that the same structures are present and exhibit the same morphology on opposite sides of the vertebra unless otherwise stated. Following Walker and Homberger (1992) and Wake (1979), the thoracic vertebrae are defined as those vertebrae possessing articulations with movable ribs, the sacral vertebrae as those vertebrae that articulate directly with the ilium (or are fused to these vertebrae posteriorly), and the lumbar vertebrae as those vertebrae that lie in between the thoracic and sacral vertebrae.

All of Flower’s (1885) euphaextian armadillo specimens had 14 dorsal vertebrae—3 lumbar and 11 thoracic. The FMNH specimens are somewhat more variable. Although most have 14 dorsal vertebrae, one Chaetophractus specimen (FMNH 60467) and the sole Euphractus specimen have 15, the former with 10 thoracic and 5 lumbar and the latter with 11 thoracic and 4 lumbar. The thoracic vertebrae of extant euphaextians are very similar to those of other mammals, with small, depressed centra and elongated, posteriorly inclined neural spines (Fig. 1; see also Sliper, 1946; Walker & Homberger, 1992). As in many other mammals, the neural spines of the anterior thoracic vertebrae are dramatically longer than those of more posterior thoracic vertebrae. The anterior thoracic vertebrae of euphaextians are unusual, however, in several respects. The centra are functionally opisthocoelous. The main anterior articular surface of each centrum is nearly flat, but it is flanked by two small lateral facets (Fig. 3A). These facets face anterolaterally, creating a convex profile for the whole anterior surface of the centrum. Similarly, the posterior surface of each centrum bears two small lateral facets that face posteromedially (Fig. 3A). This creates a concave posterior articular surface to receive the convex anterior surface. In Zaedys such functionally

Fig. 2. Thoracic and lumbar vertebrae shown in dorsal view. A, Zaedys pichiy caurinus, FMNH 104817—T6, T7, T8, L1, L2, proceeding from right to left. B, Tamandua mexicana, FMNH 69897—T12, T13, T14, L1, proceeding from right to left. C, Bradypus variegatus, FMNH 69589—T14, T15, L1, L2, proceeding from right to left. All scale bars = 1 cm. Abbreviations as in Figure 1, plus alz, anterior lateral zygaphysal facet; amz, anterior median zygaphysal facet; ax, anterior xenarthrous facet; ax/sit, fused anterior lateral zygaphysal facet and anterior xenarthrous facet; D, diaphragmatic vertebra; plz, posterior lateral zygaphysal facet; pmz, posterior medial zygaphysal facet; px, posterior xenarthrous facet.

GAUDIN: THE MORPHOLOGY OF XENARTHROUS VERTEBRAE
Fig. 2.
Fig. 2. Continued.
Fig. 3. Thoracic and lumbar vertebrae shown in cranial and caudal views. A, Zacatops pichiya caurinus, FMNH 10481—T6 (cran.), T6 (caud.), T7 (cran.), T7 (caud.), T8 (cran.), proceeding from right to left. B, Tamandua mexicana, FMNH 69593—T12 (caud.), T13 (cran.), T13 (caud.), T14 (cran.), proceeding from right to left. C, Bradypus variegatus, FMNH 69586—T15 (cran.), T15 (caud.), L1 (cran.), L1 (caud.), L2 (cran.), proceeding from right to left. All scale bars = 1 cm. Abbreviations as in Figures 1 and 2, plus cran, cranial view; caud, caudal view; lca, lateral centrum articulation; lf, lateral foramen for ventral branch of spinal nerve; rfpx, fused rib facet and posterior xenarthrous facet.

specimens examine T3 posteriorly.

The anterioriorm not only bear its underside, but a ventrally directed of the metapophysis xenarthrous joint (l
specimens examined. In Zaedyus they occur from T3 posteriorly.

The anteriormost xenarthrous articulations are between the sixth and seventh thoracic vertebrae. The small anapophysis of the sixth thoracic vertebra not only bears a lateral zygapophyseal facet on its underside, but also a small, flat, ovate facet on its dorsal surface (Figs. 2A, 3A, 4A). This longitudinally elongated dorsal facet articulates with a ventrally directed facet carried on the underside of the metapophysis of T7, forming the first true xenarthrous joint (Figs. 3A, 4A). The facet on T7 is actually borne on a small anterior projection that emerges from the base of the metapophysis but lies well above the lamina of the neural arch. The anterior xenarthrous facet of T7, coupled with the normal horizontal zygapophyseal facet on the lamina of the neural arch, forms a slot that receives the anapophysis of T6 (Fig. 2A). Owen (1851a) analogized this interlocking of vertebrae to a carpenter’s “mortise and tenon” joint.

The seventh thoracic vertebra is the diaphragmatic vertebra, defined by Sliper (1946) as that in which the anterior zygapophyseal facets are
Fig. 4. Zaudicus pichiy caurinus. FMNH 104817: thoracic and lumbar vertebrae shown in right lateral view. A, stereophotographs of T6 and T7. B, stereophotographs of T7 and T8. C, T8 and T9. D, T11 and L1. Scale bar = 1 cm. Abbreviations as in Figures 1 and 2, plus ax/p, xenarthrous intervertebral joint; ax/1alz, fused anterior lateral zygaphyseal facet and anterior xenarthrous facet; ax/2px, xenarthrous intervertebral joint between secondary and posterior xenarthrous facets; px/p, fused posterior lateral zygaphyseal facet and posterior xenarthrous facet; px/2, secondary posterior xenarthrous facet; spn, foramen foraminalis for spinal nerve roots.

horizontally oriented and the posterior zygaphyseal facets are roughly vertical. T7 is the anterior most vertebra to bear a distinct, although small, metapophysis. The metapophyses become progressively elongated posteriorly (Figs. 2A, 4B-D). By the ninth thoracic vertebra, the metapophysis is as long as the neural spine, and by the first lumbar vertebra, the metapophysis exceeds the neural spine in height. On the seventh thoracic vertebra, the base of the metapophysis lies posterior to the anterior zygaphyseal facet. On T8, however, the base of the metapophysis contacts the anterior edge of the lamina (Figs. 2A, 3A). This more fully divides the anterior zygaphyseal facet into medial and lateral components.

The portion of the anterior zygaphyseal facet that is medial to the base of the metapophysis (i.e., the anterior median zygaphyseis) strongly resembles the postdiaphragmatic anterior zygaphyseal facets of other mammals (Pick & Howden, 1977; Walker & Homberger, 1992) and is homologized with these facets by Owen (1851a) and others (Hoffstetter 1958, 1982; Lessertisseur & Saban, 1967; Gaudin & Biewener, 1992; Rose & Emry, 1993). I concur with this homology. The facet is concave and transversely elongated. The medial half of the facet is horizontal and faces dorsally. The lateral half is vertical, rolling up onto the base of the metapophysis and facing medially. This facet articulates with a convex, ventrolateral anterior edge of the l...
convex, ventrolaterally oriented facet on the posterior edge of the lamina of T7 (Fig. 3A).

The portion of the zygaphyseal facet lateral to the base of the metapophysis in T8 is similar in position to the lateral anterior zygaphyseal facet of T7. It is, however, oriented much more obliquely (indeed, it is nearly vertical) and lies further laterally on the neural arch. It abuts a thin intervertebral facet on its dorsomedial edge (Fig. 3A). The third facet, also positioned lateral to it...
The anapophysis of T7 is enlarged relative to that of T6, a trend that continues posteriorly (Fig. 4A-D). As noted by Owen (1851a), this enlargement primarily represents an increase in vertical thickness, accompanied by a more modest increase in length. As the anapophysis becomes deeper, it participates in bearing, laterally, the facet for the head of the rib (starting at T8; Fig. 4C). Not only is the anapophysis of T8 larger than that of T7, but the two facets it carries on its inner surface, the lateral zygapophyseal and the xanthothrus facet, are confluent (Fig. 3A). The lateral zygopaphysyal and xanthothrus facets are similarly confluent on the anterior edge of T9. The intervertebral joints of T9/T10 and T10/T11 are virtually identical to those of T8/T9. In each case there are two sets of intervertebral joints, one medial to the base of the diaphysis, representing the medially zygopaphysyal joint, and one lateral to the base of the metaphysis, representing the conjointed lateral zygopaphysyal and xanthothrus joints.1

The intervertebral joint between T11 and L1 differs from the T10/T11 intervertebral joint in a number of important respects. The diaphysis, which is progressively reduced posteriorly beginning with T8 (Fig. 4A-C), is rudimentary on T11 (Fig. 4D). Concomitant with the reduction of the diaphysis, the foramen for the dorsal branch of the spinal nerve, which lies between the diaphysis and anapophysis anteriorly, occupies a progressively more caudal position on the side of the anapophysis of T8-T10 (compare Fig. 4B with C). It also changes orientation, from a vertical course to a horizontal, posteriorly directed course. At the 11th and last thoracic vertebra, the foramen reaches the caudal edge of the anapophysis (Fig. 4D). The groove leading to this opening divides the articular facets carried on the anapophysis into separate dorsal and ventral facets. In Chaetopterus a similar dorsal articulation on the ultimate thoracic vertebra contains two facets, a lateral zygopaphysyal and a xanthothrus facet (see footnote 4). In Zanclus and Eurypranes, these facets are fused. As in more anterior xanthothrus joints, the spinal nerve comes to the metamorphosis of the neural arch. The facet below the suture is the articular surface of the anapophysis, not 1851a; see Tolypeutes homologous with the anapophysis in the thoracic vertebrae.

The anapophysis elongate than th thus be attributed to the neural archs in the rowing of the pec men is present in all morphology of the intervertebral foramen.

Tolypeutes matac

This specimen is still unfused vical and lumbar. The left and right fused in all but the leading 15 dorsals at the 11th thoracic vertebra. The lumbar vertebrae are variably Tolypeutes. The specimens with 11 th (FMNH 121540, 1 with 12 th (FMNH 122233, 1 with 12 th (FMNH 122233, 1 have a typical thoracic vertebra, vertebrae and 11 thoracic, 3 fused to include count. The last h to the first sacral condition is not observed in a

1 This confirms the lumbar vertebrae in mammals are plus the vertebrae plus a cuneiform, the anterior ti in the possees are termed vertebrae that serve cranial head of two.

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GAUDIN: THE
enlarged relative to those posteriorly (Fig. 1851a); this enlargement in vertical dimension is a more modest indication that the anapophysial facet(s) above the spinal nerve contacts the ventral neural surface of the metapophysis and the lateral neural surface of the neural arch. The serial homology of the neural facet below the spinal nerve is more difficult to ascertain. Its articulation posteriorly with the dorsalfacet of the transverse process (a pleuroapophysis, not parapophysis, contra Owen, 1851a; see Tolyopeutes below) suggests, however, homology with the facet on the lateral surface of the anapophysis that receives the head of the rib in the thoracic vertebrae.

The anapophysis of T11 appears much more elongate than that of T10 (Fig. 4C, D). This can be attributed to the reappearance of the intervertebral foramen at T11 and the concomitant narrowing of the pedicle. The intervertebral foramen is present in all the lumbar vertebrae. The morphology of the intervertebral articulations is virtually unchanged from T1/L1 to L3/S1.

### Tolyopeutes matacus (FMNH 124569 [juv.])

This specimen is a juvenile. The neural arches are still unfused to the centrum. Similarly, the cervical and lumbar ribs remain unfused. However, the left and right halves of the neural arches are fused in all but the cervical vertebrae. The specimen has 15 dorsal vertebrae—11 thoracic and 4 lumbar. The numbers of thoracic and lumbar vertebrae are variable in adult members of the genus Tolyopeutes. The FMNH collections include individuals with 11 thoracic and 4 lumbar vertebrae (FMNH 121540, 124570, 153773) as well as individuals with 12 thoracic and 5 lumbar vertebrae (FMNH 122233). Flower (1885) characterizes Tolyopeutes as possessing only 14 dorsal vertebrae (11 thoracic, 3 lumbar), but I suspect that he failed to include the last lumbar vertebra in his count. The last lumbar vertebra is typically fused to the first sacral vertebra in adult specimens. This condition is not uncommon in xenarthrans. It has been observed in the eugomphilids Euphractus and Chaetophractus, the giant armadillo Priodontes in certain extinct genera of mylodontid sloths (Owen, 1842; Stock, 1925).

The anterior thoracic vertebrae of Tolyopeutes differ somewhat from those of Zoedyus. They lack the transverse processes of the neural arch. Although the pedicles are low and longitudinally elongated, the ventral spinal foramen is present (Fig. 5A). The dorsal branch of the spinal nerve emerges through a notch between the large diaphysis and the rudimentary anapophysis. Only a single pair of zygopophyseal facets is present, and the zygopophyseal surface is narrower mediolaterally in Tolyopeutes than in Zoedyus, especially in adult specimens.

In FMNH 124569, the diaphragmatic vertebra is T7, and the anterior thoracic articular facies lies between this vertebra and the preceding one. In Zoedyus, this joint is formed by the dorsal surface of a small anapophysis and the ventral surface of the metapophysis, which is rudimentary in this specimen (Fig. 5A). Unlike Zoedyus, this xenarthran joint between T6 and T7 occurs only on the right side of the specimen. The position of the first xenarthran joint is apparently somewhat variable in Tolyopeutes. In FMNH 124540, the first xenarthran joint also occurs between T6 and T7, but on the left rather than the right side. Moreover, the diaphragmatic vertebra in this specimen is T8 rather than T7. In FMNH 124570, the diaphragmatic vertebra is T7, but the first xenarthran joint occurs between T7 and T8.

As was the case with Zoedyus, in Tolyopeutes the vertebra following the diaphragmatic vertebra bears a large metapophysis whose base reaches the anterior margin of the lamina. This creates three sets of intervertebral joints between T7 and T8: (1) a joint medial to the base of the metapophysis, the medial zygopophyseal joint; (2) a joint lateral to the base of the metapophysis, formed by facets on the dorsal surface of the anapophysis and the ventral surface of the metapophysis; and (3) a joint lateral to the base of the metapophysis, formed by facets on the ventromedial surface of the anapophysis and the lateral surface of the neural arch (Fig. 5A). It is not possible to determine in this juvenile specimen whether or not these two lateral joint facets are confluent in the thoracic vertebrae. They are separate, however, in the thoracic vertebrae of at least one adult specimen (FMNH 153773), becoming confluent in the lumbar vertebrae of both the adult and juvenile specimens. As in Zoedyus, these two joint facets presumably

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DIANA: GEOLOGY

GAUDIN: THE MORPHOLOGY OF XENARTHROUS VERTEBRAE
Figure 5. *Tolypeutes martius*, FMNH 124569 (juv). A, series of thoracic vertebrae (T5-T8) shown in left lateral view; B, series of lumbar vertebrae (L1-L3) shown in left lateral view. Scale bar = 1 cm. Abbreviations as in Figures 1 and 4, plus lrf, lumbar rib facet.

The intervertebral articulations of the thoracic vertebrae differ significantly from that of T11/L1 and those of the lumbar vertebrae. The ventral spinal foramen resumes a typical intervertebral condition in T11 and all subsequent lumbar vertebrae (Fig. 5B). The dorsal branch of the spinal nerve, which emerges ventral to the anapophysis in the majority of the thoracic vertebrae, i.e., between the pedicel of the following vertebra and the anapophysis, develops articulation with the ribs (Fig. 5B). This is a common feature in the cervical vertebrae, but in the thoracic vertebrae it becomes a feature of the transverse processes.

MacPhee (1994) mentioned that a kind of intervertebral fusion in the lumbar vertebrae might be considered a necessary process or characteristic feature of the intervertebral articulations of some of the larger mammals. The specimen FMNH 124568 was examined and found to have a broad fusion of some vertebral pedicles to the intervertebral articulations. However, in some other cases of thoracic vertebrae, such as in *Tolypeutes martius*, the sacral articulation of the intervertebral articulations is not yet developed in the thoracic vertebrae, and the sacral articulation is in the thoracic vertebrae.

**Other Cingulates**

The number of nodes varies among species. In *Dasyurus hallucatus* (Amann, 1985), the number of nodes varies from 13 to 16. Thoracic vertebrae, many of which are present in the *Dasyurus hallucatus* (Flower, 1885), and others in *Dasyurus eremicus* (Flower, 1885). The number of nodes varies from 2 to 5 in *Dasyurus hybrida* (Flower, 1885). Despite variation in the number of nodes, the intervertebral articulations of the thoracic vertebrae are consistent across species.
ysis in the majority of thoracic vertebrae, emerges medial to the anapophysis of T11 and the lumbar vertebrae, i.e., between the anapophysis and the pediel of the following vertebra. Below the opening for the dorsal branch of the spinal nerve, the anapophysis develops a laterally directed facet for articulation with the last thoracic and the lumbar ribs (Fig. 5B). This facet is absent in a slightly younger specimen (FMNH 124568, in which the right and left neural arches of the posterior thoracic vertebrae are still unfused). In adult specimens it becomes a facet between the anapophysis and transverse process.

MacPhee (1994, p. 174) suggested that xenarthrous intervertebral articulations are produced through “a kind of ‘sacralization’ of the lower part of the free spine,” a hypothesis that he believed could be confirmed by the discovery of accessory processes or transitory supplementary intervertebral articulations in the early developmental stages of some xenarthran or even non-xenarthran mammal. The sacral vertebrae of juvenile specimen FMNH 124569 and the younger FMNH 124568 were examined for evidence of such processes or articulations. In the anterior sacral vertebrae the pedicles of successive vertebrae are broadly fused lateral to the metapophysis and dorsal to the intervertebral foramina (Fig. 6). It is unclear, however, whether these lateral areas of fusion represent anapophyses, fused sacral ribs, or some other type of structure. Moreover, the xenarthrous articulations between L4 and S1, typical of older Tolyphostes (including FMNH 124569), had not yet developed in FMNH 124568. This suggests that sacral fusion and the development of xenarthran in the thoracic and lumbar vertebrae are unrelated.

**Other Cingulates**

The number of dorsal vertebrae is somewhat more variable among dasypodid (sensu Engelman, 1985) armadillos than in euphractans. The total number of dorsal vertebrae varies between 13 and 16. Thoracic counts range from 13 in Protodontes (FMNH 25271) to 9 in Dasypus hybridus (Flower, 1885). The number of lumbar vertebrae varies from 2 in Protodontes (perhaps 3, given the fusion of the last lumbar to the sacrum in this species) to 5 in Dasypus novemcinctus and some Dasypus hybridus (Flower, 1885; Gaudin & Biewener, 1992).

Despite variation in vertebral number, the morphology of the xenarthrous articulations among living adult armadillos is remarkably constant. The anteriormost xenarthrous facets typically occur in the vicinity of the diaphragmatic vertebra, between the diaphragmatic vertebra and either the preceding or the succeeding vertebra (although occasionally xenarthrous joints occur between the first and second prediaphragmatic vertebrae; see Tolyphostes above). The first xenarthrous joints form between the dorsal surface of a small anapophysis and the ventral surface of a small metapophysis. As the metapophysis enlarges posteriorly and its base reaches the anterior edge of the lamina (as almost always occurs in the first postdiaphragmatic vertebra), the zygapophyseal facet is divided in two. One portion comes to lie medial to the base of the metapophysis. It articulates with a facet on the posterioromedial portion of the lamina of the diaphragmatic vertebra. The second portion comes to lie lateral to the base of the metapophysis, on the most lateral portion of the lamina. It articulates with a facet borne on the medial surface of the anapophysis of the diaphragmatic vertebra. It usually becomes confluent with the xenarthrous facet in the first few postdiaphragmatic vertebrae. The xenarthrous facet is carried on the ventralateral surface of the metapophysis and articulates with the dorsomedial surface of the anapophysis. These three types of joints—medial zygapophyseal, lateral zygapophyseal, and xenarthrous—are present in all the postdiaphragmatic thoracic vertebrae. A second type of xenarthrous joint is also usually present in armadillos. It is found in the lumbar vertebrae, where it forms between the ventral surface of the anapophysis and the dorsal surface of the transverse process of the following vertebra. A very similar joint is found in the ultimate or penultimate thoracic vertebra, formed by the ventral surface of the anapophysis and the dorsal surface of the rib or transverse process of the following vertebra.

Although the condition of the xenarthrous articulations cannot be ascertained in glyptodonts because of extensive fusion among the dorsal vertebrae (Hoffstetter, 1958; Gillette & Ray, 1981), the dorsal vertebrae remain unfused in several close relatives (following Engelman, 1985; Patterson et al., 1989) of the glyptodonts, the panoptheres and eupatine armadillos. In panoptheres typical xenarthrous articulations “begin to appear at the anterior end of the thoracic section, and are well developed in the posterior thoracic and lumbar vertebrae” (Edmund, 1985, p. 88). A posterior thoracic vertebra illustrated by Edmund (1985,
Fig. 6. *Tolypeutes matacus*, FMNH 124569 (juv.). A–C, sacral vertebrae shown in right lateral, ventral, and dorsal views. Scale bar = 1 cm.

fig. 9) shows confluent xenarthrous and lateral zygapophyseal facets on the anapophysis and what is perhaps an anapophyseal facet for articulation with the head of the rib. A specimen of *Proeutatus* (FMNH P12912), a eutatine armadillo from the late early to early middle Miocene Santa Cruz Formation of Patagonia (Scott, 1903–1904), also has a typical cingulate pattern. FMNH P12912 includes the last five thoracic and first lumbar vertebrae in articulation. The diaphragmatic vertebra is the second in the series. The most anterior xenarthrous articulation occurs between the diaphragmatic vertebra and the first prediaphragmatic vertebra, formed by the ventral metapophysis of the former and the dorsal anapophysis of the latter. Facets medial and lateral to the metapophyseal base are present in the postdiaphragmatic vertebrae, with a third set of facets present between the anapophysis and transverse process in the last thoracic and first lumbar vertebrae.

*Priedontes* constitutes the only major exception to the cingulate pattern of xenarthrous articulations. The giant armadillo possesses all of the articulations described above. It is characterized, however, by several posterior thoracic apophyseal facets on the dorsal by two pairs of facets dorsal edge of the anapophyseal facets. The corresponding facets of the lamina of the extra facet of *Priedontes*.

**Vermilingua**

*Tamandua mexicanus*

The vertebralcolumn species *Tamandua* (FMNH 22398, 5854 and 93176 [juv.]), is primarily on *T. mexicanus* 3B, 8).

The number of higher in pilosans in the thoracic port numbers of thoracic *Tamandua* vary. FMNH lumbar vertebrae; 2 lumbar vertebrae

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however, by several additional sets of facets in the posterior thoracic and lumbar vertebrae (Fig. 7). Anteriorly, these vertebrae have a single midline facet on the dorsal surface of the lamina, flanked by two pairs of facets also situated on the anterodorsal edge of the lamina, cranial to the zygapophyseal facets. The extra facets articulate with corresponding facets on the posteroventral edge of the lamina of the preceding vertebra. The presence of the extra facets is clearly a derived feature of *Priodontes*.

### Vermilingua

**Tamandua mexicana**

The vertebral columns of five specimens of the species *Tamandua mexicana* were examined (FMNH 22398, 58545 [juv.], 69597, 93095 [juv.], and 93176 [juv.]). The description below is based primarily on *T. mexicana*, FMNH 69597 (Figs. 2B, 3B, 8).

The number of dorsal vertebrae tends to be higher in pilosans than in cingulates, particularly in the thoracic portion of the column. The actual numbers of thoracic and lumbar vertebrae in *Tamandua* vary. FMNH 69597 has 17 thoracic and 2 lumbar vertebrae; FMNH 22398 has 18 thoracic and 2 lumbar vertebrae. Both Cuvier (1836a) and Flower (1885) cite specimens of *Tamandua* with 17 thoracic and 3 lumbar vertebrae.

The anterior thoracic vertebrae of *Tamandua* are less strongly modified than those of cingulates, with much taller, narrower pedicels and normal intervertebral foramina. The diapophyses, though large, are less elevated than in the armadillos, and the head of the rib articulates exclusively with the anterodorsal portion of a single vertebral centrum (Fig. 8). These vertebrae are unusual, however, in four respects. First, the large neural spines are of uncommonly uniform height throughout the thoracic region, decreasing only slightly in height posteriorly. Second, these neural spines are markedly robust and elongated anteroposteriorly (Fig. 8). Third, the zygapophyseal articular facets are widely separated from the midline of the vertebral lamina (Fig. 2B). On the anterior edge of the lamina this separation is produced by a broad, rounded, midline indentation. Fourth, the zygapophyseal facets themselves are quite wide mediolaterally. Indeed, as can be seen in anterior and posterior views (Fig. 3B), the facets extend farther laterally than the vertebral centra, a morphology in sharp contrast to that found in the armadillos (Fig. 3A) and to the generalized mammalian condition (Fig. 1; Flower, 1885; Jenkins & Parrington, 1976; Jenkins & Schaff, 1988; Walker & Homberger, 1992).

All of the thoracic vertebrae have distinct diapophyses that increase in size posteriorly. There
is no trace, however, of an anapophysis in any prediaphragmatic vertebra (Figs. 2B, 8). The diaphragmatic vertebra is T13. The first xenarthrous articulation occurs between the diaphragmatic vertebra and T14. As in Zaedyus, the base of the enlarged metapophysis on the first postdiaphragmatic vertebra reaches the anterior edge of the lamina, dividing the wide anterior zygapophyseal facet in half (Fig. 2B). The portion remaining medial to the metapophysis is a concave medial zygapophyseal facet that faces dorsomedially. It articulates with a convex, ventrolaterally oriented facet on the posterior edge of the lamina of T13 (Fig. 3B). This medial joint appears identical to the relatively vertical zygapophyseal articulations found in the posterior thoracic and lumbar vertebrae of non-xenarthran mammals.

Lateral and ventral to the metapophysis of T14, a mortise-and-tenon-style articulation is formed with the well-developed anapophysis of T13. In anterior view, the facet lateral to the base of the metapophysis of T14 is parabolic in shape (Fig. 3B), with its dorsal portion facing ventrally and its ventral portion facing dorsally. The ventral portion is nearly identical in position, size, shape, and orientation to the lateral half of the anterior zygapophyseal facet of T13, which is likewise borne on a lateral extension of the anterior vertebral lamina. I believe it to be the serial homologue of the outer half of the anterior zygapophyseal facet. The dorsal portion is a true xenarthrous facet borne on the ventral surface of a small anterior process projecting from the base of the metapophysis. The anapophysis of T13 has dorsal and ventral facets that are continuous medially. The dorsal facet is a xenarthrous facet. The ventral facet, though separate from the metapophysis, is appressed to it and is the true anapophysis of T13 (Figs. 3B, 8).

Nearly identical intervertebral and intervertebral facets occur between the vertebrae of T14 and T13. The anapophyses of T13 and T14 are third pair of intervertebral facets between L2 and S1. A ventrolaterally directed anapophysis articulates with a facet on the dorsal surface of the vertebra above.

Several early juvenile individuals (FMNH 58545) are described in the material of the sacral ribs of the sacrum. These facets are those of the neural arches. The neural arches are apparently not well-developed in the juvenile stages. These facets are those of the neural arches. The neural arches are apparently not well-developed in the juvenile stages.

The neural arches are apparently not well-developed in the juvenile stages. These facets are those of the neural arches. The neural arches are apparently not well-developed in the juvenile stages.
articulation is formed by the base of the neural arches of the sacral vertebrae are unfused (in contrast to both juvenile Tolypeutes specimens described above). This specimen has fairly typical adult-style xenarthrous articulations between the posterior thoracic and the lumbar vertebrae, beginning at the diaphragmatic vertebrae and extending back to the joint between L1 and L2. However, the lumbosacral joint differs markedly from the adult morphology. The last lumbar vertebra bears a large, anteroposteriorly broad transverse process. This in turn carries a very small anapophysis that lies immediately lateral to a notch for the dorsal branch of the spinal nerve. The anapophysis does not contact the fused transverse process/sacral rib of S1. The last lumbar and first sacral vertebrae are joined by a single pair of wide facets. These facets extend laterally from the base of the neural spine to the medial margin of the notch for the dorsal spinal nerve. In S1 the facet passes around the base of the metaphysis, but it is much more extensive medial to this process. The intervertebral connections between subsequent sacral vertebrae (S1–S3) are virtually identical to those described at the lumbosacral joint. Although the sacral ribs of all three sacral vertebrae appear to carry small anapophyses, there is no indication that these participate in supplementary articulations.

A slightly older juvenile Tamandua (FMNH 93176) with unfused sacral vertebrae but fused neural arches was examined to ascertain ontogenetic changes in the sacral intervertebral articulations. The sacral vertebrae of this specimen are joined not by synovial joints but by three areas of rugose bone. One joins the laminae near the midline, representing the aforementioned sacral joints of the younger Tamandua specimen. The second unites the vertebral centra. The third zone of attachment is a massive area of rugose bone situated lateral to the metaphysis and dorsal to the intervertebral foramina, presumably representing a broad zone of contact between the sacral ribs and their attendant anapophyses. It does not involve the metaphyses or vertebral laminae, and thus it bears little resemblance to the xenarthrous connections of the dorsal vertebrae.

Other Vermilingua

As its close relative Tamandua, the number of thoracic and lumbar vertebrae in the giant anteater Myrmecophaga is variable—15 thoracic and 3 lumbar or 16 thoracic and 2 lumbar (Cuvier, 1836b; Owen, 1851a; Flower, 1885). The pygmy anteater Cyclopes has 16 thoracic and 2 lumbar vertebrae (Flower, 1885; FMNH 61853, 69869, 69971). The vertebrae of Myrmecophaga are virtually identical to those described above for Tamandua, except that the joint between the anapophysis of the last lumbar and the sacral rib is also represented between the ultimate and penultimate lumbar vertebrae. In these vertebrae, the joint lies between the ventrolateral surface of the anapophysis and the dorsal surface of the transverse process of the succeeding vertebra (Flower, 1885).

The vertebrae of Cyclopes are likewise similar to those of Tamandua. Cyclopes lacks the joint between the anapophysis of the L2 and the sacral rib. More interestingly, rudimentary anapophyses are present in the first prediaphramatic vertebra (and sometimes in the second), and xenarthrous articulations occur between the diaphragmatic and prediaphramatic vertebrae. These xenarthrous are formed between the dorsal surface of the rudimentary anapophysis and the ventral surface of an anterior projection of the metaphysis.

Tardigrada

Bradyurus variatus

The vertebral columns of 2 specimens of Bradyurus variatus were examined (FMNH 68919,
diapophyses, causing gitudinally elongate This is also quite re tion. The first disti borne by T14. The vertebral are progres T15 is the diapt from that of other x mentary interverteb small anaphyposis t the base of the fuse 2C, 3C, 9). The anaph a lateral projection s tension lies lateral tc of L1. As in the pther xenarthrans, t of L1 reaches the a In contrast to other synovial joint does anaphyposis and the metapophysis (Fig. 4).

The anaphyposis of T15, and it bears directed facet on its This facet articulate lateral to the base of the surface on L2 is of the neural arch, at the curved, upright by the base of the articulation between the lamina of L2 is of seal joints of arms and it is hence harm ever interestingly, a dorsal L1, or an anterior pi facets on the metapodypus. There is apj joint between these.

The intervertebra and between L3 an 68919, however, pos teach at 8 T3 posteriorly. These are situated on the anterodorsal edge of the posterodorsal edge of the vertebral centrum and the anterior edge of the pedicel of the succeeding vertebra. The zygapophyseal facets of the thoracic vertebrae of Bradypus strongly resemble those of Tamandua. They are transversely oval and widely separated by a broad, rounded, midline notch on the anterior edge of the lamina (Fig. 2C). As in anteaters, these zygapophyseal facets extend lateral to the vertebral centra in anterior view. The lateral extension of the zygapophyses becomes increasingly prominent in more posterior thoracic vertebrae.

As in Tamandua, there is no trace of an anaphyposis in any anterior thoracic vertebra. There are rudimentary metapophyses present in most thoracic vertebrae (from at least T3 posteriorly). These are situated on the anterodorsal edge of the

\*This is not the case in posterior view, due to the presence of elongated tubercles that extend dorsolaterally from the caudal edge of the centrum and articulate with the head of each rib.

**FIELDIANA: GEOLOGY**

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diaphyses, causing the diaphyses to be longitudinally elongated in dorsal view (Fig. 2C). This is also quite reminiscent of the anteater condition. The first distinct metapophysis is small and borne by T14. The metapophyses of succeeding vertebrae are progressively larger (Fig. 2C).

T15 is the diaphragmatic vertebra. It differs from that of other xenarthrans in lacking supplementary intervertebral articulations. T15 bears a small anapophysis that extends posteriorly from the base of the fused diaphysis/15th rib (Figs. 2C, 3C, 9). The anapophysis closely approximates a lateral projection of the lamina of L1. This extension lies lateral to the base of the metapophysis of L1. As in the postdiaphragmatic vertebrae of other xenarthrans, the base of the metapophysis of L1 reaches the anterior margin of the lamina. In contrast to other xenarthrans, however, a true synovial joint does not occur between the small anapophysis and the area lateral to the base of the metapophysis (Fig. 9A).

The anapophysis of L1 is much larger than that of T15, and it bears a flat, circular, ventromedially directed facet on its medial edge (Figs. 2C, 3C). This facet articulates with a similar facet located lateral to the base of the metapophysis of L2. This lateral facet on L2 is carried on a lateral extension of the neural arch, and it is narrowly divided from the curved, upright medial zygopophyseal facet by the base of the metapophysis (Fig. 2C). The articulation between the anapophysis of L1 and the lamina of L2 is nearly identical in position, shape, and orientation to the lateral zygopophyseal joints of armadillos and anteaters (Fig. 9), and it is hence homologized with these joints. Interestingly, a dorsal facet on the anapophysis of L1, or an anterior projection or ventrally directed facet on the metapophysis of L2, is absent in Bradypus. There is apparently no true xenarthrous joint between these vertebrae.

The intervertebral joints between L2 and L3 and between L3 and S1 are virtually identical to that between L1 and L2 in FMNH 68919. FMNH 68919, however, possesses an additional set of articular facets between L3 and S1. The transverse process of L3 in this specimen bears a wide, shallow, ovate articulating facet on its distal end. The facet forms a synovial joint with a similar facet lying on the anterior edge of the transverse process/sacral rib of S1. This joint provides the only evidence of nonzygapophyseal supplementary intervertebral articulations in this genus. The joint is of further significance because it does not involve the anapophysis at all, in contrast to the supple-

Hapalops

The vertebral columns of four specimens of Hapalops from the Miocene Santa Cruz Formation of South America (Scott, 1903–1904) were examined. These specimens included Hapalops longipalatus, FMNH P13146, a mounted skeleton with a nearly complete series of vertebrae; Hapalops sp., FMNH P13145, a partially prepared (ventral surface only) block of articulated lumbar and sacral vertebrae; Hapalops sp., FMNH P131133, a specimen with several discontinuous strings of articulated thoracic vertebrae; and Hapalops sp., FMNH P15318, an articulated series of vertebrae composed of the first lumbar and ultimate and penultimate thoracic elements. The latter specimen is the best preserved and is emphasized in the description below (Figs. 10, 11).

Scott (1903–1904) estimated the number of thoracic vertebrae to be between 21 and 22 in the type specimen of Hapalops longiceps, with 3 lumbar vertebrae present. FMNH P13146 has 22 thoracic and 3 lumbar vertebrae, although the column is incomplete, with several thoracic vertebrae and their accompanying ribs reconstructed in plaster. The anterior thoracic vertebrae are typically pilosan. They have tall pedicles and well-developed intervertebral foramina. The zygapophyseal facets are remarkably wide, even more than in living pilosans. In pilosans and euphractan armadillos, the maximum width of the zygapophyseal facets is about twice the maximum anteroposterior length. In Hapalops the width is two-and-a-half times the length (Table 1). The anterior zygapophyseal facets are separated from one another by a rounded midline notch somewhat narrower than that observed in Bradypus and Tamandua. As in the living anteater and sloth, these facets extend further laterally than the vertebra centra. The facets become even wider posteriorly and are slightly curved in a horizontal plane, with the medial portion extending out from the midline anterolaterally and the lateral part oriented almost directly laterally (Fig. 10).

The anterior thoracic vertebrae of Hapalops are more reminiscent of anteaters than Bradypus in several respects. The neural spines are quite tall and elongated anteroposteriorly. They are of rel-
relatively uniform height, decreasing only slightly from the middle of the thoracic series posteriorly. As in *Tamandua*, the articulation for the head of the rib is positioned on the anterodorsal corner of a single vertebral centrum (Fig. 11). The diapophyses of *Hapalops* are much taller than those of the *Bradyapus*. They are longitudinally elongated, as are those of other pilosans, due to the presence of rudimentary metapophyses extending from the anterior edge of the diapophyses. The metapophyses become progressively larger posteriorly. The first freestanding metapophysis occurs on T15 in FMNH P13146 (T18 in Scott, 1903-1904, pl. 30). As in *Bradyapus* and *Tamandua*, anapophyses are absent on all anterior thoracic vertebrae.

The diaphragmatic vertebra of FMNH P13146 is T19, as in Scott's (1903-1904) specimens of *Hapalops longiceps* and *H. elongatus*. Like *Tamandua*, the first supplementary intervertebral articulation occurs between the diaphragmatic and postdiaphragmatic vertebrae. In addition, the diaphragmatic vertebra is the anteriormost thoracic vertebral that bears a T19 has a small anapophysis facet ventrally. This isontally and separate posterior zygapophyseal vertical joint is closer to the midline.

The two posterior joints with correspond edge of T20. As in otters on the anterior formed by division c zygapophyseal facet. sis of T20 reaches thbra, dividing the zyg and lateral portions. facet is concave. Its and its lateral half is ulates in typical fash posterior zygapophyseal. The lateral zygapophyseal, nearly flat (it sally), and oriented slightly ventrolateral surface of an anterior

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**FIG. 10. Hapalops sp., FMNH P15318; 19th through 21st thoracic vertebrae shown in dorsal view (cranial end toward the top of the page). Scale bar = 1 cm. Abbreviations as in Figures 1, 2, and 10, plus rh, rachitomous foramen.**

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**FIG. 11. Hapalops sp., FMNH P15318; 19th through 21st thoracic vertebrae shown in left lateral view. Scale bar = 1 cm. Abbreviations as in Figures 1, 2, and 10, plus rh, rachitomous foramen.**

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**TABLE 1. Ratio of t axis) of the anterior zyg

<table>
<thead>
<tr>
<th>Taxon</th>
<th>FMNH</th>
<th>SMNH</th>
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<tbody>
<tr>
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<td></td>
</tr>
<tr>
<td>Euphractus sexcinctus</td>
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<td>Chaetophractus villosus</td>
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<td>153773</td>
<td>125140</td>
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<td>Tamandua mexicana</td>
<td>69625</td>
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<td>Bradyapus variegatus</td>
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<td>Hapalops sp.</td>
<td>P13133</td>
<td>P15318</td>
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<tr>
<td></td>
<td>(mid-TV)</td>
<td>(T19 mea)</td>
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**TABLE 1. Ratio of t axis) of the anterior zygapophysis facet.**

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**FIELDIANA: GEOLOGY**

**GAUDIN: THE MOI**
TABLE 1. Ratio of maximum width (parallel to long axis) to maximum anteroposterior length (orthogonal to long axis) of the anterior zygaphyseal facets of the prediaphragmatic thoracic vertebrae in Xenarthra.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Total no. of TV</th>
<th>Vertebra</th>
<th>Maximum width (mm)</th>
<th>Maximum length (mm)</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zaeus pichly</td>
<td>11</td>
<td>T3</td>
<td>3.8</td>
<td>1.6</td>
<td>2.4</td>
</tr>
<tr>
<td>FMNH 104817</td>
<td></td>
<td>T6</td>
<td>3.5</td>
<td>1.7</td>
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</tr>
<tr>
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<td>11</td>
<td>T3</td>
<td>5.7</td>
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<tr>
<td>FMNH 152051</td>
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<td>T5</td>
<td>5.9</td>
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<td>2.3</td>
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<tr>
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<td>10</td>
<td>T5</td>
<td>6.8</td>
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<td>2.1</td>
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<tr>
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<td></td>
<td>T7</td>
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<td>2.4</td>
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<tr>
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<tr>
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<tr>
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<tr>
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<td>?mid-TV</td>
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<td>2.5</td>
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<tr>
<td>FMNH P13133 (mid-TV measured)</td>
<td></td>
<td></td>
<td>14.8</td>
<td>6.0</td>
<td>2.5</td>
</tr>
</tbody>
</table>

TV = thoracic vertebrae; T1, T2, T3 = first thoracic vertebra, second thoracic vertebra, third thoracic vertebra, etc.

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Another type of articulation is the metapophysis and the dorsal surface of the anapophysis. These are sporadically present in FMNH P13146 (e.g., on the right side only of the intervertebral joint between T22 and L1, and on both sides of L2/L3). Xenarthrous joints, are clearly absent in the thoracic intervertebral joints, even those bearing supplemental articular facets. The presence of xenarthrous joints could not be confirmed at L1/L2 or L3/S1 because of poor preservation.

Other Tardigrada

The extant tree sloth Choloepus and the extinct ground sloth families Mylodontidae, Megatheriidae, Nothrotheriidae, and Megalonychidae are, like other pilaon, characterized by a relatively large number of thoracic vertebrae and a small number of lumbar vertebrae. Thoracic vertebral counts among the extinct forms range from 15 in Glossostherium and Paramylodon (Flower, 1885; Stock, 1925) to 22 in Hapalops. The highest number among non-Santacrucian ground sloths is 19, which occurs in the Pliocene nothothertid Pronothokrtochus (FMNH P14503) and the Pleistocene megalonychid Megalocnus (Matthew & Paula Couto, 1959, pl. 26). The number of thoracic vertebrae in Choloepus ranges between 22 and 24, the highest among living mammals (Flower, 1885). The tardigrades characteristically possess three lumbar vertebrae, although some Choloepus and some Hapalops have four (Flower, 1885; Scott, 1903–1904), and the Santacrucian genus Schizosthenus has five (AMNH 9244; Scott, 1903–1904). In several genera, one or more of the lumbar vertebrae are fused to the sacral vertebra (Glossostherium, Owen, 1842; Paramylodon, Stock, 1925; Megalocnus, Matthew & Paula Couto, 1959; Acratocnus, AMNH 177616–177619).

The anterior thoracic vertebrae among tardigrades are typically much like those described in Hapalops, with tall, anteroposteriorly elongated neural spines and diapophyses, and wide anterior and posterior zygapophysial facets that extend further laterally than the vertebral centra and are separated by a small midline notch. The zygapophysial facets appear to be particularly wide among the Santacrucian megalonychids (sensu Gaudin, 1993) and the nothitheriids (Fig. 12). The zygapophysial facets of Eremotherium (Paula Couto, 1978) and Seclidotherium (Gervais, 1855) are unusual in that they are not elongated mediolaterally but instead are almost circular in shape. They are, however, very widely separated from one another on either side of the midline and, at least in Seclidotherium, their lateral margins lie lateral to the outer margins of the centra.

The anterior zygapophyseal facets of the Pleistocene West Indian megalonychid Megalocnus, although retaining the elongated ovate shape, are oriented anterolaterally at an angle of approximately 45° to the midsagittal plane. The facets are also more widely separated on either side of the midline than is usual for ground sloths. In the extinct Puerto Rican genus Acratocnus (Anthony, 1918) and the extant genus Choloepus (FMNH 147993, 127422), the facets are oriented almost directly anteriorly and separated by a very broad, rounded, midline notch very reminiscent of that in Bradypus. The thoracic vertebrae of these two taxa, particularly in Choloepus, also resemble Bradypus in the degree of reduction of the vertebral processes.

One other noteworthy modification of the thoracic vertebrae appears in the anterior and middle thoracic vertebrae of certain large mylodontid and megatheriid ground sloth genera. In these forms some of the thoracic vertebrae bear an additional articular facet both anteriorly and posteriorly. The facets are unpaired and lie on the midline. The anterior facet lies on the dorsal surface of the lamina, with its anterior margin situated approximately at the level of the posterior zygapophyseal surface. The midline facets (Owen, 1851b, 1978), the large-bodied Megalocnus (Foster, 1987), and don harlani (Stock, 1913) are the closely related G. In almost all tardigrade species, the anterior thoracic articulation is a lateral, rather indistinct area for an extension of the thoracic articulation is an external metapophysis and possibly a lumbosacral joint.

A second accesso-
ly at the level of the posterior margin of the anterior zygapophyal facets. The posterior facet is borne on the undersurface of the neural spine. These midline facets have been noted in Megatherium (Owen, 1851b), Eremotherium (Paula Couto, 1978), the large-bodied Santacruzanus genus Planops (Hoffstetter, 1961), the scelidotheres (McDonald, 1987), and the mylodontines Paramylodon harlani (Stock, 1925) and “Mylodon” garnani (Allen, 1913). They are absent, however, in the closely related Glossotherium (Owen, 1842).

In almost all tardigrades accessory intervertebral articulations make their initial appearance in the posterior thoracic vertebrae. As in Hapalops, accessory articulations usually occur as a single articular surface between the ventral surface of a rather indistinct anapophysis and the dorsal surface of an extension of the vertebral lamina lying lateral to the base of the metapophysis. These articulations extend from the joint between the diaphragmatic and postdiaphragmatic vertebrae to the lumbosacral joint. In the majority of taxa, this lateral zygapophyal articulation is flat, although in Planops (Hoffstetter, 1961) and Paramylodon harlani (Stock, 1925) it curves dorsomedially onto the lateral surface of the metapophysis and the medial edge of the anapophysis.

A second accessory articulation, a true xenarthrous facet between the dorsal surface of the anapophysis and the ventral portion of the metapophysis, occurs only rarely among tardigrades. It has, however, been observed in three genera from the Miocene Santa Cruz formation of Patagonia; Hapalops, where it may be variably present, as noted above; Schizotherium, where again its presence is variable (observed in FMNH P13137 but not in AMNH 9244 or in specimens described by Scott, 1903–1904); and Preotherium, a genus closely related to Planops (Scott, 1903–1904).

In most tardigrades separate medial and lateral zygapophyal facets do not occur anterior to the diaphragmatic vertebra, but several taxa exhibit at least incipient separation of the facets in the prediaphragmatic vertebra. In the Santacruzanus genus Pelecyodon (AMNH 9240), the anterior zygapophyal surface of the diaphragmatic vertebra is formed by two contiguous facets oriented approximately 120° to one another. The medial facet is oriented horizontally, and the lateral facet slopes ventrolaterally. The posterior zygapophyal facets on the prediaphragmatic vertebra are similarly constructed. A very similar morphology has been described by Stock (1925) in Paramylodon harlani, where these angled medial and lateral facets are variably expressed between the prediaphragmatic and diaphragmatic vertebrae. The angled facets may appear bilaterally, on one side only, or be absent. These angled medial and lateral facets have also been observed in Megalonyx, including AMNH FLA-103-1986, in which the abutting, angled medial and lateral posterior zygapophyses are present on one side, while on the other side the two posterior facets are widely separated, with the vertical medial facet and horizontal lateral facet typical of diaphragmatic vertebrae in other sloths.

The accessory articulations are smaller and fewer in number in sloths compared to those of other xenarthrans. However, the articulations are reduced even further in several tardigrade genera. In the North American Pleistocene genus Nothrotheriops, the morphology of the articulations is much like that described above for Hapalops. The diaphragmatic vertebra occurs in the posterior lumbar vertebrae, however, rather than in the posterior thoracic vertebrae. As in other sloths, Nothrotheriops has three lumbar vertebrae, the second of which is the diaphragmatic vertebra, so that the accessory intervertebral articulations occur only between L2 and L3 and between L3 and S1 (Stock, 1925). In Choloepus the reduction is even more significant. The diaphragmatic vertebra of Choloepus hoffmani (FMNH 127422, 147993) is the 21st, or antepenultimate, thoracic, a fairly typical position for a tardigrade. Metapophyses are well developed on T21 and more posterior vertebrae. The anapophysis first appears as a small nubbin on T23 and becomes progressively larger on L1, L2, and L3. Nevertheless, the only accessory articulation present occurs at the lumbosacral joint, and even then only on one side of that joint (FMNH 127422 = left; FMNH 147993 = right). In a juvenile Choloepus specimen (FMNH 127421) only slightly younger than the juvenile Tolypeutes (FMNH 124569) described above (based on the degree of fusion of the neural arches in the midline), the accessory articulations are absent, as are metapophyses and anapophyses. When present, the accessory intervertebral joint of Choloepus resembles that of other tardigrades, taking the form of a lateral zygapophyal articulation between the ventral surface of the anapophysis and the dorsal surface of a facet situated immediately lateral to the base of the metapophysis.
Conclusions

Morphological Summary

The morphological data described above are summarized in Appendix Table 1 (p. 36). The intervertebral articulations between the thoracic and lumbar vertebrae of xenarthrans can be placed into four distinct categories.

1. Normal zygaphysyal facets. The intervertebral articulations between the anterior thoracic vertebrae in most xenarthrans differ little from the thoracic zygaphysyal facets found in other mammals (Fig. 1; Walker & Homberger, 1992). Morphological departures from the normal mammalian pattern include widening of the anterior and posterior zygaphyses in pilosans and euphractan armadillos (Table 1, Fig. 3B), so that the zygaphyses extend further laterally than the vertebral centra. In addition, pilosans possess a broad midline notch that separates the anterior zygaphysyal facets (Fig. 2B, C).

Typical mammalian zygaphyses are present only in the prediaphragmatic vertebrae of the majority of xenarthrans. The exceptions are the living tree sloths Bradypus and Choloepus, in which the normal mammalian morphology extends from one (Bradypus) to six vertebrae (Choloepus) posterior to the diaphragmatic vertebrae. In addition, in euphractan armadillos and some extinct sloths, the zygaphyses of some prediaphragmatic thoracic vertebrae begin to show evidence of incipient division into distinct medial and lateral facets (see below).

2. Medial zygaphysyal facets. In all xenarthrans (except glyptodonts, in which the vertebrae are fused), the postdiaphragmatic vertebrae bear on each side a curved, vertically oriented intervertebral facet that lies medial to the metapophysis and adjacent to the midline anteriorly (Fig. 13). Posteriorly, the corresponding facet lies at the base of the neural spine adjacent to the midline. As noted above, the facets are homologized with the zygaphysyal facets of other mammals by Owen (1851a) and others (Hoffstetter, 1958; Lessertisseur & Saban, 1967; Gaudin & Biewener, 1982; Rose & Emry, 1993; contra Flower, 1885; Grassé, 1955; Vaughn, 1986). These facets are structurally identical to those present in the postdiaphragmatic vertebrae of other mammals (see Fig. 1). Given this fact, and their near-universal distribution within Xenarthra, I see no reason to doubt this homology.

In several xenarthran taxa, the medial portion of the zygaphysyal facet of some prediaphragmatic vertebrae is separated from the lateral portion by a small groove or ridge. This separation occurs in the first prediaphragmatic vertebra of several ground sloth taxa. In the euphractan armadillos it may occur as far forward as the third thoracic vertebra.

3. Lateral zygaphysyal facets. A majority of xenarthran taxa possess an anterior facet on each side of the postdiaphragmatic vertebrae that lies on a lateral extension of the vertebral lamina, situated immediately lateral to the base of the metapophysis (Fig. 13). A corresponding facet is found posteriorly, on the ventromedial surface of the anapophysis. As noted by Jenkins (1970) for Tamentua, these face
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Tampandua, these facets closely resemble in structure and position the lateral portion of the zygaphophysis of the prediaphragmatic vertebrae. I therefore suggest that these facets are serially homologous with the lateral parts of the zygaphophyseal articulations of the prediaphragmatic vertebrae. These facets are considered accessory zygaphophyseal articulations, termed “lateral zygaphophyseal facets,” and are distinct from true “xenarthral” facets.

The homology of these lateral zygaphophyseal articulations is less secure than that of the medial zygaphophyseal facets because their taxonomic distribution is not entirely congruent with the taxonomic distribution of the medial facet. Two taxa, the tree sloths Bradypus and Choloepus, lack lateral zygaphophyseal articulations at least some of the postaxial vertebrae. However, the normal zygaphophyseal articulations are poorly developed in both of these taxa, with successive vertebrae fitting together only loosely. Moreover, the vertebral processes are weak in both taxa. It therefore seems likely that the absence of lateral zygaphophyseal facets in these taxa represents a secondary reduction.

4. True xenarthral facets. There are several different types of facets found in various xenarthran taxa that can be categorized as true “xenarthral” accessory intervertebral articulations.

The most common is a facet borne, on each side, on the ventrolateral surface of an extension projecting from the base of the metapophysis; the corresponding posterior facet lies on the dorsal surface of the anapophysis (Fig. 13). Such facets are found on the diaphragmatic and postaxial vertebrae of all cingulates and verminigus, and may extend as far forward as the second prediaphragmatic vertebra in these groups. These facets are also variably present in a few genera of early megalonychiform sloths (Hapalops, Schismothemus, Protopitherium), and hence they likely represent the primitive condition for tarsigrades as well. They are often fused to the lateral zygaphophyseal facets.

A second type of facet occurs on the ventrolateral surface of the anapophysis of some thoracic vertebrae in armadillos for articulation with a rib. Such facets are found on T8–T10 (the penultimate thoracic vertebra) in Zedaus (Fig. 4C) and T6 or T7–T9 (again the penultimate thoracic vertebra) in Dasyusus, but have not been observed in any pilosans. These articular surfaces do not serve an intervertebral function. However, the anapophysis of the last thoracic vertebra of cingulates carries a ventral articular facet that apparently corresponds to the facet just described for more anterior vertebrae. In the ultimate thoracic vertebra it articulates with a facet carried on the dorsal surface of the transverse process of L1 (Fig. 4D). This type of articulation continues posteriorly through the lumbar vertebrae to the sacroiliac joint. A similar facet is present between the vertebral portion of the anapophysis and the dorsal portion of the transverse process/sacral rib in Myrmecophaga (at L1/L2 and the lumbarosacral joint) and Tamandua (at the lumbarosacral joint only), but not in Cynocephalus. This type of facet is unknown in sloths, although some specimens of Bradypus are characterized by an articulation formed between the distal tip of the transverse process of L3 and the anterior edge of the sacral rib.

Finally, the vertebrae of several groups of xenarthrans possess unpaped midline facets that may be generally categorized as xenarthral. The anterior facet is typically found on the dorsal surface of the vertebral lamina, posterior to the zygaphophyseal articulations and anterior to the base of the neural spine. The posterior facet lies on the undersurface of the neural spine. These facets are particularly characteristic of large-bodied xenarthrans, such as the giant armadillo Prionodon (Fig. 7) and megatherid, scelidotherine, and some mylodontine ground sloths.

Phylogeny and Evolution of Xenarthral Vertebrae

When the data on intervertebral articulations are plotted on a phylogeny of Xenarthra (Fig. 14), a number of features may be identified that appear to be primitive characteristics of xenarthral vertebrae. The diaphragmatic thoracic vertebrae probably have abnormally wide zygaphyses, although this feature is absent in many cingulates. The metapophyses are large, especially in the posterior thoracic and lumbar vertebrae. In the postdiaphragmatic vertebrae, these large metapophyses split the zygaphophyseal articulations into separate medial and lateral joints. In addition, each metapophysis bears a ventral articular facet that articulates with the dorsal surface of the anapophysis of the preceding vertebra. Large anapophyses may also be a primitive characteristic of xenarthral vertebrae. However, the anapophyses are only weakly developed in sloths and in the anterior xenarthral vertebrae of cingulates.

The goal of the present study was not only to
analyze the morphology of xenarthrous vertebrae across the Xenarthra as a whole, but also to understand the structural evolution of these accessory intervertebral facets. Although determining the primitive morphology of xenarthrous vertebrae is an important step in understanding their evolution, a more complete explanation requires information on intermediate conditions leading to the appearance of fully developed xenarthrales.

The difficulty in determining the structural genesis of xenarthrous intervertebral facets stems from what MacPhee (1994, p. 174) described as an “apparent absence of any recognizable intermediate condition between nonarthry and xenarthry.” As mentioned above, however, MacPhee (1994, p. 174) suggested that the development of accessory intervertebral facets may be the result of a process of “sacralization,” whereby the posterior dorsal vertebrae become more solidly attached to one another in a manner analogous to the intimate union characteristic of mammalian sacral vertebrae. Such an analogy seems particularly apt for an animal such as Scutisorex (Lessertisseur & Saban, 1967; Kingdon, 1984), in which the posterior thoracic and lumbar vertebrae are united latetly by closely interlocking bony

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excrecences. It is less clear whether the analogy can be usefully applied to xenarthrans, in which the vertebrae are not synostosed laterally or connected by tight fibrous joints but rather are connected by extra synovial joints that limit intervertebral mobility (Gaudin & Biewener, 1992). Whereas MacPhee (1994) noted that the sacral elements in some mammals remain unfused throughout life and hence might serve as an appropriate xenarthran analogue, the fused condition is certainly primitive for xenarthrans, and perhaps for mammals as a whole (Jenkins & Schaff, 1988; Kielan-Jaworowska & Gambaryan, 1994; but see also unfused sacral vertebrae in Jenkins & Parrington, 1976; Krebs, 1991; Marshall et al., 1995).

In support of MacPhee’s (1994) hypothesis is the observation that in several xenarthran taxa some or all of the lumbar vertebrae are fused to the sacral vertebrae. This lumbar sacral fusion occurs in the dasyurid armadilloes *Friedontes* and *Tolypeutes*, in the euphractan armadilloes *Euphractus* and *Chaetophractus*, in glyptodonts (Gillette & Ray, 1981), in some mylodontine sloths (Owen, 1842; Stock, 1925), and in some West Indian megalonychid sloths (Matthew & Paula Couto, 1959). Nevertheless, the phylogenetic distribution of lumbar sacral fusion suggests that it is a derived feature of these lineages and not a primitive feature of Xenarthra. Moreover, in the juvenile specimens of *Tolypeutes* and *Tamandua* described above, the lumbar sacral joint is the last to develop accessory intervertebral joints. This observation would seem to argue against a claim of some structural continuity between sacral and more anterior vertebrae.

MacPhee (1994) asserted that the demonstration of accessory intervertebral joints in the sacrum of developing xenarthrans (or indeed non-xenarthran mammals) would strongly support the sacralization hypothesis. No evidence of accessory synovial joints is present, however, in the skeletal remains of very young juvenile individuals representing all three major subgroups of xenarthrans (armadillos, anteaters, tree sloths) in FMNH collections. Indeed, in the youngest *Tamandua* specimen examined the sacral anapophyses do not contact the succeeding vertebrae. Rather, the sacral vertebrae were joined through wide

zymoglyphous facets reminiscent of those in the anterior thoracic vertebrae. In a young juvenile *Choloepus* specimen, the sacral vertebrae lacked anapophyses altogether. It would seem at present that there is little evidence in support of sacralization as the process through which xenarthran articulations originated.

In contrast to MacPhee’s (1994) claim, I suggest that documented structural intermediates between xenarthrous and nonxenarthrous vertebrae do exist. Among tardigrades, the xenarthran articulations are reduced relative to the primitive condition for the order as a whole. The reduction includes not only a diminution in the number of intervertebral joints that possess accessory articulations (see Bradypax, Notrotheriops, and Choloepus, above), but also a simplification of the accessory articulations themselves. The vast majority of sloths lack a xenarthran joint between the ventral surface of the metapophysis and the dorsal surface of the anapophysis. Weakly developed anapophyses are universally characteristic of sloth vertebrae. Sloths retain only the wide prediaphragmatic zygoglyphous facets, large metaphyses, and medial and lateral postdiaphragmatic zygoglyphous facets characteristic of primitive xenarthran vertebrae. Even these medial and lateral postdiaphragmatic zygoglyphous facets may be restricted to the last few lumbar vertebrae in several taxa, most notably the extant tree sloths.

The presence of xenarthran joints between the metapophysis and anapophysis in several relatively early sloth genera, e.g., *Hapalops* and *Prephotherium*, suggests that the xenarthralia in sloths are reduced secondarily. Although the manner in which these facets are reduced need not parallel the process by which they originate, I believe that the sloth condition, as the only known structural intermediate between xenarthry and nonxenarthry, represents the best available tool for understanding the evolutionary origin of xenarthran vertebrae.

Using the condition in sloths as a model, I suggest that the first step in the evolution of xenarthran articulations was a widening of the zygoglyphous facets and enlargement of the metaphyses, both becoming more extensive in progressively more posterior thoracic and lumbar vertebrae. The widening of the zygoglyphous facets should increase the lateral moment of resistance of the joints and hence enhance the stability of the vertebral column in lateral bending (see below). The enlarged metaphyses would provide a larger area for origin of the epaxial transverso-
spinalis muscles. At the joint between the diaphragmatic and first postdiaphragmatic vertebrae, the metapophyses would become sufficiently large to split the widened zygaphyseal facets perforce into separate medial and lateral zygaphyseal joints. These medial and lateral zygaphyseal joints would then continue posteriorly to the lumbosacral joint.

The second step in the evolution of xenarthrans would involve the development of the other two primitive features of xenarthrous vertebrae, an enlarged anapophysis and a xenarthrous joint between the dorsal surface of the anapophysis and the ventrolateral surface of the metapophysis. These two structurally linked modifications would serve to further enhance the stability of the spinal column, particularly in lateral and dorsal bending (Gaudin & Biewener, 1992). The final steps in the evolution of the xenarthrous vertebrae would involve the appearance of the various types of specialized xeranthesian facets in the major xenarthran subgroups, e.g., the joints between anapophyses and transverse processes in cingulates and some anteaters. These presumably function to provide additional stiffness to the vertebral column while preserving a certain degree of mobility. Secondary loss of some of these facets in sloths might be the result of their switch from a digging to a more terrestrial or semi-aquatic habit (Gaudin, 1993; White, 1993a,b).

The above model contrasts with that of MacPhee (1994) in postulating that xenarthrans develop from the posterior thoracic vertebrae back rather than from the sacral vertebrae forward. The new model accords well with the observation that xenarthrous articulations in living xenarthrans tend to become more complex caudally, and that these more complex caudal articulations appear later in development (see Tolypeutes and Tamandua above). It conforms with what is known about the mechanics of the mammalian spine. The mammalian backbone tends to exhibit maximum flexibility in the mid-dorsal region, in the vicinity of the diaphragmatic vertebrae (Slijper, 1946; Jenkins, 1974). Thus one might predict that adaptations to reduce spinal mobility might first appear in this region. Finally, the model fits well with what is known about the functional morphology of xenarthrous vertebrae. Gaudin and Biewener (1992; see also Gaudin, 1993) have recently reaffirmed the idea that Xenarthra represents an offshoot of early placental mammals that were previously specialized for digging. They note further that in digging mammals, the axial musculoskeletal system has a particularly important role to play in resisting the large dorsal and lateral reaction forces generated by digging. The axial skeleton of xenarthrans is stiffened relative to the primitive mammalian condition in dorsal and lateral bending. The appearance of wide zygaphyses in early xenarthrans would effectively increase the lateral moment of resistance of the vertebrae, stiffening the intervertebral joints in lateral bending. Because xenarthrans dig primarily with their forelimbs, the vertebral column is loaded as a cantilever, with loads increasing posteriorly. This would account for the progressive increase in width of the zygaphyseal facets in more caudal vertebrae. Large metapophyses would result from hypertrophy of transversospinalis muscles, which, according to Gaudin and Fortin (unpubl. data), play an important role in stabilizing the vertebral column during dorsal bending. Again, these muscles would be expected to increase in size posteriorly in concert with the increase in dorsal bending forces.

It is of particular interest that the above model of xenarthrous vertebral evolution does not initially include enlargement of the anapophyses. Enlarged anapophyses have been considered by several authors (Simpson, 1931; Ding, 1987; Storch, 1981; see below) as indicating incipient xenarthra. However, Gaudin and Fortin (unpubl. data) note that the longissimus dorsi muscles, which take their origin from the anapophyses, are not enlarged in xenarthrans relative to the primitive mammalian condition and likely play little or no role in enhancing dorsal and lateral stiffness. Further, Gaudin and Biewener (1992) were able to cut the anapophyses in the posterior lumbar vertebrae of Dasypus without significantly decreasing either dorsal or lateral stiffness. Gaudin and Biewener (1992) presented evidence from strain gauge analyses suggesting that enlarged anapophyses serve to reduce shear stress in dorsal bending, to augment the lateral moment of resistance in lateral bending, and to transmit forces from the forelimbs to the robust pelvic girdle and hind limbs in both dorsal and lateral bending. Nevertheless, the functional and phylogenetic evidence appears to indicate that enlarged anapophyses are not a necessary structural antecedent of xenarthrous intervertebral articulations.

Relationship of Xenarthra to Early Cenozoic Fossil Taxa

The final goal of the present study was to utilize the above conclusions on the structural evolution of xenarthrans to evaluate several enigmatic legged assemblages. Close ties to the Paleocene mammals with rudimentary limbs from Paleogene strata (e.g., Gaudin et al., 1991, 1992; Gunther et al., 1991, 1992) suggest that these ungulate-like remains from China (e.g., Dian, a purported ante Messel fauna of Germany) may be linked to the Paleocene xenarthrans. However, the highly derived Late Paleocene (or Early Eocene) metatherians of the genus Allocecomy sus were not considered in this study. It is possible that the evolution of Allococecomy sus from xenarthrans is not well understood, and additional material from this group may reveal a closer relationship with xenarthrans. Further, the functional and phylogenetic evidence presented here suggests that xenarthrans and the early Cenozoic metatherians (e.g., Eocene Hesperocyonidae, and Oligocene Paenungulata) are not closely related. Therefore, it is unlikely that xenarthrans are the direct ancestors of the early Cenozoic metatherians. Finally, the functional and phylogenetic evidence presented here suggests that xenarthrans and the early Cenozoic metatherians are not closely related. Therefore, it is unlikely that xenarthrans are the direct ancestors of the early Cenozoic metatherians.
A significant role to play in the evolution of xenarthrans was the development of an axial skeleton of xenarthran construction, which was broadly similar to the primitive mammalian condition. The axial and lateral elements of the anaphyses in early Cenozoic xenarthrans were relatively large and had a larger anteposterior length than in laterally bending vertebrates. This increase in anteposterior length is suggested to have been due to an increase in the number of anteposterior vertebrae, stiffening the vertebral column and allowing for greater lateral bending. The anaphyses in xenarthrans are also much wider than those in laterally bending vertebrates.

A close phylogenetic link between palaeoedonts and xenarthrans has been proposed based on various lines of evidence, including the morphology of the vertebral column (see Emery, 1970, for contrast interpretations). In his description of the vertebral column of the palaeoedont *Metachirostomys* (Simpson, 1931, p. 334), stated that "the character [of xenarthran articulations] is not definitely incipient in *Metachirostomys*,... its morphology seems... an ideal point of departure for the origin of the secondary articulations." Yet Matthew (1918, p. 629), in his description of the Late Paleocene (or Early Eocene; see Gunnell & Gingerich, 1993) genus *Palaeotherium*, could find no recognizable foreshadowing of the peculiar 'xenarthral' articulations characteristic of true xenarthrans.

In part the discrepancy results from the poor state of preservation of the vertebral column of *Palaeotherium*. Other palaeoedonts lack preserved vertebrae (Rose, 1978, 1979), and hence shed no light on the problem. Better preserved material exists from the Early and Middle Eocene, representing both families of palaeoedonts (Eopoliotheriidae and Metachirostomidae). In the *Eochotheriidae* *Allochirostomia* and *Metachirostomidae*, certain similarities to xenarthran vertebrae can be observed (Simpson, 1931; Rose et al., 1992). The metaphyses are enlarged, particularly in the posterior thoracic vertebrae in the vicinity of the diaphragmatic vertebra. Unlike xenarthrans, however, the metaphyses become progressively smaller in more posterior lumbar vertebrae. In the posterior thoracic vertebrae, there is an uncertainty whether the thoracic zygapophyseal facets belong to the thoracic or the posterior lumbar vertebrae. They are narrow anteriorly and posteriorly, and the zygapophyseal facets are narrow anteriorly and posteriorly, and the zygapophyseal facets are angularly projected posteriorly. Rose et al. (1992, p. 226) describe the lumbar prezygapophyseal facets of *Allochirostomia* as "broad." Broad zygapophyseal facets have also been observed in the lumbar vertebrae of the Early Eocene *Eochotheriidae* *Pentapassalus* (USNM 20028, Gaudin, pers. observ.) and the diaphragmatic vertebra of *Metachirostomidae* (USNM 26132, Gaudin, pers. observ.). They are not so broad, however, as in xenarthrans, in which width often exceeds anteposterior length by a factor of two or more (Table 1).

Simpson (1931, fig. 12c) figured narrow anterior zygapophyseal facets on the 10th or 11th thoracic vertebra of *Metachirostomidae*, but these facets are situated well lateral to the midline. In no case, however, are there distinct medial and lateral zygapophyseal facets observed in any palaeoedont. The anaphyses of palaeoedonts are enlarged (Simpson, 1931; Rose et al., 1992), again in the vicinity of the diaphragmatic vertebrae. Although relatively deep on T12 and T13 of *Allochirostomia* (Rose et al., 1992, fig. 3, the anaphyses of palaeoedonts tend to be dorsoventrally and laterally narrow and spine-like. In this respect they more closely resemble the anaphyses of carnivores than those of xenarthrans (Rose et al., 1992; Rose & Emry, 1993). Furthermore, there is no indication of articular surfaces between the anaphyses and the succeeding metaphyses or transverse processes.

On balance, it would appear that palaeoedont vertebrae share few, if any, of the derived characteristics of xenarthran vertebrae unequivocally. The strongest similarity between the vertebrae of the two groups is the enlargement of the metaphyses. This specialization, however, is known to occur in many groups of fossorial mammals (Gaudin & Fortin, unpubl. data), and hence may likely be convergently acquired.

Among other supposed similarities to xenarthrans, Ding (1987, p. 92) noted the posterior thoracic vertebrae of *Eochotheriidae*, which bear "largely elongated projections under the mammalian process [= metapophysis], which are incipiently developed xenarthran articulations." As in xenarthrans and palaeoedonts, the posterior thoracic vertebrae are characterized by well-developed metaphyses. A pair of large vertebral processes extend lateral to the metaphyses, but do not form joints with the metaphyses. These lateral processes (Ding, 1987, fig. 7) apparently represent large anaphyses. In the posterior thoracic vertebrae, the anaphyses arise anteriorly from the back of the thoracic vertebrae, and are thus basal to the diaphragm. In the thoracic vertebrae, the anaphyses are short, anteriorly elongated transverse processes, the latter reminiscent of those found in extinct sloths.

**GAUDIN: GEOLOGY**
anapophyses are relatively deep in the thoracic vertebrae, but are oriented more dorsally than among unequivocal xenarthrans. The anapophysse of the lumbar vertebrae are not illustrated in lateral view, and the width of the zygaphyseal facets in Ermanodon is unclear. They are described as "oval" in the anterior thoracic vertebrae, increasing in size posteriorly (Ding, 1987, p. 92). However, the zygaphyseal joints of the lumbar vertebrae are enlarged, as are those of pholidolphins (Emry, 1970); such a condition is uncommon among true xenarthrans, where enrollment occurs in only a few derived taxa (e.g., Euphractus, Priodontes). There is no evidence of any accessory intervertebral articulations in Ermanodon, be they lateral zygaphyses or xenarthrous joints between anapophysese, metasteses, and transverse processes.

As with the palaeanodonts, the case for strong shared derived similarity between the vertebrae of Ermanodon and undoubted xenarthrans is weak. The most notable resemblances are the enlarged metasteses and anapophysese. However, the former are widespread among living forms, as noted above. The latter differ slightly in their morphology from those of xenarthrans. Moreover, it is not clear that enlarged anapophysese are characteristic of Xenarthra primitively.

Eurotamandua presents the most striking claim for derived resemblance between the vertebrae of undoubted xenarthrans and a non-South American early Cenozoic taxon. As in palaeanodonts and Ermanodon, the vertebrae of Eurotamandua possess large metasteses, beginning three to four vertebrae anterior to the diaphramatic vertebra and extending posteriorly through the lumbar vertebrae (Storch, 1981). Similarly, enlarged anapophysese are present in the diaphramatic region of the vertebrae. Unlike what is found in palaeanodonts and Ermanodon, the anterior thoracic vertebrae of Eurotamandua are more reminiscent of armadillo (but not anteater) vertebrae, with elongated, anteroposteriorly narrow neural spines, broad laminae, and elevated diaphyses. The most remarkable aspect of the vertebral morphology in this genus, however, is the purported possession of true accessory intervertebral articulations.

The diaphramatic vertebra of Eurotamandua, the last thoracic according to Storch (1981), has a large anapophysese that appears to be both dorsal and ventral articular facets. By analogy with unequivocal xenarthrans, the former would represent either a xenarthrous facet between the vertebral bodies, or an anapophysese/metakypophysal xenarthrous facet. The ventral articulation would then represent a xenarthrous joint between the anapophysese and the transverse process of the first lumbar vertebra. Note that a joint between the anapophysese and transverse process is not a primitive characteristic of xenarthrans or anteaters, according to the phylogenetic distribution presented above (Fig. 14). Storch (1981) suggests that less elaborate accessory intervertebral articulations can also be observed between the diaphragmatic and the preceding vertebra, and perhaps even at the next anterior intervertebral junction.

Unfortunately, there remain a number of difficulties that render Storch's (1981) morphological assessments open to question. Several subsequent workers have been unable to verify the presence of the xenarthrous articulations in Eurotamandua (Rose & Emry, 1993; Szalay & Schrenk, 1994). Szalay and Schrenk (1994, p. 48A) state that "xenarthry cannot be corroborated (and not only because of the nature of preservation)."

The lumbar vertebrae, which on the basis of comparison with undoubted xenarthrans would have been expected to show the most well-developed xenarthrous articulations, are preserved with only the dorsalmost portions of the vertebrae exposed. This prevents observation of any lateral accessory joints. In addition, the morphology of the accessory joints themselves, particularly those of the diaphramatic vertebrae, is unusual (Storch, 1981, fig. 8). The two vertebrae anterior to the diaphramatic vertebra have narrow, spine-like anapophysese, very similar to those found in palaeanodonts and unlike anything known in Xenarthra. These anapophysese allegedly articulate with a small concave facet or depression on the pedicle of the succeeding vertebra. This latter facet lies midway between the base of the metamorphosis dorsally and the base of a second process ventrally. The more ventral process apparently carries a facet for the rib tubercle distally, and hence it must represent a ventrally situated diaphysis. This type of articulation, between the anapophysese anteriorly and the metamorphosis and diaphysis posteriorly, is not present in any known xenarthran.

In summary, the case for strong shared derived similarity between the vertebrae of Ermanodon and xenarthrans, as well as for similarities between the vertebrae of undoubted xenarthrans and those of Eurotamandua, rests on few morphological evidence, the paucity of available material, and the paucity of comparisons.

Acknowledgments

My thanks go first to those who so skillfully ext
In summary, the case for derived resemblance between the vertebrae of *Eurotamandua* and undoubted xenarthrans remains less than compelling. Like palaeanodonts and *Eranodon, Eurotamandua* does possess enlarged metaphyses and anapophyses, but these are of equivocal phylogenetic utility. The width of the zygopophyses in *Eurotamandua* cannot be assessed from the published descriptions and figures. Storch (1981) claims that accessory intervertebral articulations are present, including a possible lateral zygopophyseal joint and xenarthran joints between the anapophysis and metaphysis, the anapophysis and transverse process, and the anapophysis/metakopophysis and diapophysis. However, the latter joint is unknown in undoubted xenarthrans, and the presence of all such joints has been questioned by subsequent workers.

On the basis of vertebral morphology, there is at present little evidence that would clearly suggest a close phylogenetic relationship between true xenarthrans and palaeanodonts, *Eranodon*, or *Eurotamandua*. Assessment of the vertebral morphology in the latter two taxa is hindered by the paucity of available material and the incomplete preservation of the existing material. More complete information on the vertebral column of either *Eranodon* or *Eurotamandua* (in particular the latter) would allow a more reliable assessment to be made of their potential ties with Xenarthra. Good material is available for Eocene and Oligocene palaeanodonts. The Paleocene material in this group is still poorly known, and thus it is difficult to arrive at a more complete understanding of any phylogenetic link between this group and the Xenarthra. In light of the present study, it is possible that restudy of the younger palaeanodont material, focusing in particular on the morphology of the zygopophyses, might yield additional derived characteristics linking xenarthrans and palaeanodonts. For now, however, these early Cenozoic taxa provide little help in elucidating the evolutionary history of the peculiar intervertebral articulations that characterize Xenarthra. Our best guide to understanding the structural evolution of xenarthran vertebrae would appear to be continued study of the functional, ontogenetic, and phylogenetic history of these articulations among the xenarthrans themselves.

Acknowledgments

My thanks go first and foremost to Julia Scott, who so skillfully executed all the artistic renditions in this report. For providing access to specimens under their care, including the loan of the figured specimens, I am grateful to Larry Heaney, Bruce Patterson, and Bill Stanley of the Division of Mammals, Field Museum of Natural History, and John Flynn and Bill Simpson of the Department of Geology, Field Museum of Natural History. I thank Gerry DeFlevis, Laura Panko, and two anonymous reviewers for their comments on an earlier draft of this manuscript. The research on which this report is based was supported by a UC Foundation Faculty Research Grant from the University of Tennessee at Chattanooga.

**Literature Cited**


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FIELDIANA: GEOLOGY


**APPENDIX TABLE 1. Summary of Morphological Data**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. of TV</th>
<th>No. of LV</th>
<th>Diaphragmatic vertebra</th>
<th>MP</th>
<th>AP</th>
<th>Spinal nerves</th>
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<tr>
<td><em>Zaedyus pichiy</em> FMMH 23809, 104817</td>
<td>11</td>
<td>3</td>
<td>T7, T7-L3 (104817)</td>
<td>T6-L3</td>
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<td>Ventral branch: intervertebral foramina between pedicles of successive vertebrae, T1 and T2, T11-L3; within pedicles, T3-T10. Dorsal branch: in lamina between ap and dp, T3-T10; medial to ap, T11-L3.</td>
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<td><em>Chaetophractus villosus</em> FMMH 60467, 122023, 134611</td>
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<td>T3-L4</td>
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<td>Ventral branch: within pedicle, T1-T10; intervertebral foramina, T11-L4. Dorsal branch: perforates lamina, T2-T4; perforates ap, T3-T10 (two holes in T7-T9); medial to ap, T11-L4.</td>
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<tr>
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<td>T4-L3</td>
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<td>Ventral branch: within pedicle, T1-T10; intervertebral foramina, T11-L3. Dorsal branch: perforates lamina, T3-T7; perforates ap, T8-T10; medial to ap, T11-L3.</td>
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<td><em>Tolypeutes matacus</em> FMMH 121540, 124568 (juv.), 124569 (juv.), 124570, 153773</td>
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<td>3</td>
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<td>T13-L2</td>
<td>Spinal nerves emerge through typical intervertebral foramina</td>
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<td>T13-L2</td>
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<td>16</td>
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<td>T1-L2</td>
<td>T13-L2</td>
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<td><em>Bradyus variegatus</em> FMMH 68919, 69589</td>
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<td>T15-L3</td>
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<tr>
<td><em>Choleoepus hoffmani</em> FMMH 127421 (juv.), 127422, 147993</td>
<td>23</td>
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<td>T21, T21-L3</td>
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<td><em>Hapalopus sp.</em> FMMH P13133, P13145, P13146, P15318</td>
<td>21-22</td>
<td>3</td>
<td>T19, T19-L3</td>
<td>T1-L3</td>
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ALZ or alz = anterior lateral zygapophyseal facet; AMZ or amz = anterior medial zygapophyseal facet; AP or ap = anapophysis; AX = anterior xeromorphic facet; dp = diapophysis; (l) = left side only; L1, L2, L3 = first lumbar vertebra, second lumbar vertebra, third lumbar vertebra, etc.; LV = lumbar vertebra; MP or mp = metapophysis; PLZ or plz = posterior lateral zygapophyseal facet; PMZ or pmz = posterior medial zygapophyseal facet; PX = posterior xeromorphic facet; (r) = right side only; S1, S2 = first sacral vertebra, second sacral vertebra, etc.; TI, T2 = first thoracic vertebra, second thoracic vertebra, etc.; tp = transverse process; TV = thoracic vertebrae.

* Information in table derived from this specimen, except for thoracic and lumbar vertebral counts.

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<th>PMZ and PLZ</th>
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<th>PX</th>
<th>Notes</th>
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<td>T2–L3</td>
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<td>Opisthocoelus centra, T1–T9; rib head articulates between</td>
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<td>pmz abuts plz</td>
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<td></td>
<td></td>
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<td>T3(r)/T4(l)–L4</td>
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<td></td>
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<td></td>
<td>from L3–L5; dorsal tp:</td>
<td>ap (for rib): T8–T10;</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>L1–L5</td>
<td>ventral ap: T11–L4</td>
<td></td>
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</tr>
<tr>
<td><em>Euphractus sexcinctus</em></td>
<td>T5–L4</td>
<td>T4–L3</td>
<td>Ventral mp: T7–L4,</td>
<td>Dorsal ap: T6–L3,</td>
<td>L4 fused to S1; medial zygaphyses enrolled as in</td>
</tr>
<tr>
<td>FMNH 152051</td>
<td>amnz abuts alz</td>
<td>pmz abuts plz</td>
<td>confluent with alz</td>
<td>confluent with plz</td>
<td>pangolins; opisthocoelus centra; rib head as <em>Zaedus</em></td>
</tr>
<tr>
<td></td>
<td>from T5–T9</td>
<td>from T4–T8</td>
<td>from T9–L4; dorsal tp:</td>
<td>from T8–L3; lateral</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>L1–L4</td>
<td>ap (for rib): T8–T10;</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ventral ap: T11–L4</td>
<td></td>
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<tr>
<td><em>Teothereutes matacus</em></td>
<td>T9–S1</td>
<td>T8–L4</td>
<td>Ventral mp: T7(r)/T8(l)–</td>
<td>Dorsal ap: T6(r)/T7</td>
<td>Rib head as <em>Zaedus</em></td>
</tr>
<tr>
<td>(juv.)</td>
<td></td>
<td></td>
<td>S1, confluent with alz</td>
<td>(l)–L4, confluent</td>
<td></td>
</tr>
<tr>
<td>FMNH 124569</td>
<td></td>
<td></td>
<td>with plz in LV</td>
<td>with plz in LV;</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ventral ap (for thoracic, lumbar, and sacral ribs): T11–L4</td>
<td></td>
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</tr>
<tr>
<td><em>Tamaquella mexicana</em></td>
<td>T14–S1</td>
<td>T13–L2</td>
<td>Ventral mp: T14–S1,</td>
<td>Dorsal ap: T13–L2,</td>
<td>Rib head articulates exclusively with anterior centrum;</td>
</tr>
<tr>
<td>FMNH 69597</td>
<td></td>
<td></td>
<td>confluent with alz</td>
<td>confluent with plz</td>
<td>neural spines robust, uniform height; anterior zygaphyses</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>in all; dorsal sacral rib: S1</td>
<td>in all; ventral ap: L2</td>
<td>separated by midline notch; thoracic zygaphyses wide,</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>extending lateral to centrum</td>
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</tr>
<tr>
<td><em>Cyclopse didactylus</em></td>
<td>T15–S1</td>
<td>T14–L2</td>
<td>Ventral mp: T13–S1,</td>
<td>Dorsal lamina: T12–T13; dorsal ap: T14–L2</td>
<td>Rib head, neural spines, zygaphyses as *Tamaqua-</td>
</tr>
<tr>
<td>FMNH 69569</td>
<td></td>
<td></td>
<td>confluent with alz</td>
<td></td>
<td>lla*</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>in all</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bradyrus variabilis</em></td>
<td>L2–S1</td>
<td>L1–L3</td>
<td>Absent</td>
<td>Absent</td>
<td>Rib head articulates between posterior centrum and ante-</td>
</tr>
<tr>
<td>FMNH 69589</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>rior pedicel; all vertebral processes reduced; neural</td>
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<td></td>
<td></td>
<td></td>
<td>spines uniform height; anterior zygaphyses separated by</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>midline notch</td>
</tr>
</tbody>
</table>

*physeal facet; AP or ap L2, L3 = first lumbar r mp = metaphyseal; L2, L3 = first lumbar vertebra, etc.; T1, T2 vertebrae.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>AMZ and ALZ</th>
<th>PMZ and PLZ</th>
<th>AX</th>
<th>PX</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Choleopus hoffmani</em></td>
<td>S1 (r)</td>
<td>L3 (r)</td>
<td>Absent</td>
<td>Absent</td>
<td>Vertebral processes as in <em>Bradytus</em>; anterior zygopophyses separated by midline notch as in <em>Bradytus</em></td>
</tr>
<tr>
<td>FMNH 147993</td>
<td>T20–S1</td>
<td>T19–L3</td>
<td>P13146 only—ventral mp; L1 (right side only), L3</td>
<td>P13146 only—dorsal ap; T22 (right side only), L2</td>
<td>Rib head, neural spines as <em>Tamandua</em>; zygopophyses of anterior thoracics very wide, extending lateral to centrum; anterior zygopophyses separated by narrow midline notch</td>
</tr>
</tbody>
</table>

1 From T7–T9, the lateral zygopophyseal facet is divided in two in this specimen. The “lateral” lateral zygopophyseal facet articulates with the medial surface of the anapophysis of the preceding vertebra.