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The Morphology of Xenarthrous Vertebrae (Mammalia: Xenarthra)

Timothy J. Gaudin

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The Morphology of Xenarthrous Vertebrae (Mammalia: Xenarthra)

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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 (Palaeandonta, *Ernanodon*, and *Eurotamandua*) 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 Palaeandonta, *Ernanodon*, and *Eurotamandua* revealed few resemblances to undoubted 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 palaeandonts, *Ernanodon*, or *Eurotamandua*.

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-

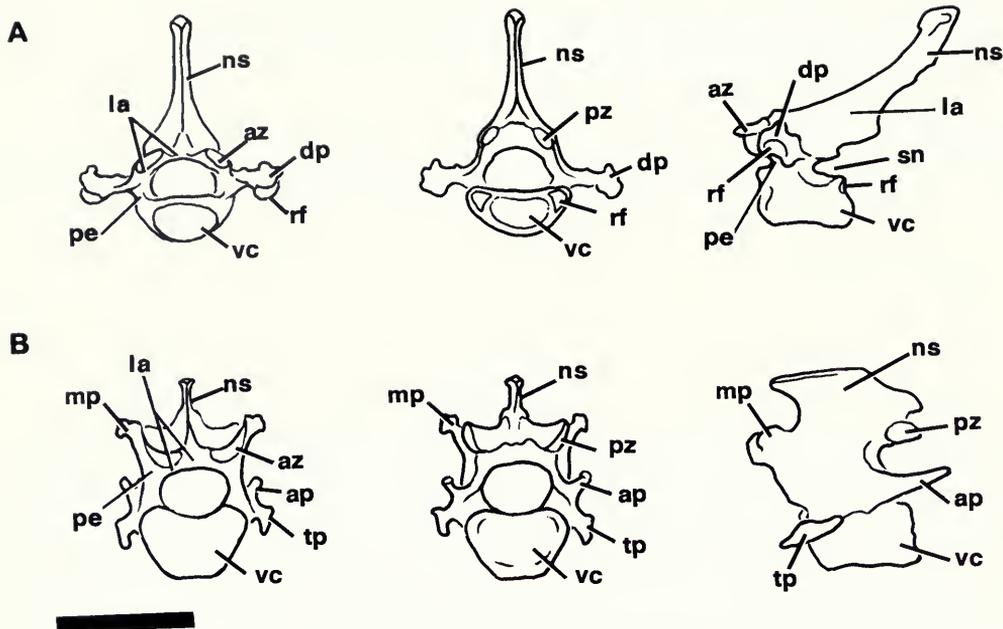


FIG. 1. *Mephitis mephitis*, UTCM 521: thoracic and lumbar vertebrae shown in anterior, posterior and left lateral views (proceeding left to right). A, T4, B, L3. Scale bar = 1 cm. Abbreviations: ap, anapophysis; az, anterior zygapophyseal facets; dp, diapophysis; la, lamina; mp, metapophysis; ns, neural spine; pe, pedicel; pz, posterior zygapophyseal facet; rf, rib facet; sn, notch for emergence of spinal nerve; tp, transverse process; vc, vertebral centrum.

ticular 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 "xenarthrales," are well developed in xenarthrans that span a wide range of locomotory habits, including a subterranean armadillo (*Chlamyphorus*), fossorial armadillos and anteaters (e.g., *Dasybus*, *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. Xenarthrales 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 xenarthrous 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 xenarthrales has been used as a "litmus test" for determining phylogenetic relatedness to the Xenarthra. The pangolins and armadillos were originally included with xenarthrans under the taxonomic grouping Edentata, but they were subsequently removed to separate orders largely because they lacked xenarthrales (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 Xenarthra on the basis of "incipient" development of xenarthrales. These include the Palaeodonta (Simpson, 1931), a group known from Paleocene to Oligocene deposits of North America and Europe, and *Ernanodon* (Ding, 1987), a Late Paleocene genus from China. Both *Ernanodon* and the palaeodont *Metacheiromys* have enlarged anapophyses in the posterior dorsal vertebrae. Similarly enlarged anapophyses can be

found, however, among a number of unrelated groups of mammals, e.g., felids and geomyid rodents (Rose & Emry, 1993). Hence such processes are not necessarily structural antecedents of true xenarthrous articulations. The purported Middle Eocene anteater *Eurotamandua*, from the Messel fauna of Germany, allegedly possesses true xenarthrous articulations (Storch, 1981). Unfortunately, several subsequent authors have been unable to verify the presence of accessory intervertebral articulations in this taxon (Rose & Emry, 1993; Szalay & Schrenk, 1994). Novacek and his colleagues (Novacek, 1986; Novacek & Wyss, 1986; Novacek et al., 1988) resurrected the taxonomic grouping Edentata, including pangolins, palaeonodonts, and xenarthrans, 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 xenarthrales may be overemphasized.

Part of the difficulty in determining the phylogenetic significance of xenarthrales, and in identifying xenarthrales or incipient xenarthrales in early Cenozoic taxa potentially allied to Xenarthra, lies in the fact that the morphology of these articulations among unquestioned 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)¹ wrote the first brief description of such joints. They were not formally named, however, until Gill (1886, p. 66)² coined the term "xenarthral" (Gk., *xenos* = "strange," *arthron* = "joint") in order to distinguish xenarthran vertebrae from normal, "nomarthral" vertebrae. Simpson (1931, 1948) used the adjective "xenarthrous" 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 & Emry, 1993). The joints have also been referred to by the noun "xenarthrales" (e.g., Frechkop, 1949; Grassé, 1955; Hoffstetter, 1958; DeBlase & Martin, 1981; Storch 1981),³ and the condition of possessing such joints has been termed "xenarthry" (e.g., Lessertisseur & Saban, 1967; Hoffstetter, 1982; Novacek & Wyss, 1986). The first detailed morphological description of xenarthrous 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 anterior-most 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 xenarthrous articulations along the whole length of the vertebral column, but only in the vermilinguan *Myrmecophaga* (Flower, 1885). He also briefly summarized the form of the xenarthrous facets in the sloth genus *Bradypus*. Interestingly, Flower differed from Owen in deciding which facets to designate as the normal zygapophyseal facets and which to designate as supplementary. Owen (1851a) consistently recognized the medialmost pair of intervertebral facets, those lying medial to the metapophyses, as the normal zygapophyseal facets. Flower (1885, figs. 22–24) designated a set of facets lying lateral to the metapophyses as the homologues of the typical mammalian zygapophyses.

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

¹ Curiously, the joints are not described in a contemporaneous edition of Cuvier's *Recherches sur les ossements fossiles*, where, e.g., the vertebrae of the anteater *Myrmecophaga* are described as "unremarkable" (Cuvier, 1836b, p. 208).

² Glass (1985) 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 Ineducabilia, a group including the Bruta (= Xenarthra + Pholidota + Tubulidentata). Vertebral morphology is not mentioned in the ordinal level description of Bruta.

³ Gaudin and Biewener (1992) and Gaudin (1993) refer to the joints as "xenarthrae," a term which I had assumed was standard usage. Unfortunately, I can now find no historical source for the term. Although I do not believe I invented the term, I have chosen to abandon it for the apparently more widely used "xenarthrales."

dially is followed by Hoffstetter (1958, 1982), Lessertisseur and Saban (1967), and Gaudin and Biewener (1992). Jenkins (1970) notes that in *Tamandua* the distinct facets designated as “zygapophyses” by Owen (1851a) and Flower (1885) are distinct only in the lumbar vertebrae. In the posterior thoracic vertebrae, the medial and lateral facets become confluent.

The problem of identifying which facets are xenarthrous and which represent the typical mammalian zygapophyseal facets is exacerbated by variability in the number and form of the intervertebral joints among xenarthrans and by the lack of any modern comprehensive study of the problem. It is known that in some living xenarthrans, e.g., the giant armadillo *Priodontes*, there are as many as six pairs of intervertebral articulations (Grassé, 1955; see below). In others the number of facets is reduced, so that in many ground sloths, e.g., *Hapalops*, there are only two pairs of intervertebral facets, one set of zygapophyses, and one set of supplementary joints (Scott, 1903–1904; see below). This variability has gone largely unnoticed, as most modern studies that make any mention of the morphology of xenarthrales illustrate only a single joint in a single species, and describe this joint in a few brief sentences (Grassé, 1955; Hoffstetter, 1958, 1982; Vaughn, 1986; Gaudin & Biewener, 1992). Jenkins (1970) describes regional variation in the morphology of xenarthrales, but only in *Tamandua tetradactyla*.

Finally, the problem of the origin of xenarthrales has been inadequately treated in the literature. Gaudin and Biewener (1992), Gaudin (1993), and Gaudin and Fortin (unpubl. data) considered the functional reasons for the evolution of these facets but did not address their actual structural antecedents. MacPhee (1994, p. 174) suggested that the facets arose through the “sacralization” of the lumbar and posterior thoracic vertebrae, but he noted the paucity of evidence to substantiate this claim. To date no study has examined the structural origin of xenarthrales from either a developmental or paleontological perspective.

The present study reexamines the morphology of xenarthrous vertebrae throughout the Xenarthra. Following Owen (1851a), both regional intraspecific variation and interspecific variation across the various xenarthran suborders are addressed. Nearly all of the extant xenarthran genera have been examined in detail, as well as the fossil genera housed in the Field Museum of Natural History (FMNH) collections, plus an assortment of

ground sloth genera from other North American museums. The descriptions provided below, however, will focus on five representative taxa: the extant armadillos *Zaedyus* and *Tolypeutes*, the extant anteater *Tamandua*, the extant 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 Xenarthra.

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. p. caurinus*, FMNH 104817 (Figs. 2A, 3A, 4A–D). It should be noted at the outset that vertebrae are bilaterally symmetrical structures. Nearly all of

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) euphractan 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 anterior thoracic vertebrae of extant euphractans are very similar to those of other mammals, with small, depressed centra and elongated, posteriorly inclined neural spines (Fig. 1; see also Slijper, 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 euphractans 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 *Zaedyus* such functionally

opisthocoelous centra are found in all thoracic vertebrae except the last two.

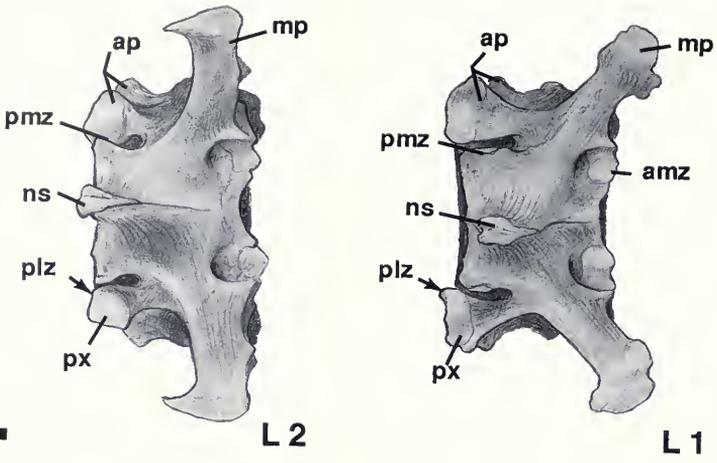
The pedicels of the anterior thoracic vertebrae are extremely low and broad anteroposteriorly. Beginning with the third thoracic vertebra, these long, low pedicels occlude the intervertebral foramina from which the spinal nerves typically emerge. Hence the neural arch of each thoracic vertebra from T3 through T10 is perforated by two foramina: one for the ventral branch of each spinal nerve, perforating the pedicel itself, and one for the dorsal branch of each spinal nerve, perforating the lamina of the vertebra just behind the root of the diapophysis (Fig. 4B). The latter process is much higher in euphractans than is typical for mammals; this is due at least in part to the vertically depressed nature of the neural arch. The articular facet for the head of the rib is likewise more dorsally situated. It lies between the anterodorsolateral part of the vertebral centrum and the posterolateral surface of the pedicel of the preceding vertebra.

Finally, the zygapophyseal facets of the anterior thoracic vertebrae are unusual in certain respects. The anterior zygapophysis bears a typical flat, ovate facet situated immediately to one side of the midline. The long axis of this facet runs anteroposteriorly, and the facet faces dorsally. The anterior zygapophyseal facet articulates with a similar ventrally directed facet on the underside of the lamina of the preceding vertebra. Both the anterior and posterior zygapophyseal facets, however, are contiguous or confluent with a second set of facets laterally (Figs. 2A, 3A). These atypical lateral zygapophyseal articulations are also flat and ovate, but with their long axes oriented transversely. Their presence dramatically widens the zygapophyseal articular surface. The anterior lateral zygapophyseal facet faces dorsally and slightly laterally. It articulates with a ventrally facing facet borne on the underside of a rudimentary anapophysis (or accessory process) that projects posteriorly from the root of the diapophysis (Fig. 3A). The anterior and posterior lateral zygapophyseal facets are present in all euphractan

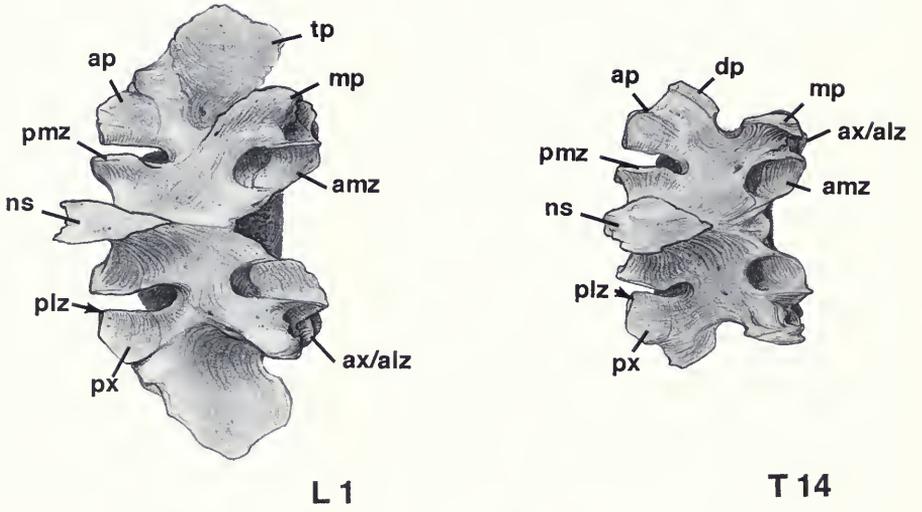
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FIG. 2. Thoracic and lumbar vertebrae shown in dorsal view. **A**, *Zaedyus pichiy caurinus*, FMNH 104817—T6, T7, T8, L1, L2, proceeding from right to left. **B**, *Tamandua mexicana*, FMNH 69597—T12, T13, T14, L1, proceeding from right to left. **C**, *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 zygapophyseal facet; amz, anterior medial zygapophyseal facet; ax, anterior xenarthrous facet; ax/alz, fused anterior lateral zygapophyseal facet and anterior xenarthrous facet; **D**, diaphragmatic vertebra; plz, posterior lateral zygapophyseal facet; pmz, posterior medial zygapophyseal facet; px, posterior xenarthrous facet.

A



B



C

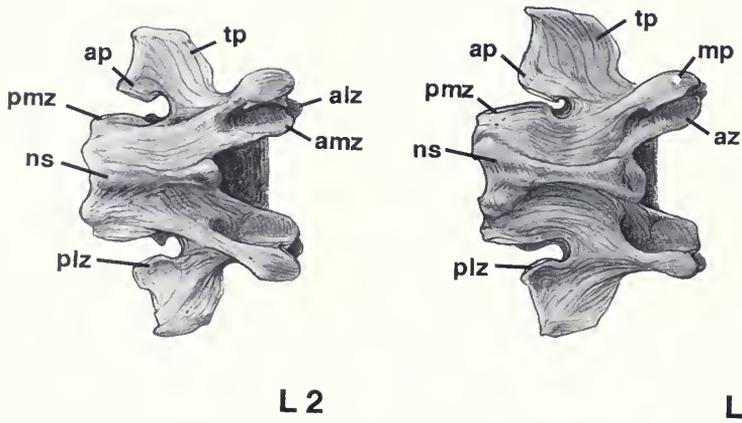
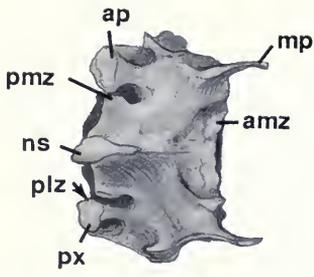
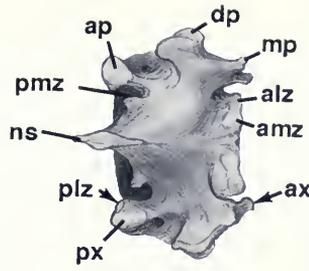


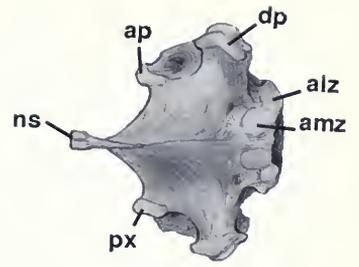
FIG. 2.



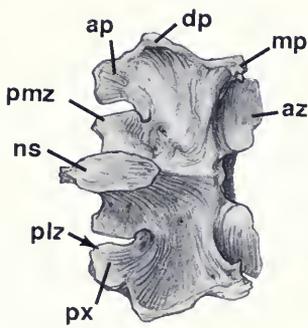
T 8



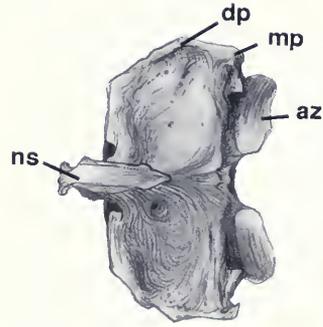
T 7 (D)



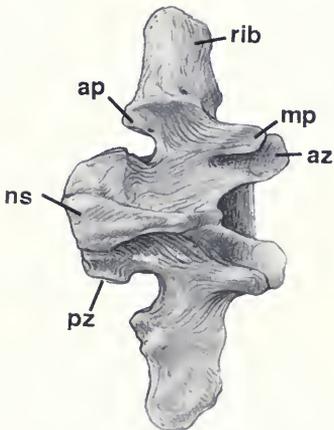
T 6



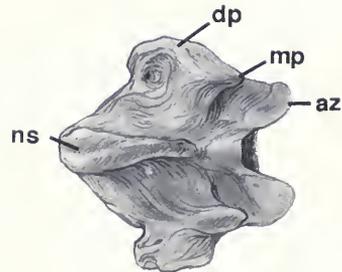
T 13 (D)



T 12



T 15 (D)



T 14

FIG. 2. Continued.

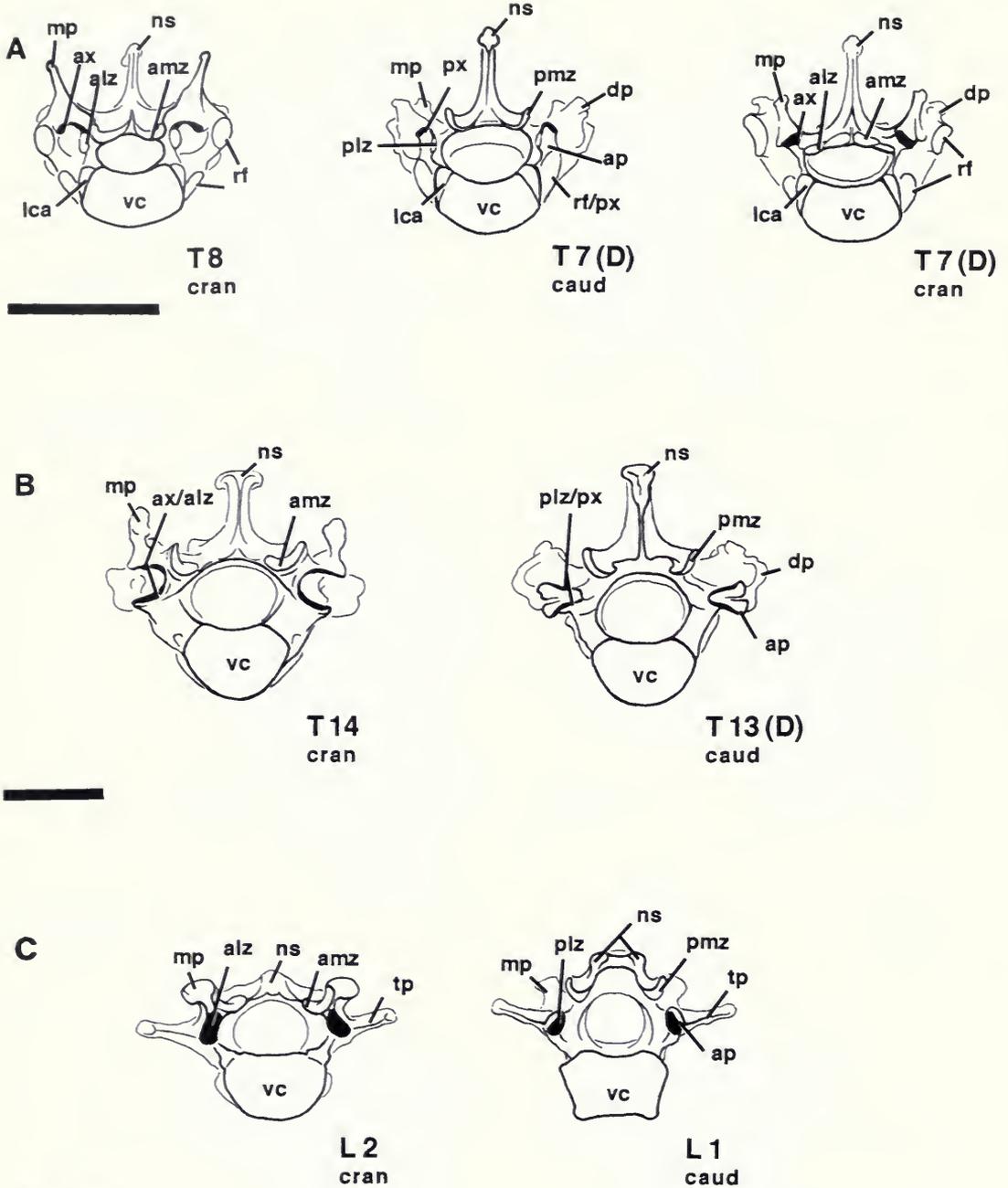
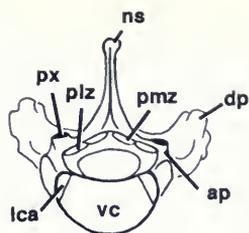
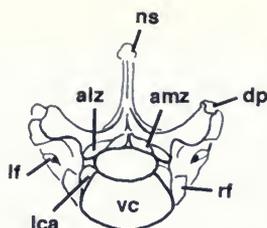


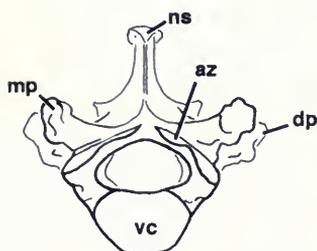
FIG. 3. Thoracic and lumbar vertebrae shown in cranial and caudal views. **A**, *Zaedyus pichiy caurinus*, FMNH 104817—T6 (cran.), T6 (caud.), T7 (cran.), T7 (caud.), T8, (cran.), proceeding from right to left. **B**, *Tamandua mexicana*, FMNH 69597—T12 (caud.), T13 (cran.), T13 (caud.), T14 (cran.), proceeding from right to left. **C**, *Bradypus variegatus*, FMNH 69589—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; rf/px, fused rib facet and posterior xenarthrous facet.



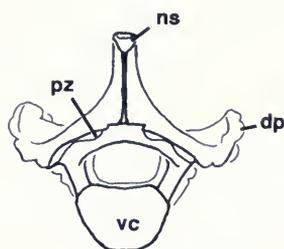
T6
caud



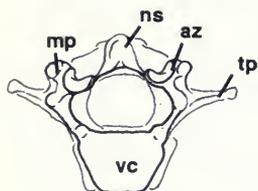
T6
cran



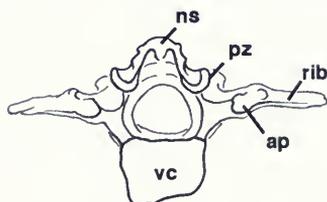
T13 (D)
cran



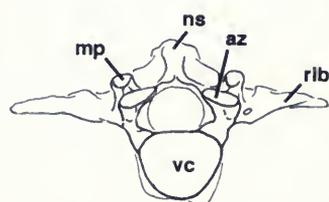
T12
caud



L 1
cran



T15 (D)
caud



T15 (D)
cran

FIG. 3. Continued.

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 Slijper (1946) as that in which the anterior zygapophyseal facets are

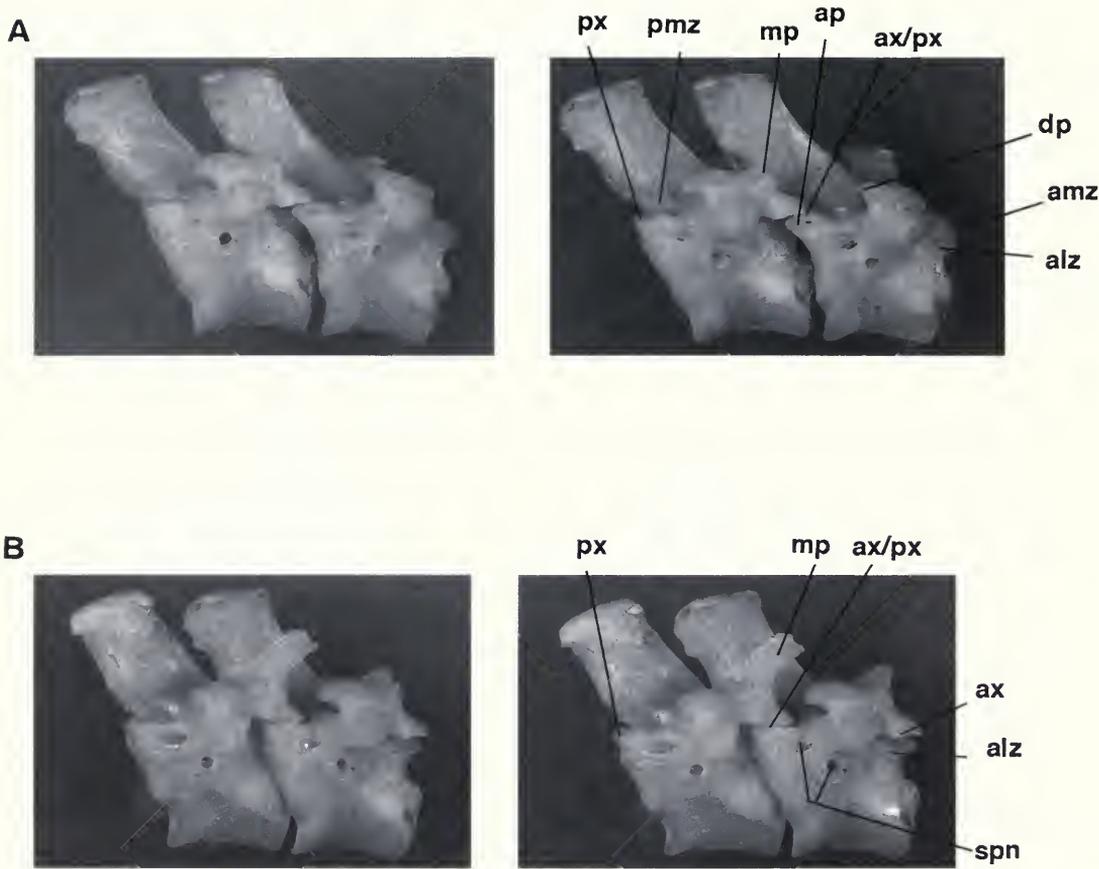


FIG. 4. *Zaedyus pichiy caurinus*. FMNH 104817: thoracic and lumbar vertebrae shown in right lateral view. **A**, stereophotographs of T6 and T7. **B**, stereophotographs of T7 and T8. **C**, T8 and T9. **D**, T11 and L1. Scale bar = 1 cm. Abbreviations as in Figures 1 and 2, plus ax/px, xenarthrous intervertebral joint; ax 1/alz, fused anterior lateral zygapophyseal facet and anterior xenarthrous facet; ax 2/px 2, xenarthrous intervertebral joint between secondary anterior and posterior xenarthrous facets; px 1/plz, fused posterior lateral zygapophyseal facet and posterior xenarthrous facet; px 2, secondary posterior xenarthrous facet; spn, foramen/foramina for spinal nerve roots.

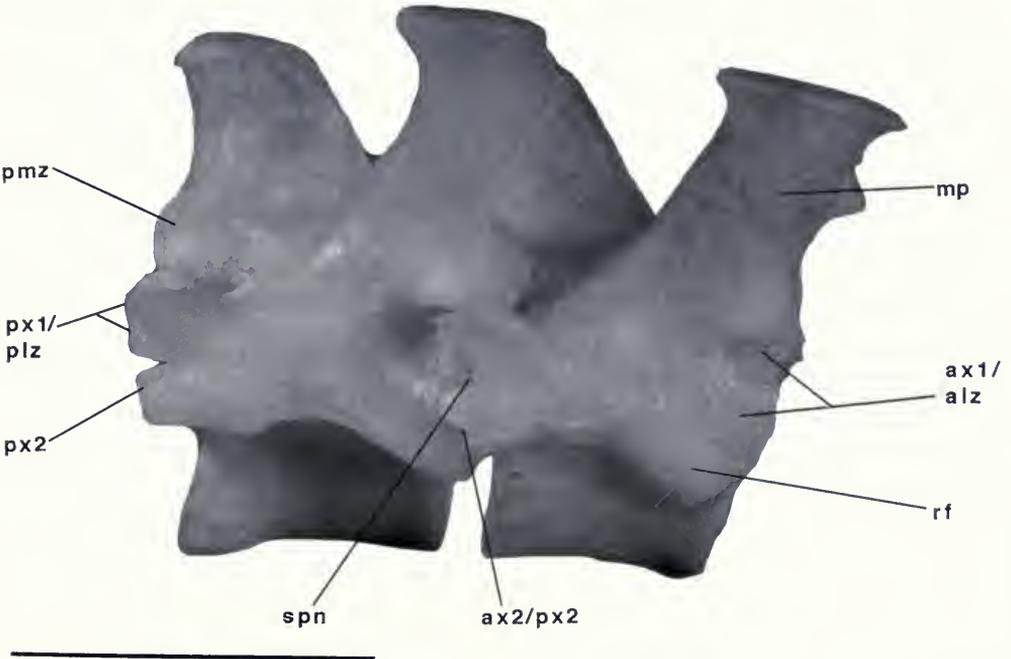
horizontally oriented and the posterior zygapophyseal facets are roughly vertical. T7 is the anteriormost vertebra to bear a distinct, although small, metapophysis. The metapophyses become progressively elongated posteriorly (Figs. 2A, 4B–D). By the ninth thoracic vertebra, the metapophysis is as long 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 zygapophyseal 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 zygapophyseal facet into medial and lateral components.

The portion of the anterior zygapophyseal facet that is medial to the base of the metapophysis (i.e., the anterior median zygapophysis) strongly resembles the postdiaphragmatic anterior zygapophyseal facets of other mammals (Pick & Howden, 1977; Walker & Homberger, 1992) and is homologized with these facets by Owen (1851a) and others (Hoffstetter 1958, 1982; Lesertisseur & 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

C



D



convex, ventrolaterally oriented facet on the posterior edge of the lamina of T7 (Fig. 3A).

The portion of the zygapophyseal facet lateral to the base of the metapophysis in T8 is similar in position to the lateral anterior zygapophyseal

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 third intervertebral facet on its dorsomedial edge (Fig. 3A). The third facet, also positioned lateral to the

base of the metapophysis, is nearly identical to the anterior xenarthrous facet on T7. It is situated on the ventral surface of a small anterior projection at the base of the metapophysis (Figs. 3A, 4B). The facet faces primarily ventrally, although it bears a concave medial lappet that extends onto the lamina and faces laterally. The two facets lateral to the metapophysis articulate with the anapophysis of T7, forming the medial wall of a deep pocket that receives the anapophysis in mortise and tenon fashion (Figs. 3A, 4B). The anapophysis on T7 bears a convex dorsal facet, the xenarthrous facet, as well as a flat, ventromedially oriented facet that appears to be the serial homologue of the lateral posterior zygapophyseal facet of T6. Unlike T6, however, this lateral posterior zygapophyseal facet is not in contact with the medial posterior zygapophyseal facet. Rather, the two are divided by a distinct notch (Figs. 2A, 3A).

Because of its apparent serial homology with portions of the more anterior zygapophyseal facets, I have not applied the term "xenarthrous" to the distinct lateral zygapophyseal articulation of T7/T8 and more posterior vertebrae in *Zaedyus* and other euphractans (as well as other xenarthrans described below). Rather, in order to enhance precision and avoid confusion, I will restrict the term "xenarthrous articulation" to those accessory intervertebral joints that are clearly distinct from the zygapophyseal system of facets. It should be noted that this usage differs markedly from that of most previous authors, who identify a single set of "normal" zygapophyseal facets, either medial or lateral, and then several sets of "xenarthrous" facets (Owen, 1851a; Flower, 1885; Grassé, 1955; Hoffstetter, 1958, 1982; Lesertisseur & Saban, 1967; Vaughn, 1986; Gaudin & Biewener, 1992; Rose & Emry, 1993). This usage also differs from that of Jenkins (1970), who merely identifies facets as dorsal, ventral, or intermediate pre- and postzygapophyses without distinguishing "normal" from "xenarthrous" facets. I believe there are two sets of "normal" facets in xenarthrans, i.e., facets that can be homologized with zygapophyseal facets in more anterior vertebrae. One set lies medial to the metapophysis, the other lateral. Previous authors disagree on which set is normal because they assume that only one set can be normal. I believe that in addition to these two sets of "normal" zygapophyseal facets, xenarthrans possess extra "xenarthrous" facets that lack serial homologues in more anterior vertebrae.

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 xenarthrous facet, are confluent (Fig. 3A). The lateral zygapophyseal and xenarthrous 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 metapophysis, representing the medial zygapophyseal joint, and one lateral to the base of the metapophysis, representing the conjoined lateral zygapophyseal and xenarthrous joints.⁴

The intervertebral joint between T11 and L1 differs from the T10/T11 intervertebral joint in a number of important respects. The diapophysis, which is progressively reduced posteriorly beginning with T8 (Fig. 4A–C), is rudimentary on T11 (Fig. 4D). Concomitant with the reduction of the diapophysis, the foramen for the dorsal branch of the spinal nerve, which lies between the diapophysis 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 nearly 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 *Chaetophractus* a similar dorsal articulation on the ultimate thoracic vertebra contains two facets, a lateral zygapophysis and a xenarthrous facet (see footnote 4). In *Zaedyus* and *Euphractus*, these facets are fused. As in more anterior xenar-

⁴ The point at which the lateral facets fuse in euphractans is somewhat variable. In *Euphractus*, the two facets are never separate. In *Chaetophractus*, however, they remain separate all the way back to the second lumbar vertebra. Moreover, in the latter genus the lateral zygapophysis is split into two facets starting at T7. These two lateral zygapophyseal facets remain separate until T10. Similar facets have also been observed in adult specimens of *Tolypeutes* (FMNH 121540, 153773).

throus joints, the anapophyseal facet(s) above the spinal nerve contacts the ventrolateral surface of the metapophysis and the lateral surface of the neural arch. The serial homology of the ventral facet below the spinal nerve is more difficult to ascertain. Its articulation posteriorly with the dorsal surface of the transverse process (a pleurapophysis, not parapophysis, *contra* Owen, 1851a; see *Tolypeutes* 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 pedicel. The intervertebral foramen is present in all the lumbar vertebrae. The morphology of the intervertebral articulations is virtually unchanged from T11/L1 to L3/S1.

Tolypeutes matacus (FMNH 124569 [juv.])

This specimen is a neonate. The neural arches are still unfused to the centra. Similarly, the cervical and lumbar ribs remain unfused.⁵ 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 *Tolypeutes*. The FMNH collections include individuals with 11 thoracic and 4 lumbar vertebrae (FMNH 121540, 124570, 153773) as well as individuals with 12 thoracic and 3 lumbar vertebrae (FMNH 122233). Flower (1885) characterizes *Tolypeutes* 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 euphractans *Euphractus* and

Chaetophractus, the giant armadillo *Priodontes*, and in certain extinct genera of mylodontid sloths (Owen, 1842; Stock, 1925).

The anterior thoracic vertebrae of *Tolypeutes* differ somewhat from those of *Zaedyus*. They lack the functionally opisthocoelel centra. Although the pedicels are low and longitudinally elongated, only the ventral spinal foramen is present (Fig. 5A). The dorsal branch of the spinal nerve emerges through a notch between the large diapophysis and the rudimentary anapophysis. Only a single pair of zygapophyseal facets is present, and the zygapophyseal surface is narrower mediolaterally in *Tolypeutes* than in *Zaedyus*, especially in adult specimens.

In FMNH 124569, the diaphragmatic vertebra is T7, and the anteriormost xenarthrous articulation lies between this vertebra and the preceding one, T6. As in *Zaedyus*, this joint is formed between the dorsal surface of a small anapophysis and the ventral surface of the metapophysis, which is rudimentary in this specimen (Fig. 5A). Unlike *Zaedyus*, this xenarthrous joint between T6 and T7 occurs only on the right side of the specimen. The position of this first xenarthrous joint is apparently somewhat variable in *Tolypeutes*. In FMNH 124540, the first xenarthrous 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 xenarthrous joint occurs between T7 and T8.

As was the case with *Zaedyus*, in *Tolypeutes* 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 zygapophyseal 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 surfaces 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 *Zaedyus*, these two joints presumably

⁵ This confirms that the transverse processes of the lumbar vertebrae in adult armadillos (like those of other mammals) are pleurapophyses, i.e., rib attachments of the vertebra plus a fused rib (*contra* Owen, 1851a). The neonatal lumbar vertebrae lack any lateral projections, precluding the possibility that the adult transverse processes are parapophyses, i.e., lateral projections of the vertebra that serve as the site of attachment for the ventral head of two-headed ribs (Wake, 1979; Kardong, 1995).

A**B**

FIG. 5. *Tolypeutes matacus*, 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, 2, and 4, plus lrf, lumbar rib facet.

represent xenarthrous and lateral zygapophyseal articulations.

As occurs in *Zaedyus*, the anapophysis and metapophysis become progressively larger in the more caudal dorsal vertebrae in FMNH 124569. Also, the intervertebral articulations of the tho-

racic 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 anapoph-

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 pedicel 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 pedicels of successive vertebrae are broadly fused lateral to the metapophyses 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 *Tolypeutes* (including FMNH 124569), had not yet developed in FMNH 124568. This suggests that sacral fusion and the development of xenarthrales in the thoracic and lumbar vertebrae are unrelated.

Other Cingulates

The number of dorsal vertebrae is somewhat more variable among dasypodid (*sensu* Engelmann, 1985) armadillos than in euphractans. The total number of dorsal vertebrae varies between 13 and 16. Thoracic counts range from 13 in *Priodontes* (FMNH 25271) to 9 in *Dasypus hybridus* (Flower, 1885). The number of lumbar vertebrae varies from 2 in *Priodontes* (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 mor-

phology 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 *Tolypeutes* 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 posteromedial 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 ventrolateral 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 Engelmann, 1985; Patterson et al., 1989) of the glyptodonts, the pampatheres and eutatine armadillos. In pampatheres 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,

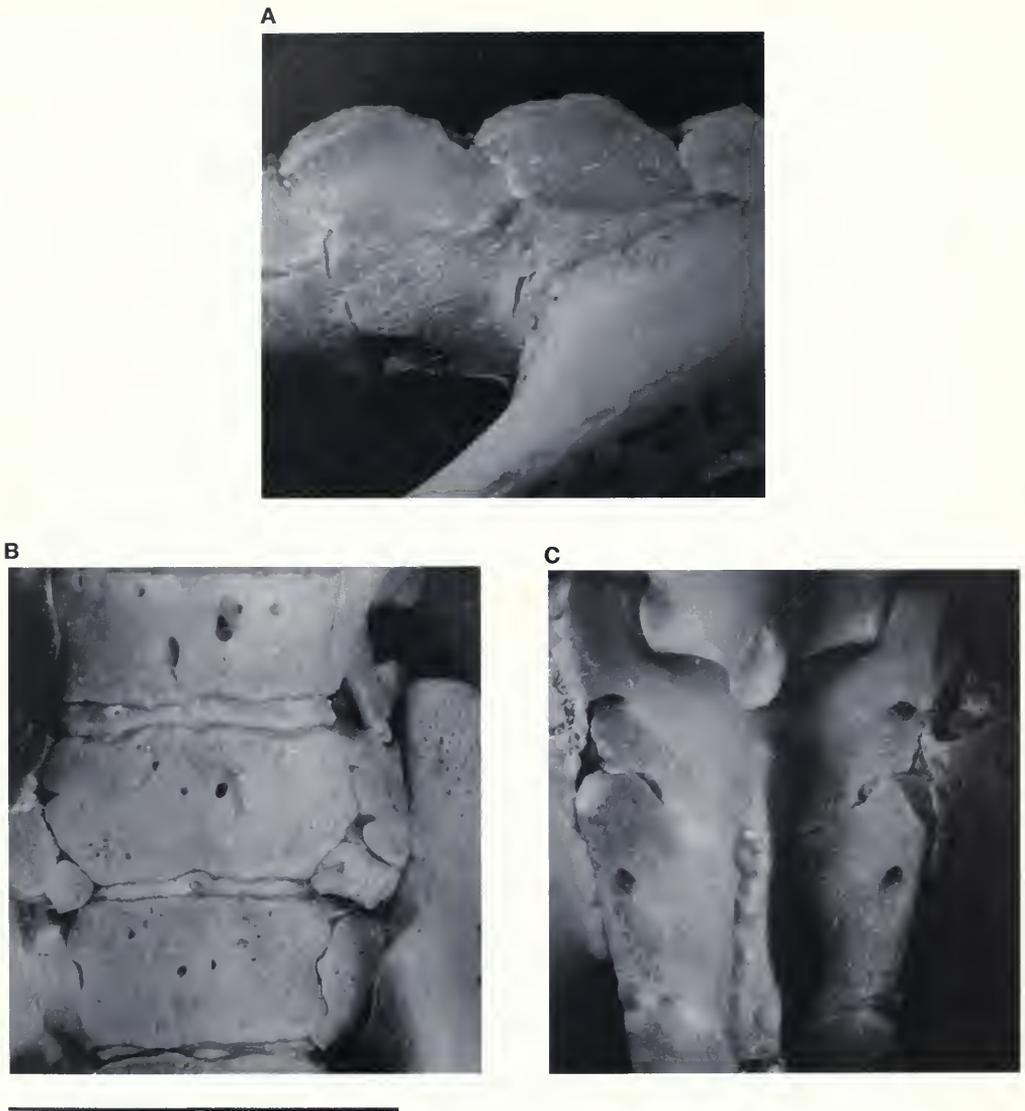


FIG. 6. *Tolypeutes matacus*, FMNH 124569 (juv.). A-C, sacral vertebrae shown in right lateral, ventral, and dorsal views. Scale bar = 1 cm.

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 dia-

phragmatic 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.

Priodontes 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,

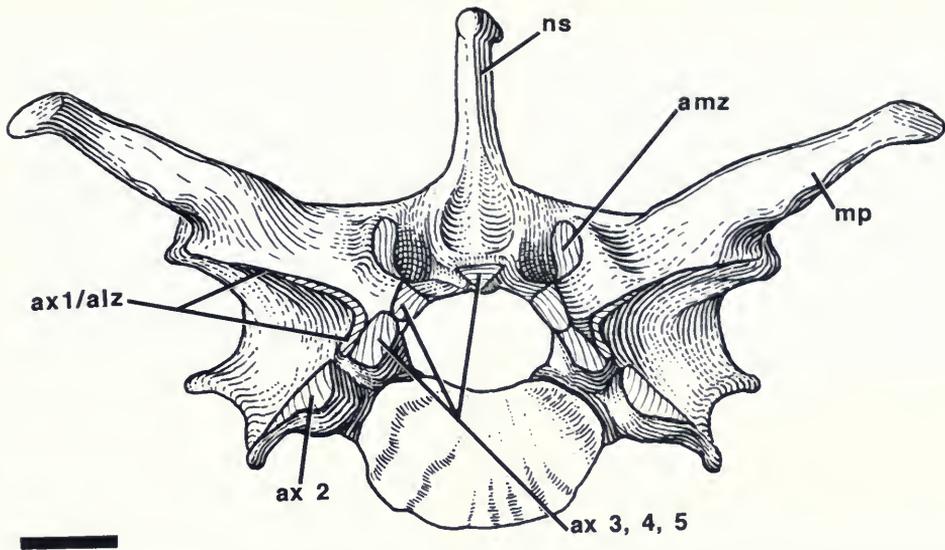


FIG. 7. *Priodontes maximus*, FMNH 25271; first lumbar vertebra shown in cranial view. Scale bar = 1 cm. Abbreviations as in Figures 1, 2, and 4, plus ax 3, 4, 5, third, fourth, and fifth anterior zygopophyseal facets, respectively.

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 zygopophyseal 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 zygopophyseal 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 zygopophyseal facets themselves are quite wide mediolaterally. Indeed, as can be seen in anterior and posterior views (Fig. 3B), the facets extend further 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 metapophyses that increase in size posteriorly. There

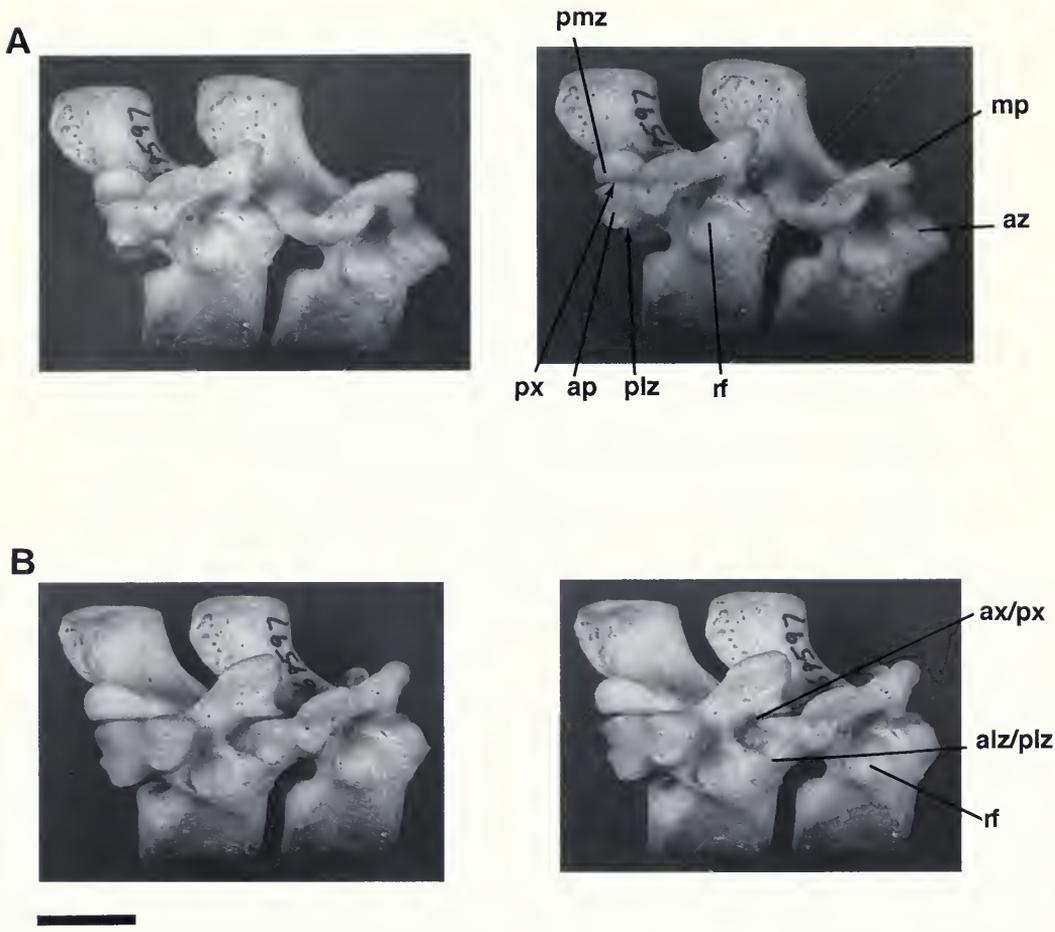


FIG. 8. *Tamandua mexicana*, FMNH 69597: stereophotographs of thoracic vertebrae shown in right lateral view. A, T12 and T13, B, T13 and T14. Scale bar = 1 cm. Abbreviations as in Figures 1, 2, and 4, plus alz/plz, lateral zygapophyseal joint.

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 zygapophysis 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 sep-

arated from the medial zygapophyseal facet by a deep notch, is apparently a lateral zygapophyseal facet (Figs. 3B, 8).

Nearly identical intervertebral articulations occur between the vertebrae caudal to T13/T14. The major morphological changes in these more posterior vertebrae include a gradual increase in the size of the metapophyses and a gradual decrease in size of the diapophyses. Unlike the situation in *Zaedyus*, the anapophyses of the posterior thoracic vertebrae do not articulate with the ribs. It is therefore not surprising that articulations between the anapophyses and transverse processes at T17/L1 and L1/L2 are absent. There is, however, a third pair of intervertebral articulations that forms between L2 and S1. The anapophysis of L2 bears a ventrolaterally directed facet on its lateral edge. It articulates with a dorsomedially oriented facet on the dorsal surface of the sacral rib of S1.

Several early juvenile specimens of *Tamandua* were available, including one very young specimen (FMNH 58545) in which the left and right 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 vertebra 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 metapophysis, 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 articu-

lations. 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 metapophysis 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 metapophyses or vertebral laminae, and thus it bears little resemblance to the xenarthrous connections of the dorsal vertebrae.

Other Vermilinguas

As in 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, 69969, 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 L2 and the sacral rib. More interestingly, rudimentary anapophyses are present in the first prediaphragmatic vertebra (and sometimes in the second), and xenarthrous articulations occur between the diaphragmatic and prediaphragmatic vertebrae. These xenarthrales are formed between the dorsal surface of the rudimentary anapophysis and the ventral surface of an anterior projection of the metapophysis.

Tardigrada

Bradyus variegatus

The vertebral columns of 2 specimens of *Bradyus variegatus* were examined (FMNH 68919,

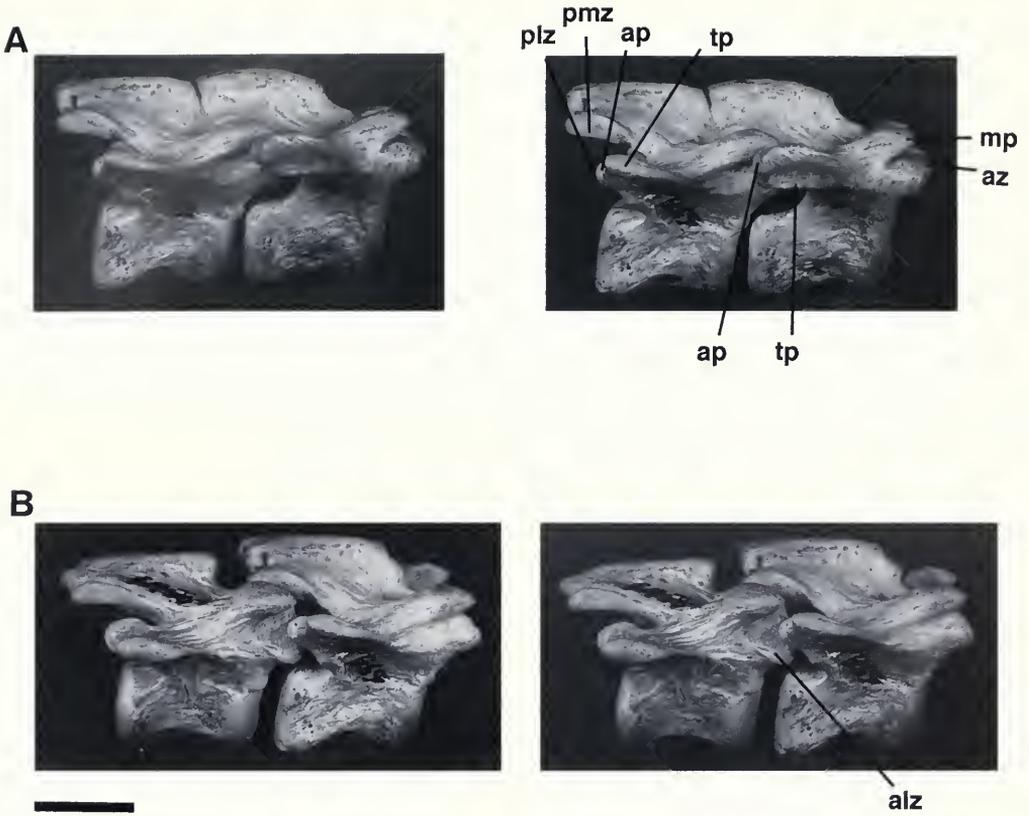


FIG. 9. *Bradypus variegatus*, FMNH 69589. Stereophotographs of thoracic and lumbar vertebrae shown in right lateral view. **A**, T15 and L1. **B**, L1 and L2. Scale bar = 1 cm. Abbreviations as in Figures 1 and 2.

69589). The description below is based primarily on FMNH 69589 (Figs. 2C, 3C, 9), which has 15 thoracic and 3 lumbar vertebrae. The numbers of thoracic and lumbar vertebrae within the genus vary; there are between 14 and 16 thoracic vertebrae and either 3 or 4 lumbar vertebrae (Flower, 1885).

The anterior thoracic vertebrae of *Bradypus* resemble those of anteaters in that the pedicels are tall and narrow and normal intervertebral foramina are present. Similarly, no dramatic difference in the height of the neural spines exists between the anterior and posterior thoracic vertebrae, although the height of the neural spines does gradually diminish posteriorly. The neural spines are much shorter in *Bradypus* than in armadillos and anteaters (Figs. 3C, 9). The rib articulations occur at roughly the same level as was observed in *Tamandua*. The head of the rib articulates between successive vertebrae, as in armadillos but not anteaters. The lower rib facet is shifted somewhat anteriorly relative to that in armadillos, lying on

the posterodorsal edge of the vertebral centrum and the anterior edge of the pedicel of the succeeding vertebra. The zygapophyseal facets of the anterior 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.⁶ The lateral extension of the zygapophyses becomes increasingly prominent in more posterior thoracic vertebrae.

As in *Tamandua*, there is no trace of an anapophysis 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

⁶ 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.

diapophyses, causing the diapophyses 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 diapophysis/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 zygapophyseal 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 zygapophyseal 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 69589. 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 articular facet at 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 supplementary

articulations found in other xenarthrans. The anapophysis of L3 in FMNH 68919 is situated well medially and forms a typical lateral zygapophyseal articulation.

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 P13133, 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 pedicels 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 vertebral 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-

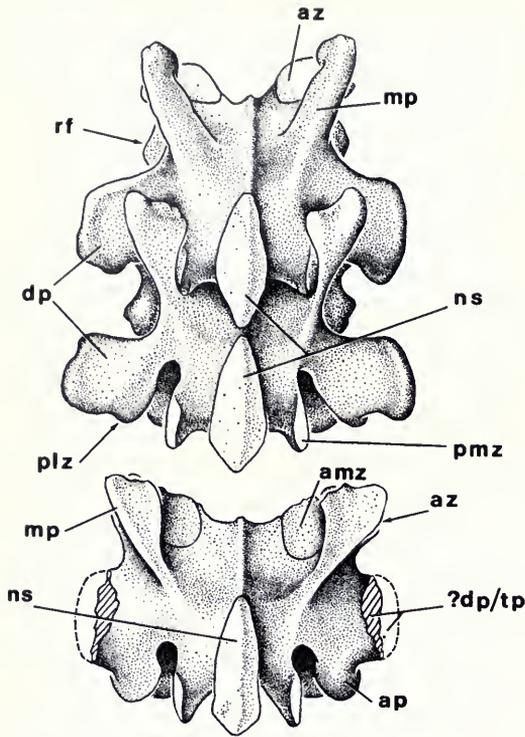


FIG. 10. *Hapalops* sp., FMNH P15318; 19th through 21st thoracic vertebrae shown in dorsal view (cranial end toward the top of the page). Scale bar = 1 cm. Abbreviations as in Figures 1 and 2, plus ?dp/tp, possible diapophysis or transverse process.

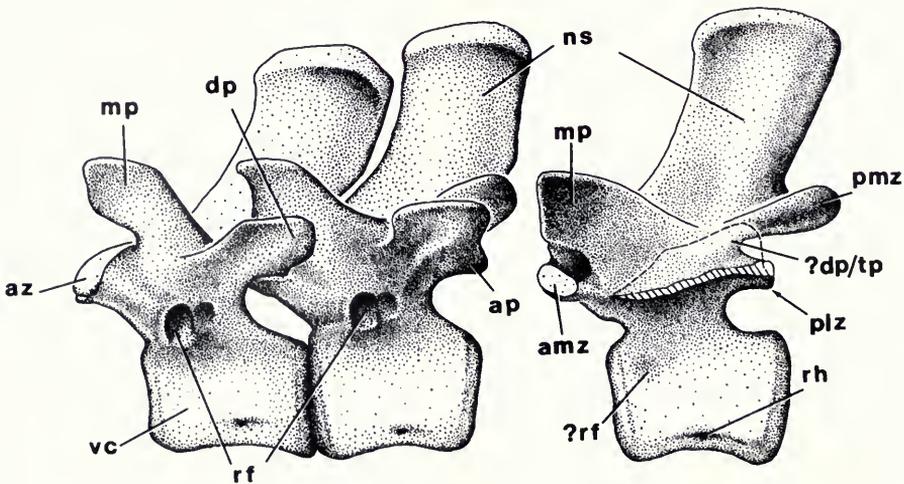


FIG. 11. *Hapalops* sp., FMNH P15318; 19th through 21st thoracic vertebrae shown in left lateral view. Scale bar = 1 cm. Abbreviations as in Figures 1, 2, and 10, plus rh, rachitiform foramen.

actively 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 *Bradypus*. 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 *Bradypus* 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*.⁷ Like *Tamandua*, the first supplementary intervertebral articulation occurs between the diaphragmatic and post-diaphragmatic vertebrae. In addition, the diaphragmatic vertebra is the anteriormost thoracic

⁷ There may be some variation in the position of the diaphragmatic vertebra in *Hapalops*. In FMNH P15318, the third and last vertebra in the series, the presumed 21st thoracic vertebra, has broken transverse processes and a very weak depression on the anterolateral surface of the centrum for articulation with the head of the rib. These rib facets are very strongly developed on T20 and T19 (Fig. 11). This raises the possibility that the vertebra labeled T21 is in fact the first lumbar, and the diaphragmatic vertebra is the penultimate thoracic vertebra.

TABLE 1. Ratio of maximum width (parallel to long axis) to maximum anteroposterior length (orthogonal to long axis) of the anterior zygapophyseal facets of the prediaphragmatic thoracic vertebrae in Xenarthra.

Taxon	Total no. of TV	Vertebra	Maximum width (mm)	Maximum length (mm)	Ratio
<i>Zaedyus pichi</i>	11	T3	3.8	1.6	2.4
FMNH 104817		T6	3.5	1.7	2.1
<i>Euphractus sexcinctus</i>	11	T3	5.7	1.9	3.0
FMNH 152051		T5	5.9	2.6	2.3
		T8	6.8	3.2	2.1
<i>Chaetophractus villosus</i>	10	T3	4.1	3.6	1.1
FMNH 60467		T5	6.2	2.4	2.6
		T7	5.5	2.7	2.0
<i>Tolypeutes matacus</i>	11				
FMNH 153773 (T4 measured)		T4	2.8	1.4	2.0
FMNH 121540 (T6 measured)		T6	2.4	1.7	1.7
<i>Tamandua mexicana</i>	17	T5	5.2	2.9	1.8
FMNH 69597		T8	5.4	3.2	1.7
		T11	5.7	3.3	1.7
<i>Bradypus variegatus</i>	16	T4	5.3	2.8	1.9
FMNH 69589		T8	5.2	2.4	2.2
		T11	5.3	2.8	1.9
<i>Hapalops</i> sp.	22?				
FMNH P13133 (mid-TV measured)		?mid-TV	14.9	5.9	2.5
FMNH P15318 (T19 measured)		T19	14.8	6.0	2.5

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

vertebra that bears any trace of an anapophysis. T19 has a small anapophysis extending back from the posteromedial portion of the large diapophysis. The anapophysis bears a small flat articular facet ventrally. This facet is oriented nearly horizontally and separated by a wide notch from the posterior zygapophysis, which forms a semicylindrical vertical joint surface lying more dorsal and closer to the midline (Fig. 10).

The two posterior facets on T19 form synovial joints with corresponding surfaces on the anterior edge of T20. As in other xenarthrans, the two facets on the anterior edge of T20 are apparently formed by division of the wide thoracic anterior zygapophyseal facet. The base of the metapophysis of T20 reaches the anterior edge of the vertebra, dividing the zygapophyseal facet into medial and lateral portions. The medial zygapophyseal facet is concave. Its medial half lies horizontal, and its lateral half is oriented vertically. It articulates in typical fashion with the semicylindrical posterior zygapophyseal facet of T19 (Fig. 10). The lateral zygapophyseal facet is ovate transversely, nearly flat (it is very slightly convex dorsally), and oriented almost horizontally (it dips slightly ventrolaterally). It is borne on the dorsal surface of an anterolateral extension of the lamina

and articulates with the anapophyseal facet of T19 (Fig. 11).

The intervertebral joints between the more posterior thoracic and lumbar vertebrae, including that between the last lumbar and first sacral vertebrae, are nearly identical to those described for T19/T20. The only notable difference in the more posterior joints is an increase in the size of the anapophysis, corresponding to an increase in size of the thin, anteroposteriorly broad pleurapophysis of the lumbar vertebrae.

As in *Bradypus* but in contrast to other xenarthrans, *Hapalops* typically lacks true xenarthrous articulations, i.e., joints between the ventral and/or lateral surface of the metapophyseal base and the dorsal or medial surface of the anapophysis. The postdiaphragmatic vertebrae of FMNH P15318 bear distinct depressions on the lateral surface of the metapophyseal bases immediately dorsal and medial to the lateral zygapophyseal facets (Fig. 11). These, however, do not have polished articular surfaces, nor is there any evidence of corresponding facets on the anapophyses of T19 and T20. True xenarthrous facets are also absent in FMNH P13133 and P13145, as well as in Scott's (1903–1904) *Hapalops* material. Small xenarthrous articulations between the ventral surface of

the metapophysis and the dorsal surface of the anapophysis 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 articulations. The presence or absence 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 pilosans, 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 *Glossotherium* 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 nothrotheriid *Pronothrotherium* (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 *Schismotherium* has five (AMNH 9244; Scott, 1903–1904). In several genera, one or more of the lumbar vertebrae are fused to the sacral vertebrae (*Glossotherium*, 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 zygapophyseal facets that extend further laterally than the vertebral centra and are separated by a small midline notch. The zygapophyseal facets appear to be particularly wide among the Santacrucian megalonychimorphs (*sensu* Gaudin, 1993) and the nothrotheriids (Fig. 12). The zygapophyseal facets of *Eremotherium* (Paula Couto, 1978) and *Scelidothorium* (Gervais, 1855) are unusual in that they are not elongated mediolaterally but instead are almost circular in

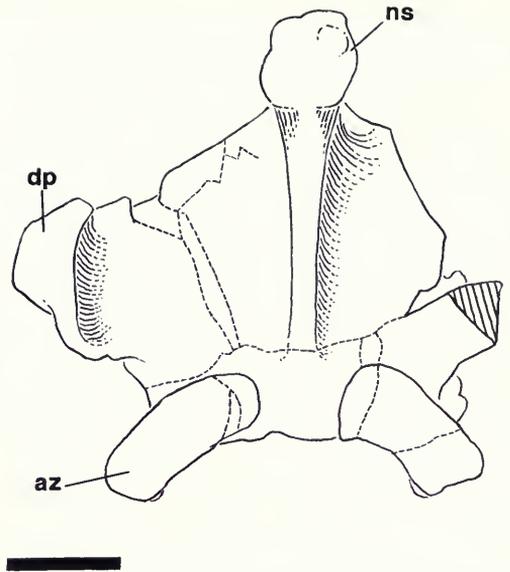


FIG. 12. *Pronothrotherium typicum*, FMNH P14467: isolated mid-thoracic vertebra shown in dorsal view (cranial end toward the bottom of the page). Scale bar = 1 cm. Abbreviations as in Figure 1.

shape. They are, however, very widely separated from one another on either side of the midline and, at least in *Scelidothorium*, 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 approximate-

ly at the level of the posterior margin of the anterior zygapophyseal 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 Santacrucian genus *Planops* (Hoffstetter, 1961), the scelidotheres (McDonald, 1987), and the mylodontines *Paramylodon harlani* (Stock, 1925) and “*Myلودon*” *garmani* (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 zygapophyseal 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; *Schismotherium*, where again its presence is variable (observed in FMNH P13137 but not in AMNH 9244 or in specimens described by Scott, 1903–1904); and *Prepothierium*, a genus closely related to *Planops* (Scott, 1903–1904).

In most tardigrades separate medial and lateral zygapophyseal 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 Santacrucian genus *Pelecycodon* (AMNH 9240), the anterior zygapophyseal 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 zygapophyseal facets on the prediaphragmatic vertebra are similarly constructed. A very similar morphology has been described by Stock (1925) in *Paramylodon har-*

lani, 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 zygapophyseal articulation between the ventral surface of the anapophysis and the dorsal surface of a facet situated immediately lateral to the base of the metapophysis.

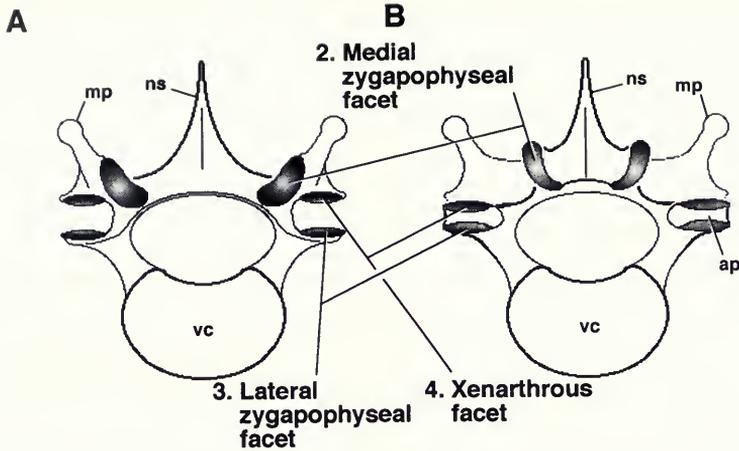


FIG. 13. Diagrammatic representation of the morphology of typical xenarthran intervertebral facets in the posterior thoracic or lumbar vertebrae. **A**, anterior view; **B**, posterior view. Abbreviations as in Figure 1.

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

Typical mammalian zygapophyses 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 zygapophyses of some prediaphragmatic thoracic vertebrae begin to show evidence of incipient division into distinct medial and lateral facets (see below).

2. *Medial zygapophyseal facets.* In all xenar-

thrans (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 zygapophyseal facets of other mammals by Owen (1851a) and others (Hoffstetter, 1958, 1982; 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 zygapophyseal 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 zygapophyseal 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

Tamandua, these facets closely resemble in structure and position the lateral portion of the zygopophysis of the prediaphragmatic vertebrae. I therefore suggest that these facets are serially homologous with the lateral parts of the zygopophyseal articulations of the prediaphragmatic vertebrae. These facets are considered accessory zygopophyseal articulations, termed "lateral zygopophyseal facets," and are distinct from true "xenarthrous" facets.

The homology of these lateral zygopophyseal articulations is less secure than that of the medial zygopophyseal 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 zygopophyseal articulations in at least some of the postdiaphragmatic vertebrae. However, the normal zygopophyseal 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 zygopophyseal facets in these taxa represents a secondary reduction.

4. *True xenarthrous facets.* There are several different types of facets found in various xenarthran taxa that can be categorized as true "xenarthrous" 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 postdiaphragmatic vertebrae of all cingulates and vermilinguas, 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 megalonychimorph sloths (*Hapalops*, *Schismotherium*, *Prepothorium*), and hence they likely represent the primitive condition for tardigrades as well. They are often fused to the lateral zygopophyseal 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 *Zaedyus* (Fig. 4C) and T6 or T7–T9 (again the penultimate thoracic vertebra) in *Dasybus*, but have not been observed in any pilosan. These articular surfaces do not serve an intervertebral function. However, the anapophysis of the last thoracic vertebra of cingulates carries

a ventrolateral 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 lumbosacral joint. A similar facet is present between the ventral portion of the anapophysis and the dorsal portion of the transverse process/sacral rib in *Myrmecophaga* (at L1/L2 and the lumbosacral joint) and *Tamandua* (at the lumbosacral joint only), but not in *Cyclopes*. 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 unpaired midline facets that may be generally categorized as xenarthrous. The anterior facet is typically found on the dorsal surface of the vertebral lamina, posterior to the zygopophyseal 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 *Priodontes* (Fig. 7) and megatheriid, scelidotheriine, and some mylodontine ground sloths.

Phylogeny and Evolution of Xenarthrous 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 xenarthrous vertebrae. The prediaphragmatic thoracic vertebrae probably have abnormally wide zygopophyses, 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 zygopophyseal articulations into separate medial and lateral joints. In addition, each metapophysis bears a ventrolateral articular facet that articulates with the dorsal surface of the anapophysis of the preceding vertebra. Large anapophyses may also be a primitive characteristic of xenarthrous vertebrae. However, the anapophyses are only weakly developed in sloths and in the anterior xenarthrous vertebrae of cingulates.

The goal of the present study was not only to

Cingulata

- 1) Wide zygapophyseal facets (only in euphractans)
- 2) Enlarged metapophyses
- 3) Enlarged anapophyses (only in post. thor. and lumb. vert.)
- 4) Medial and lateral zygapophyseal facets in post-diaphragmatic vertebrae
- 5) Xenarthrous articulations between: metapophysis and anapophysis anapophysis and rib (thor. vert.) anapophysis and transverse process (lumb. vert.) neural spine and lamina (*Tolypeutes* & *Priodontes* only)

Vermilingua

- 1) Wide zygapophyseal facets
- 2) Enlarged metapophyses
- 3) Enlarged anapophyses
- 4) Medial and lateral zygapophyseal facets in post-diaphragmatic vertebrae
- 5) Xenarthrous articulations between: metapophysis and anapophysis anapophysis and transverse process (lumbo-sacral joint, *Tamandua* & *Myrmecophaga* only)

Tardigrada

- 1) Wide zygapophyseal facets
- 2) Enlarged metapophyses (in most taxa)
- 3) Weak anapophyses
- 4) Medial and lateral zygapophyseal facets in post-diaphragmatic vertebrae (in most taxa)
- 5) Xenarthrous articulations between: metapophysis and anapophysis (several Santacrucian genera) neural spine and lamina (large ground sloths only)

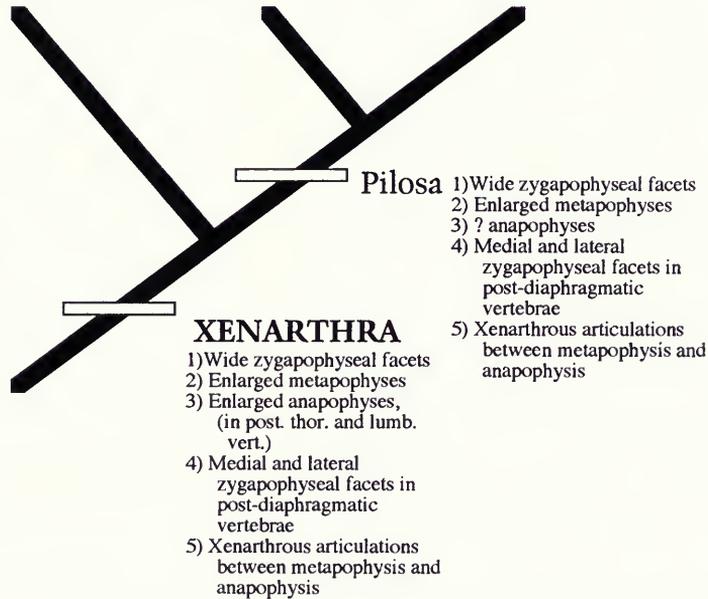


FIG. 14. Phylogeny of the Xenarthra (following Engelmann, 1985; Gaudin, 1993), showing the distribution of vertebral character states among the three major suborders, and the inferred character states at the ancestral nodes "Pilosa" and "Xenarthra." For further description of each character state, see text. Abbreviations: lumb. vert., lumbar vertebrae; post. thor. vert., posterior thoracic vertebrae; thor. vert., thoracic vertebrae.

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 inter-

mediate condition between nomarthry 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* (Lesertisseur & Saban, 1967; Kingdon, 1984), in which the posterior thoracic and lumbar vertebrae are united laterally by closely interlocking bony

excrescences.⁸ 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 lumbosacral fusion occurs in the dasyproctid armadillos *Priodontes* and *Tolypeutes*, in the euphractan armadillos *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 lumbosacral 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 lumbosacral 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

zygapophyseal 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 xenarthrous articulations originated.

In contrast to MacPhee's (1994) claim, I suggest that documented structural intermediates between xenarthrous and nomarthrous vertebrae do exist. Among tardigrades, the xenarthrous articulations are reduced relative to the primitive condition for the order as whole. The reduction includes not only a diminution in the number of intervertebral joints that possess accessory articulations (see *Bradypus*, *Nothrotheriops*, and *Choloepus*, above), but also a simplification of the accessory articulations themselves. The vast majority of sloths lack a xenarthrous 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 zygapophyseal facets, large metapophyses, and medial and lateral postdiaphragmatic zygapophyseal facets characteristic of primitive xenarthran vertebrae. Even these medial and lateral postdiaphragmatic zygapophyseal facets may be restricted to the last few lumbar vertebrae in several taxa, most notably the extant tree sloths.

The presence of xenarthrous joints between the metapophysis and anapophysis in several relatively early sloth genera, e.g., *Hapalops* and *Prepothierium*, suggests that the xenarthrales 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 nomarthry, represents the best available tool for understanding the evolutionary origin of xenarthrous vertebrae.

Using the condition in sloths as a model, I suggest that the first step in the evolution of xenarthrous articulations was a widening of the zygapophyseal facets and enlargement of the metapophyses, both becoming more extensive in progressively more posterior thoracic and lumbar vertebrae. The widening of the zygapophyses 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 metapophyses would provide a larger area for origin of the epaxial transverso-

⁸ Such bony excrescences are also present in several FMNH specimens of *Tamandua*, e.g., FMNH 137419, 140912, and 150733. All, however, are zoo specimens. It therefore seems likely that this condition is an age-related pathological state.

spinalis muscles. At the joint between the diaphragmatic and first postdiaphragmatic vertebrae, the metapophyses would become sufficiently large to split the widened zygapophyseal facets perforce into separate medial and lateral zygapophyseal joints. These medial and lateral zygapophyseal joints would then continue posteriorly to the lumbosacral joint.

The second step in the evolution of xenarthrales 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 xenarthrous 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 semiarboreal habitus (Gaudin, 1993; White, 1993a,b).

The above model contrasts with that of MacPhee (1994) in postulating that xenarthrales 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 vertebra (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 primitively specialized for digging. They note further that in digging mammals, the axial musculoskeletal sys-

tem 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 zygapophyses 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 zygapophyseal 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 xenarthry. 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 *Dasybus* 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 xenarthrales to evaluate the taxonomic affinity of several enigmatic early Cenozoic taxa with allegedly close ties to Xenarthra. Of particular concern are the Palaeanodonta, a group of fossorial mammals with reduced dentitions that is known from Paleogene strata of North America (Rose et al., 1991, 1992; Gunnell & Gingerich, 1993) and Europe (Hessig, 1982); *Ernanodon*, a taxon based on a single skeleton found in Late Paleocene sediments from China (Ding, 1987); and *Eurotamandua*, a purported anteater from the Middle Eocene Messel fauna of Germany (Storch, 1981).

Simpson (1931) proposed a close phylogenetic link between palaeanodonts and xenarthrans based on various lines of evidence, including the morphology of the vertebral column (see Emry, 1970, for contrasting interpretations). In his description of the vertebrae of the Eocene palaeanodont *Metacheiromys*, Simpson (1931, p. 334) stated that "While xenarthrous articulations are not definitely incipient in *Metacheiromys*, . . . [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 *Palaeanodon*, 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 vertebrae of *Palaeanodon*. Other Paleocene palaeanodonts 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 palaeanodonts (Epoicotheriidae and Metacheiromyidae). In the epoicotheriid *Alocodontulum* and the metacheiromiid *Metcheiromys*, certain resemblances to xenarthran vertebrae can be observed (Simpson, 1931; Rose et al., 1992). The metapophyses are enlarged, particularly in the posterior thoracic vertebrae in the vicinity of the diaphragmatic vertebra. Unlike xenarthrans, however, the metapophyses become progressively smaller in more posterior lumbar vertebrae. It is unclear whether or not the thoracic zygapophyseal facets of palaeanodonts are particularly enlarged transversely. Rose et al. (1992, p. 226) describe the lumbar prezygapophyses of *Alocodontulum* as "broad." Broad . . . , mediolateral width much greater than antero . . . anterior length) zygapophyseal facets have also . . . observed in the lumbar vertebrae of the Early Eocene epoicotheriid *Pentapassulus* (USNM

20028; Gaudin, pers. observ.) and the diaphragmatic vertebra of *Metacheiromys* (USNM 26132; Gaudin, pers. observ.). They are not so broad, however, as in xenarthrans, in which width often exceeds anteroposterior 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 *Metacheiromys*, but these facets are situated well lateral to the midline. In no case, however, are distinct medial and lateral zygapophyseal facets observed in any palaeanodont. The anapophyses of palaeanodonts are enlarged (Simpson, 1931; Rose et al., 1992), again in the vicinity of the diaphragmatic vertebra. Although relatively deep on T12 and T13 of *Alocodontulum* (Rose et al., 1992, fig. 3), the anapophyses of palaeanodonts tend to be dorsoventrally narrow and spine-like. In this respect they more closely resemble the anapophyses of carnivores than those of xenarthrans (Rose et al., 1992; Rose & Emry, 1993). Furthermore, there is no indication of articular surfaces between the anapophyses and the succeeding metapophyses or transverse processes.

On balance, it would appear that palaeanodont 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 metapophyses. 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 Xenarthra, Ding (1987, p. 92) noted the posterior thoracic vertebrae of *Ernanodon*, which bear "longitudinally elongated projections under the mammillary process [= metapophysis], which are incipiently developed xenarthrous articulations." As in xenarthrans and palaeanodonts, the posterior thoracic and lumbar vertebrae of *Ernanodon* are characterized by well-developed metapophyses. A pair of large vertebral processes extend lateral to the metapophyses, but do not form joints with the metapophyses. These lateral processes (Ding, 1987, fig. 7) apparently represent large anapophyses. In the posterior thoracic vertebrae the anapophyses arise anteriorly from the back of rather low, weakly developed diapophyses, a condition that only vaguely resembles that characteristic of most true xenarthrans. In the lumbar vertebrae, the anapophyses arise from short, anteroposteriorly elongated transverse processes, the latter reminiscent of those found in extinct sloths. The

anapophyses are relatively deep in the thoracic vertebrae, but are oriented more dorsally than among unequivocal xenarthrans. The anapophyses of the lumbar vertebrae are not illustrated in lateral view, and the width of the zygapophyseal facets in *Ernanodon* is unclear. They are described as "oval" in the anterior thoracic vertebrae, increasing in size posteriorly (Ding, 1987, p. 92). However, the zygapophyseal joints of the lumbar vertebrae are enrolled, as are those of pholidotans (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 *Ernanodon*, be they lateral zygapophyses or xenarthrous joints between anapophyses, metapophyses, and transverse processes.

As with the palaeonodons, the case for strong shared derived similarity between the vertebrae of *Ernanodon* and undoubted xenarthrans is weak. The most notable resemblances are the enlarged metapophyses and anapophyses. However, the former are widespread among digging forms, as noted above. The latter differ slightly in their morphology from those of xenarthrans. Moreover, it is not clear that enlarged anapophyses 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 palaeonodons and *Ernanodon*, the vertebrae of *Eurotamandua* possess large metapophyses, beginning three to four vertebrae anterior to the diaphragmatic vertebra and extending posteriorly through the lumbar vertebrae (Storch, 1981). Similarly, enlarged anapophyses are present in the diaphragmatic region of the vertebral column. Unlike what is found in palaeonodons and *Ernanodon*, the anterior thoracic vertebrae of *Eurotamandua* are very reminiscent of armadillo (but not anteater) vertebrae, with elongated, anteroposteriorly narrow neural spines, broad laminae, and elevated diapophyses. The most remarkable aspect of the vertebral morphology in this genus, however, is its purported possession of true accessory intervertebral articulations.

The diaphragmatic vertebra of *Eurotamandua*, the last thoracic according to Storch (1981), has a large anapophysis that apparently bears both dorsal and ventral articular facets. By analogy with unequivocal xenarthrans, the former would represent either a xenarthrous facet between the

anapophysis and metapophysis or a combined anapophyseal/metapophyseal xenarthrous facet and a lateral zygapophyseal facet. The ventral articulation would then represent a xenarthrous joint between the anapophysis and the transverse process of the first lumbar vertebra. Note that a joint between the anapophysis and transverse process is not a primitive characteristic of xenarthran or anteater vertebrae, according to the phylogenetic distributions 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 be 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 prediaphragmatic vertebrae, is unusual (Storch, 1981, fig. 8). The two vertebrae anterior to the diaphragmatic vertebra have narrow, spine-like anapophyses, very similar to those found in palaeonodons and unlike anything known in Xenarthra. These anapophyses allegedly articulate with a small concave facet or depression on the pedicel of the succeeding vertebra. This latter facet lies midway between the base of the metapophysis 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 diapophysis.⁹ This type of articulation, between the anapophysis anteriorly and the metapophysis and diapophysis posteriorly, is not present in any known xenarthran.

⁹ Storch (1981) labels it a parapophysis, but I am not aware of any mammal that possesses a true parapophysis in the posterior thoracic vertebrae. Hence I believe it more likely to represent a ventrally displaced diapophysis, articulating with the tubercle rather than the head of the rib.

In summary, the case for derived resemblance between the vertebrae of *Eurotamandua* and undoubted xenarthrans remains less than compelling. Like palaeonodons and *Ernanodon*, *Eurotamandua* does possess enlarged metapophyses and anapophyses, but these are of equivocal phylogenetic utility. The width of the zygapophyses in *Eurotamandua* cannot be assessed from the published descriptions and figures. Storch (1981) claims that accessory intervertebral articulations are present, including a possible lateral zygapophyseal joint and xenarthrous joints between the anapophysis and metapophysis, the anapophysis and transverse process, and the anapophysis/metapophysis 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 palaeonodons, *Ernanodon*, 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 *Ernanodon* 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 palaeonodons. 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 palaeonodont material, focusing in particular on the morphology of the zygapophyses, might yield additional derived characteristics linking xenarthrans and palaeonodons. 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 xenarthrous vertebrae would appear to be continued study of the functional, ontogenetic, and phylogenetic history of these articulations among the xenarthrans themselves.

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APPENDIX TABLE 1. Summary of Morphological Data

Taxon	No. of TV	No. of LV	Diaphragmatic vertebra	MP	AP	Spinal nerves
<i>Zaedyus pichiy</i> FMNH 23809, 104817 ¹	11	3	T7 (104817) or T8 (23809)	T7-L3	T6-L3	Ventral branch: intervertebral foramina between pedicels of successive vertebrae, T1 and T2, T11-L3; within pedicels, T3-T10. Dorsal branch: in lamina between ap and dp, T3-T10; medial to ap, T11-L3.
<i>Chaetophractus villosus</i> FMNH 60467 ¹ FMNH 122623, 134611	10 11	5 3	T7	T7-L5	T3-L4	Ventral branch: within pedicel, T1-T10; intervertebral foramina, T11-L4. Dorsal branch: perforates lamina, T2-T4; perforates ap, T5-T10 (two holes in T7-T9); medial to ap, T11-L4.
<i>Euphractus sexcinctus</i> FMNH 152051	11	4	T8	T8-L4	T4-L3	Ventral branch: within pedicel, T1-T10; intervertebral foramina, T11-L3. Dorsal branch: perforates lamina, T3-T7; perforates ap, T8-T10; medial to ap, T11-L3.
<i>Tolypeutes matacus</i> FMNH 121540, 124568 (juv.), 124569 (juv.), ¹ 124570, 153773 FMNH 122233	11 12	4 3	T7 (124569) or T8 (124570)	T7-L4	T8-L4	Ventral branch: within pedicel T1-T10; intervertebral foramina, T11-L4. Dorsal branch: ventral to ap; T1-T6; perforates ap, T7; medial to ap, T8-L4.
<i>Tamandua mexicana</i> FMNH 69597 ¹ FMNH 22398	17 18	2 2	T13 (69597) or T14 (22398)	T1-L2	T13-L2	Spinal nerves emerge through typical intervertebral foramina
<i>Cyclopes didactylus</i> FMNH 69969, ¹ 69971	16	2	T13 (69971) or T14 (69969)	T1-L2	T13-L2	Spinal nerves emerge through typical intervertebral foramina
<i>Bradypus variegatus</i> FMNH 68919, 69589 ¹	15	3	T15	T3-L3	T15-L3	Spinal nerves emerge through typical intervertebral foramina
<i>Choloepus hoffmani</i> FMNH 127421 (juv.), 127422, 147993 ¹	23	3	T21	T21-L3	T23-L3	Spinal nerves emerge through typical intervertebral foramina
<i>Hapalops</i> sp. FMNH P13133, P13145, P13146, P15318	21-22	3	T19	T1-L3	T19-L3	Spinal nerves emerge through typical intervertebral foramina

ALZ or alz = anterior lateral zygapophyseal facet; AMZ or amz = anterior medial zygapophyseal facet; AP or ap = anapophysis; AX = anterior xenarthrous facet; dp = diapophysis; (l) = left side only; L1, L2, L3 = first lumbar vertebra, second lumbar vertebra, third lumbar vertebra, etc.; LV = lumbar vertebrae; MP or mp = metapophysis; PLZ or plz = posterior lateral zygapophyseal facet; PMZ or pmz = posterior medial zygapophyseal facet; PX = posterior xenarthrous facet; (r) = right side only; S1, S2 = first sacral vertebra, second sacral vertebra, etc.; T1, T2 = first thoracic vertebra, second thoracic vertebra, etc.; tp = transverse process; TV = thoracic vertebrae.

¹ Information in table derived from this specimen, except for thoracic and lumbar vertebral counts.

APPENDIX TABLE 2. Summary of Morphological Data

Taxon	AMZ and ALZ	PMZ and PLZ	AX	PX	Notes
<i>Zaedyus pichiy</i> FMNH 104817	T3-S1 amz abuts alz from T3-T8	T2-L3 pmz abuts plz from T2-T7	Ventral mp: T7-S1, confluent with alz from T9-S1; dorsal tp: L1-S1	Dorsal ap: T6-L3, confluent with plz from T8-L3; lateral ap (for rib): T8 or T9-T10; ventral ap: T11-L3	Opisthocoelus centra, T1-T9; rib head articulates between anterior centrum and posterior pedicel
<i>Chaetophractus villosus</i> FMNH 60467	T4(r)/T5(l)-L5 ¹ amz abuts alz from T4/5-T8	T3(r)/T4(l)-L4 pmz abuts plz from T3-T8	Ventral dp: T5-T6; ventral mp: T7-L5, confluent with alz from L3-L5; dorsal tp: L1-L5	Dorsal ap: T4-L4, confluent with plz from L2-L4; lateral ap (for rib): T8-T10; ventral ap: T11-L4	L5 fused to S1; opisthocoelus centra; rib head as <i>Zaedyus</i>
<i>Euphractus sexcinctus</i> FMNH 152051	T5-L4 amz abuts alz from T5-T9	T4-L3 pmz abuts plz from T4-T8	Ventral mp: T7-L4, confluent with alz from T9-L4; dorsal tp: L1-L4	Dorsal ap: T6-L3, confluent with plz from T8-L3; lateral ap (for rib): T8-T10; ventral ap: T11-L3	L4 fused to S1; medial zygapophyses enrolled as in pangolins; opisthocoelus centra; rib head as <i>Zaedyus</i>
<i>Tolypeutes matacus</i> FMNH 124569 (juv.)	T9-S1	T8-L4	Ventral mp: T7(r)/T8(l)-S1, confluent with alz in LV	Dorsal ap: T6(r)/T7(l)-L4, confluent with plz in LV; ventral ap (for thoracic, lumbar, and sacral ribs): T11-L4	Rib head as <i>Zaedyus</i>
<i>Tamandua mexicana</i> FMNH 69597	T14-S1	T13-L2	Ventral mp: T14-S1, confluent with alz in all; dorsal sacral rib: S1	Dorsal ap: T13-L2, confluent with plz in all; ventral ap: L2	Rib head articulates exclusively with anterior centrum; neural spines robust, uniform height; anterior zygapophyses separated by midline notch; thoracic zygapophyses wide, extending lateral to centrum
<i>Cyclopes didactylus</i> FMNH 69569	T15-S1	T14-L2	Ventral mp: T13-S1, confluent with alz in all	Dorsal lamina: T12-T13; dorsal ap: T14-L2	Rib head, neural spines, zygapophyses as <i>Tamandua</i>
<i>Bradypus variegatus</i> FMNH 69589	L2-S1	L1-L3	Absent	Absent	Rib head articulates between posterior centrum and anterior pedicel; all vertebral processes reduced; neural spines uniform height; anterior zygapophyses separated by midline notch

APPENDIX TABLE 2. Continued

Taxon	AMZ and ALZ	PMZ and PLZ	AX	PX	Notes
<i>Choloepus hoffmani</i> FMNH 147993	S1 (r)	L3 (r)	Absent	Absent	Vertebral processes as in <i>Bradypus</i> ; anterior zygapophyses separated by midline notch as in <i>Bradypus</i>
<i>Hapalops</i> sp. FMNH P13133, P13145, P13146, P15318	T20–S1	T19–L3	P13146 only— ventral mp: L1 (right side only), L3	P13146 only— dorsal ap: T22 (right side only), L2	Rib head, neural spines as <i>Tamandua</i> ; zygapophyses of anterior thoracics very wide, extending lateral to centrum; anterior zygapophyses separated by narrow midline notch

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

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