THE EAR REGION OF EDENTATES AND THE PHYLOGENY OF THE TARDIGRADA (MAMMALIA, XENARTHRA)

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ABSTRACT—A cladistic investigation of the phylogenetic relationships among 21 extinct and extant genera of sloths (Mammalia, Xenarthra, Tardigrada) was performed on the basis of characteristics of the ear region. This study was undertaken in order to evaluate the relationship among the three traditional family groupings of extant ground sloths and the monophyletic or diphyletic origin of the two genera of extinct tree sloths. Eighty-five discrete morphological characters were analyzed using the computer program PAUP. Characters were polarized via comparisons to the following successive outgroups, all members of the suprageneric grouping Edentata: the Vermilingua, or anteaters; the Cingulata, or armadillos and glyptodonts; the Palaeoedontia; and the Pholidota, or pangolins. Three most parsimonious trees result for 21 ingroup taxa and 5 outgroup taxa; Length = 304 steps, CI = 0.605, RI = 0.710. The results of this analysis provide characters which support the monophyly of the Xenarthra as a whole, as well as its dichotomous division into the clades Cingulata and Pilosa. In addition, it strongly corroborates the monophyly of the Vermilingua and the Tardigrada. Within tardigrades, the living three-toed sloth Bradypus is suggested to represent the sister-taxon to all other sloths. The results support the monophyly of the three traditional ground sloth families Megatheriidae, Mylodontidae, and Mylodontidae (the latter two, quite strongly), and suggest that the subfamily Nothrotheriinae may represent a paraphyletic stem group for the remaining sloths. A novel relationship between the families Megalonychidae and Mylodontidae is proposed which contrasts with previous hypotheses of a close relationship between megalonychids and megatheriids. Lastly, this analysis strongly supports the derivation of the extinct two-toed sloth Choloepus from within the West Indian megatherioid ground sloths, contradicting the traditional triveminate grouping of the extinct tree sloths into a monophyletic family Bradypodidae and suggesting that the living tree sloths represent one of the most remarkable examples of convergent evolution known among mammals.

INTRODUCTION

The order Xenarthra has formed a significant component of the mammalian fauna of South America throughout its Cenozoic history, representing one of the largest and most characteristic elements of this fauna (Hoffstetter, 1958). The extinct representatives of this order are tremendously varied, both in terms of taxonomic diversity (there are at least 150 described fossil genera; Hoffstetter, 1958; Paula Couto, 1979) and morphological variability. The extinct members of the order are relatively depauperate taxonomically in comparison to their extinct counterparts, numbering only some 29 species (Wetzel, 1985). However, the range of morphologies present in these taxa is striking. Recent xenarthrans have traditionally been divided into three families (Simpson, 1945): Dasypodidae, the armored fossorial armadillos; Myrmecophagidae, the terrestrial to arboreal anteaters; and Bradypodidae, the herbivorous tree sloths.

In addition to the high degree of morphological, functional, and ecological variability displayed by the Xenarthra over the course of its history, the group is of systematic importance because of the significant place it has occupied in hypotheses of higher-level (i.e., interordinal) mammalian phylogeny that have emerged over the past 20 years. McKenna (1975) noted that xenarthrans retain a number of purportedly primitive therian characteristics, and hence placed the order as the sister-group to all other eutherians. Although McKenna's evidence for this hypothesis was subsequently criticized (McNab, 1985; Novacek, 1982, 1983; Novacek and Wyss, 1986; White et al., 1990), the relationship itself has been supported (albeit somewhat tenuously at times) by other studies, including those based on morphology (Novacek, 1982, 1991, 1996; Novacek and Wyss, 1986; Novacek et al., 1988), neuroanatomy (Kirsch et al., 1983), and molecular biology (Miyamoto and Goodman, 1986; Czelusniak et al., 1990; however, see Shoshani, 1986; Wyss et al., 1987; McKenna, 1987, 1992, for contrasting interpretations).

The Xenarthra has also been hypothesized to share a common ancestry with two other groups of largely fossorial, myrmecophagous mammals: the extant pangolins (order Pholidota) of the Old World tropics, and the extinct paleoedontans (suborder Palaeoedontia, order incertae sedis; Rose et al., 1991) from the Paleogene of North America and Europe. The common ancestry of these three taxa as a monophyletic clade Edentata has been advocated by morphologists and palaeontologists (Matthew, 1918; Simpson, 1931; Emry, 672.
(1970; Szalay, 1977; Rose, 1979; Cifelli, 1983; Nova- cek, 1986, 1990, 1992; Novacek and Wyss, 1986; No- vaccek et al., 1988; Patterson et al., 1992), but molecular systematists have strongly disputed claims of shared common ancestry between xenarthrans and pholido- tans (DeJong et al., 1985; Sarich, 1985; Miyamoto and Goodman, 1986; Czelusniak et al., 1990, but see Mc- Kenna, 1992).

The question of the interordinal relationships of the Xeniarchidae cannot be satisfactorily addressed without detailed knowledge of the interordinal relationships between xer- narthrans. Unfortunately, these relationships have long been poorly understood. Three separate lineages are clearly recognizable within the group: the Cingulata (glyptodonts and armadillos); the Vermilingua (ant- eaters); and the Tardigrada (ground sloths and tree sloths). However, these groups are quite distinct from one another from their earliest appearance in the fossil record (Hoffstetter, 1958). Early workers tended to ally the two non-armed lineages into a single natural group, the Pilosa (Flower, 1882; Lane, 1909; Simpson, 1945), although Gill (1910) pointed out that the evi- dence for such a grouping was weak. Until recently, most workers have followed Hoffstetter (1954, 1955, 1958, 1982) in depicting the relationship between the three lineages as an unresolved trichotomy (Roth, 1966; Patterson and Pascual, 1968, 1972; Paula Couto, 1979, but see Cifelli, 1983).

Recent work has begun to improve our understand- ing of xenarthran interordinal phylogeny. The cladistic studies of Engstrom (1978, 1985) have gathered strong support for the monophyly of the Pilosa. Moreover, Engstrom's studies, as well as recent papers by Webb (1985, 1989, Webb and Perring, 1985) have begun to elucidate the relationships within certain families. Nevertheless, large gaps in our knowledge still exist, especially in the most diverse of the three main xer- narthran lineages, the Tardigrada. (Note that Engel- mann (1983) labels this sloth clade "Phyllophaga," following Owen (1842). I prefer Hoffstetter's (1958, 1982) use of the term "sloth" which is an equally appropriate name that enjoys priority by at least 200 years (Brison, 1762).)

Recent recognition of the distinctness of the ground sloths and sloth genera has been recognized for some 200 years (Des- marest, 1822), the precise nature of this relationship has remained elusive, as has the nature of the rela- tionship among various groups of ground sloths. Tar- digrades are typically divided into four families: the Bradypodidae, for the two extant tree sloth genera, and the extinct families Mylodontidae, Megatheriidae, and Megalonychidae. Though this four-fold division of sloths is consistent across various published phylogue- nies and classifications, the recognized content of the families has varied. Most of this variation is due to disagreements over the systematic position of the ex- tinct nothrotheriine sloths, a group including the Plio- Pleistocene genera Nothrotheriops, Nothrotherium, Nothrolopus, and Protomastodon (Paula Couto, 1979), as well as the majority of small ground sloth genera

from the late early to early middle Miocene Santa Cruz Formation of Patagonia (Scott, 1903-1904). Some workers (Winge, 1941; Simpson, 1945; Hoffstetter, 1955, 1958; 1982) have considered this group to rep- resent a subfamily of the Megalonychidae. Other au- thors have placed the nothrotheres within the family Megatheriidae (Patterson and Pascual, 1968, 1972; Paula Couto, 1979; Engelmann, 1985). The evidence for either arrangement is scant.

With the contents of the families still under debate, our understanding of their interrelationships remains poor. Hoffstetter (1958) and Engelmann (1985) de- picted the relationship between the four groups as an unresolved tetrachotomy. Patterson and Pascual (1968, 1972) linked the megalonychids and megatherids into a monophyletic superfamily Megalonychoidea, but without character support. Perhaps even more inter- estingly (but again without character support), Pat- terson and Pascual made the audacious suggestion that the Bradypodidae is diphylectic, i.e., that the two-toed sloth Choloepus is closely related to the megalonychids, and that the three-toed sloth Bradypus is derived from the megatherids. Although osteological and behav- ioral differences exist between the two genera (Grassé, 1955a; Sunquist and Montgomery, 1973; Montgomery and Sunquist, 1978), the two taxa are remarkably sim- ilar in most comparisons one would care to make— e.g., diet, mode of locomotion, pelage, gross body mor- phology; and even the fact that algae grow in their hair (Grassé, 1955a). White (1933a, b) has provided new evidence for arboreality among at least some groups of "extinct" ground sloths; however, none of these forms display the dramatic modifications for suspensory lo- comotion that characterize the living sloths (with the possible exception of the Pleistocene genus Iscacin- nus). The extinct sloths also exhibit distinct differences from the living forms in their pelage (Moro and Woodward, 1899; Acosta, 1985), diet (Woodward, 1900; Hansen, 1978; Thompson et al., 1980), and gross skel- etal morphology. If Patterson and Pascual's (1968, 1972) hypothesis is correct, the striking stenog- enomorphisms between Bradypus and Choloepus would surely represent one of the most dramatic examples of convergent evolution known to zoologists. Patterson and Pascual's remarkable hypothesis is based in large part on Patterson's studies, until recently unpublished, of the xenarthran ear region (Patterson et al., 1989; Patterson et al., 1992). Unfortunately, as discussed in the conclusions of the Patterson et al. (1992) paper, the character evidence offered by Pat- terson in support of the various proposed relationships is very unbalanced, with some clades being discussed at length and others hardly at all. Other workers have supported the conclusions of Patterson and Pascual regarding bradypodid diplophyly based upon somewhat different lines of evidence. Unbeknownst to Patterson and other American investigators, Guth (1961) had made similar claims for bradypodid diplophyly several years earlier, based on his work on the temporal region of xenarthrans. He linked Bradypus with megatheres
and Choloepus with mylodonts, but his evidence rested on a single character. More recently, Webb (1985) examined the question of interbradypodid monophyly. He linked Bradypus with megatheruids and Choloepus with megaleontyids, the former arrangement supported by five derived osteological characters, the latter by but a single derived osteological feature. Unfortunately, Webb’s was an admittedly preliminary survey, and his use of mylodontids as an outgroup rests heavily on the weakly supported assumption that megaleontyids are indeed monophyletic, and that the two tree sloths are descended from megaleontyids and not mylodontids. Naples (1982, 1987, 1989) has noted a number of resemblances between the two living sloth genera and various extinct taxa in the muscivorousauloskeleton morphology of the jaw apparatus. However, the polynomials of her characters are either not discussed, or are based on the same weakly supported assumptions utilized by Webb.

The two questions of the interrelationship of the tardigrade families and the diphyly or monophyly of bradypodids are inextricably linked. Understanding the former is a necessary prerequisite to addressing the latter, for only then can characters be polarized in a rigorous cladistic fashion, using appropriate outgroup comparisons. To date there is no detailed systematic study which has addressed these two questions in a satisfactory and convincing manner, examining diverse representatives of all the relevant taxa.

The purpose of this paper is to provide the first detailed cladistic analysis of the phylogenetic relationships among the four families of the Tardigrada, and to attempt to test the monophyly of the Bradypodidae. I have analyzed 85 discrete osteological characters of the auditory region from the descriptions in Patterson et al. (1992), and scored them in 21 living and extinct sloth genera. The resulting data matrix has been analyzed by computer, using relevant outgroup comparisons to polarize characters. It is hoped that such an analysis will provide explicit and herefore unavail-

able character support for or against the monophyly of the Megaleontyidae and the Bradypodidae.

Abbreviations—FMNH, Field Museum of Natural History, Chicago, UCM, Museum of Paleontology, University of California, Berkeley; VPM-PU, Prince-ton University collection housed at Peabody Museum, Yale University, New Haven.

MATERIALS AND METHODS

The data discussed below are based in large part on the descriptive work of Patterson et al. (1992). Nineteen of the 21 tardigrade taxa utilized in this analysis were described in that paper. Information on the remaining two genera, the Santacrucian megaleontid Planopy and the Friesian mylodontid Pseudopropotherium, has been gathered both by examination of specimens (FMNH P11348 and VPM-PU 15346 in the case of the former genus, UCM 39957 and 38000 in the case of the latter) and from the primary literature (Scott, 1903–1904; Hirschfeld, 1985). I have examined all the specimens described in Patterson et al. (1992), except as noted in the text of this paper. Since revisions of that work were completed, I have had the opportunity to examine additional material in the collections of the following museums: Academy of Nat-

ural Sciences, Philadelphia, American Museum of Nat-

ural History, New York; George C. Page Museum, Los Angeles; Natural History Museum of Los Angeles County; and Peabody Museum, Yale University, New Haven. Thus additional information has been acquired for the genera Eremotherium, Glossotherium, Parap-

ylopon, Lestodon, Megalocnus, Megalonyx, Mor
dodon, Nothrotherium, Peyerolodon, Scelidotherium, and Schismotherium.

The following primary literature sources have been consulted in addition to the descriptions in Patterson et al. (1992) for the sloth genera listed below: Acra-


ium/Parapylopon: Owen (1842), Stock (1925), Klausk (1931a, b), Hoffstetter (1952), Hart (1953), Guth (1961). Napalopos: Scott (1903–1904), Klausk (1931a). Lest-
dodon: Klausk (1931a, b), Guth (1961). Nothrother-

ium: Stock (1917, 1925). Lull (1929). Peyer-


ka (1931a, b), Guth (1961). Schismotherium: Scott (1902–

1904), Klausk (1931a).

A list of the 85 morphological characters utilized in the analysis, and their character states, is provided in Appen-
dix 1. In those instances where the characters are described or scored somewhat differently from previous work, a reference is provided in Appendix 1. Of the 85 char-

acters, 32 are multistate (ranging from 3 to 5 states) and, of these, 11 are unordered. The character states for the ordered multistate characters have been ordered along positional, orientational, or structural morpho-
clines (Appendix 1).

The data matrix has been analyzed using the computer program PAUP, version 3.0b, by David Swoford (1989). The data have been analyzed using the heuristic search option of PAUP. It has not been possible to run either an exhaustive search or even a branch and bound analysis of the data because of the large size of the matrix. However, in an effort to avoid local minima and ensure that the shortest tree is found, 30 repetitions of the original analysis have been run, with taxa added to the starting tree in random order. All 30 repetitions yield the same set of shortest trees.

Characters have been weighted using two different schemes. In the first of these, all character state changes are given equal weight. In such a weighting scheme,
each change from one character state to another is given a weight of one, whether the character is binary or has many different states. In the second weighting scheme, each character is given equal weight. Each character is assigned a weight of 1.0, and the weight given to a character state change for each character varies with its particular number of character states. Therefore, while the change between character states in a binary character entails a weight of 1.0, character state changes in a character with three states is given a weight of 0.5, changes in a four state character are assigned a weight of 0.333, and so on. Character state changes have been optimized on the resulting trees using PAUP’s DELTRAN option. The choice of optimization scheme does not affect tree topology, though it does affect character distribution (and will tend to maximize consistency indices by reducing the number of character state reversals). This optimization was selected because it felt to be slightly more conservative in terms of assigning synapomorphies to clades in a data matrix with a substantial amount of missing data. In this optimization scheme, a character is assigned to the basal node of a clade only if there is positive evidence that the members of the clade share that character primitively. Many of the terminal taxa have been found to possess several different states of a given character. In these instances, the variability is coded into the data matrix (see Appendix 2) and treated by PAUP as polymorphism (rather than as character state uncertainty or missing data). Polymorphic changes within terminal taxa are not included in length calculations; however, the presumed primitive states for polymorphic taxa are provided in Appendix 2.

Characters have been partitioned using outgroup comparisons to at least two successive outgroups (following Maddison et al., 1984). The most proximate outgroup to the tardigrades, as discussed in the introduction, is the Vermilingua, the Anheless (Flower, 1882; Engelmann, 1978, 1985). The clade is represented in the present analysis by two taxa, the pygmy annelid Clyclopes didactylus, and a combined OTU including the genera Myrmodocophaga and Tardunodes (Myrmecophagidae of Engelmann, 1985). The former is described in detail by Patterson et al. (1992) but, as was discussed by these authors, the basicranial anatomy of the latter two are almost identical, and hence they have been lumped together. Additional information on the three anheless taxa has been provided by the work of Parker (1886), Klaauw (1931a), and Guth (1961).

The second outgroup to the Tardigrada is the Cingulata, the isomilloses and glypodonts. This clade is a large and heterogeneous assemblage. In an attempt to account for as much of its morphological diversity as possible, the group is represented in the present analysis by three separate taxa: the Glypodontida, the Euphracta, and the DasyPodidae (following Engelmann, 1978, 1985). Engelmann’s Glypodonta includes both the glypodontids proper and the pampatheres, and hence the character states given in the data matrix in Appendix 2 are a combined morphotype of the two groups derived from descriptions found in Patterson et al. (1989) of the Ploocene pamphreratites and the glypodont genera Proparasphodelophorophora (late Early to early middle Miocene, South America), Elephtherocerus (Pliocene, South America), and Haplodaphne (Oligocene, South America). Additional character information was garnered from a specimen of the Santacrucian glypodont Cochlos (VPMM-P1 15193), and from Guth (1961) and Gillette and Ray (1981). The use of so many different glypodontid taxa to form a morphotype is necessitated by the poor preservational state of the auditory region in most known glypodontids and pamphatheres. Engelmann’s (1978, 1985) taxon Euphracta is represented at its base by a large unexpanded polychotomy. Therefore, characters states are assigned to this taxon based primarily on the description in Patterson et al. (1989) of the oldest well-preserved euphractan skulls, those of the Santacrucian genus Proparasphodelophorophora. In instances where a given character is neither preserved nor observable in available specimens of Euphracta, characters are scored in the Euphracta based on descriptions of the skull morphology in the four living genera, Euphracta, Choristophracta, Zarda, and Chlamydophora (Patterson et al., 1989). Character state assignments for the DasyPodidae are based primarily on the auditory anatomy of the extant genus Tolypeutes (Patterson et al., 1989), the sister-taxon to the remaining dasypodids. Since Tolypeutes exhibits a high degree of intrageneric variability in its basicalvarian anatomy, the genera Cakaxaxus and Proparasphodelophorophora were also examined in certain instances before a character state was assigned to the DasyPodidae. The latter two genera are sister taxa, and together they form the sister group to remaining dasypodids (excluding, of course, Tolypeutes, Engelmann, 1978, 1985). The monophyly of the Ploosa and Cingulata as a whole has been used as a constraint in all analyses discussed below, as has the monophyly of the Dasypond, a clade uniting dasypodids and ephodactans to the exclusion of the glypodontans.

The focus of the present study is on relationships within the Tardigrada. While the relationships of tardigrades to other xenarthrans has been constrained a priori for the purposes of outgroup analysis, it is of some interest to know whether or not this analysis might provide characters from the ear region which are congruent with these assumed relationships. If only vermilinguas and cingulatans are used as outgroups, then characters at the base of the tree cannot be polarized in the manner chosen, and it is not possible to state whether or not a given character state change can be considered synapomorphic for either the Ploosa or the Cingulata. In order to provide information on the polarity of these 85 auditory region characters at the base of the xenarthran tree, a secondary analysis has been run, using the Paleanodontina, as represented by the relatively well-preserved and unspecialized meta-xenarthrid genera Palanodon and Metactereomy, as the first outgroup of Xenarthra (following...
ever, the optimization of several characters is modified by the presence of additional outgroups (especially characters 25, 35, 43, 61, 75, 77, and 83; see Appendices 1–3). The discussion of character state distributions will focus on that analysis in which the Pholidota and Palaeoanodonta are omitted. Similarly, an identical consensus tree is obtained whether character states are all weighted equally or all characters are weighted equally, with character states weighted according to the number of states per character (Fig. 2). The discussions of character state distributions will be based upon the results from the former weighting scheme. Characters are referred to in the following discussions according to their numbered order as given in Appendix 1.

Cohort Edentata (sensu Novacek, 1986; see Fig. 1)—There are six unambiguously-placed features which undergo character state changes at the base of the Edentata, and hence represent either pholidotan autapomorphies or synapomorphies of Xenarthra + Palaeoanodonta. The polarities of these characters are, of course, not determinable without reference to even more remote outgroups. However, the first four have been discussed at some length in Patterson et al. (1992) as derived features of a clade including xenarthrans and palaeoanodonts. They include the following: (18) ontosomomorphous prominent in Xenarthra + Palaeoanodonta, small/absent in Pholidota; (23) entosomomorphous with hollowed-out lateral surface in Xenarthra + Palaeoanodonta, with flat lateral surface in Pholidota; (29) ctenodons with small participation in floor of tympanic cavity in Xenarthra + Palaeoanodonta, absent from floor of tympanic cavity in Pholidota; and (57) stylomastoid foramen positioned lateral to distal end of tympanohyal in Xenarthra + Palaeoanodonta, positioned posteroventral to distal end of tympanohyal in Pholidota. The polarity of the other two characters is uncertain, but tentatively suggested to be as follows. In xenarthrans and palaeoanodonts, the stylomastoid foramen opens distally into a posteroventro-laterally directed groove (58), whereas the foramen opens into posteriorly directed groove in Pholidota. MacPhee (1981) reconsititutes the canal for the exit of the facial nerve in primitive eutherians as running posteroventrally laterally under the tympanohyal, and a similar condition is present in early fossil eutherians (see "un-guinaloid-type," MacPhee, 1981, also Kielan-Jaworowska, 1980, 1981). Hence its more posteriorly directed course in pholidotans is a derived feature. The glossoid of xenarthrans and palaeoanodonts is located near the opening of the porus acousticus (82), while in pholidotans the glossoid is far anterior to the porus. In early eutherians (Kielan-Jaworowska, 1980, 1981, 1984; Novacek, 1986) and early metatherians (Marshall and Muizon, 1988; see also Wake, 1990:fig. 1), the glossoid is situated very close to the porus, being separated from it only by an anteriorly compressed postglenoid process; therefore, it would appear that the unusual and highly derived pholidotan glossoid, a convex roughened surface set on a small de-
scending process of the squamosal (Grasse, 1935b), is derived in this regard as well.

It is worth noting that several of the other characters suggested by Patterson et al. (1992) as probable synapomorphies of palearaneodonts and xenarthrans, namely the postero-lateral-ventral expansion of the tympanohyal, the presence of a process extending forward from the anterior end of the criatal facet(s) termed "processus criatalis facetalis" by Paterson et al., (1989), and the enclosure of the occipital artery in a strongly developed groove or canal on the mastoid near the mastoid-squamosal suture, have not been included in this analysis because they are not relevant to relationships within the Tardigrada. Paterson et al. (1992) could find no derived similarities between the ear region of palearaneodonts and pholidotheres that were not also shared by xenarthrans.

Order Xenarthra—Only two of the characters used in the present analysis have a distribution such that they may represent xenarthran synapomorphies. Both are unambiguously placed synapomorphies. Xenarthrans are thus characterized by (6), a dorsally-oriented elongate tympanic bone and (40), the presence of the pterygoid in the body wall of the tympanic cavity. Other features which appear to distinguish the auditory region of xenarthrans from that of other edentates include a reduction in the antero-posterior length of the post-glosso-skeletal region of the skull, participation of the entotympanic in the margin of the posterior lacerate foramen (for a discussion of these two features see Paterson et al., 1992), presence of contact between entotympanic and pterygoid bones, absence of contact between tympanic and alisphenoid bones, and completion of the vertical tympano-hyalial to the mastoid. However, as with several of the edentate features discussed above, these characters have been omitted from the present analysis due to their effectively invariant distribution within Xenarthra, especially as regards the Tardigrada.

Node 1: Cingulata (Figs. 2, 3)—Armadillos, pumicehs, and glyptodonts may be diagnosed by the possession of four unambiguous synapomorphies of the auditory region, and perhaps two more features with equivocal distributions (Appendix 3).

12) Partially ossified auditory bulla—In many south american eutherians, the entosphenoid is attached to the tympanic at its anterior end only, leaving a small membranous portion of the tympanic floor through which the bulla is exposed ventrally. The entotympanic is not preserved in any known glyptodontan, and only fragmentary remnants of the tympanic have been preserved (S宫h, 1961), so the state of this character is unknown in glyptodontans. The primitive state, as exemplified by palearaneodonts, vemilungiosa, and many sloths, is to have a completely ossified auditory bulla with the entotympanic and tympanic in contact along their entire ventral margin, with little or no membranous component, and with the bulla covered ventrally.

35) Enlarged mastoid process—The enlarged post-

cess for the attachment of the sternomastoid muscle is absent or rudimentary in pholidotheres, vemilungiosa, and Palearaneodont. It is well developed in Metathecot omorphus and in sloths, but is greatly hyperrophied in the three cingulatid clades.

41) Anteroposteriorly elongate promontorium—The shape of the promontorium of the petrosal is unique among cingulates, being rounded and rather elongate anteroposteriorly, especially among glyptodontids (Pat terson et al., 1989). The petrosal tends to be obliquely flattened in pholidotheres and horizontally flattened in Palearaneodont (note that the state in these two taxa is given as unknown in Appendix 2 because the flattened state does not exist in the xenarthrans examined in this study [cf. Prionodon, Patterson et al., 1989]. The pcor sia is almost globular in Metathecot omorphus, vemilungiosa, and certain sloths, and this state is taken to be the primitive condition.

77) Glenoid inclined posterodorsally—The glenoid of cingulates possesses a distinct posterodorsal inclination. This inclination is especially marked in glypto-
donids, where the glenoid lies almost in the vertical plane. The glenoid is also posterodorsally inclined in the anteater Myrmecophaga and Tamandua. How ever, the edentate glenoid presumably slopes antero-
dorsally primitives, as it does in pangolins, palearane-
donids, and sloths.

Engelmann (1978, 1985) stated that the posterior lacerate foramen of palearaneodonts is in an unusual position, immediately posterior and inset dorsally relative to the entotympanic and petrosal (character 6551). However, this position of the posterior lacerate foramen is also found among pangolins, and as this group is placed as the sister-taxon to all other edentates in this analysis, the presumed derived state of Engelmann is treated as the primitive condition here. The posterior lacerate foramen is not sunken in palearaneodonts or cingulates, and given the delayed transformation optimization scheme employed in the study, this condition is listed as an ambiguous convergence between the two groups. Patterson et al. (1989, 1992) note that in some sloths and some cingulates, a prominent ridge of the squama is extending posterointernal to the glenoid forms a large portion of the anterior wall of the tympanic cavity. They consider this ridge, the entoglenoid process (character 83), to be a characteristic feature of xenarthrans. The entoglenoid process is apparently absent in pal eaneodonts and pangolins, and is absent or rudimentary in vemilungiosa. Therefore, the presence of a strong entoglenoid process (83(2)) is optimized as a convergence between cingulates and sloths.

Node 2: Pilosa (Figs. 2, 3)—As was the case with the cingulates, the monophyly of a clade containing sloths and anteaters may be diagnosed by four unequivocal synapomorphies. There are an additional three equivocal characters which may also serve as synapomor phies for this clade (Appendix 3). The unambiguous characters are as follows.

50) Subarcuate fossa dorsal to internal auditory meatus—The subarcuate fossa is usually weak or rudi-
FIGURE 2. Hypothesized phylogeny of the Tardigrada based on PAUP analysis of 21 extinct and extant species and their outgroups in the Vermilingua and Cingulata. This tree represents a strict consensus taken from three most parsimonious trees of length = 304 steps (CI = 0.405; RI = 0.80; retention index, an approximation of Archie's (1995) "homoplasy excess ratio") = 0.712. Characters are weighted such that all character states received equal weight. See text and Appendix 3 for listing of characters at each state per character. Characters indicating antitheatere and antitheatere conditions when characters are used in addition to the two sets of trees for the two additional character sets at each state per character.
mentary in adult edentates (Novacek, 1986; Novacek and Wyss, 1986). The fossa is generally more prominent in juveniles and is quite well-developed in the palement genera Cycloter and Tamandua. In palaeontodons the condition of the fossa is unknown. Primitively, as seen in pangolins and cingulates, the fossa lies dorsal and well posterior to the internal auditory meatus, so that the posterior border of the fossa lies completely posterior to the posterior border of the meatus. In vermilingua and in many sloths, on the other
hand, the subarcuate fossa is displaced anteriorly so that it comes to lie almost directly dorsal to the internal auditory meatus, with its anterior border lying near the anterior edge of the internal auditory meatus.

63) Enlarged posterior lacerum foramen—Though Novacek (1986) has suggested that an enlarged posterior lacerum foramen might be characteristic of all edentates, an enlarged foramen is, in fact, only present in Palaeotornis (Matthew, 1910) and the Pilosa. The posterior lacerum foramen remains rather small in M. tembercius and pholidota, and is quite small in cingulates, and hence this condition is taken to be primitive for edentates as a whole.

79) Glenoid with lateral shelf—Naples (1987) has pointed out that, in the sloth genera Bradypus and Neotropicals, the zygomatic process of the squamosal forms a ridge which extends ventral to the lateral side of the glenoid and retains lateral movement of the mandibular condyle. This feature appears to be widely distributed among sloths, and is also weakly developed in anteaters. It does not appear to be developed, however, among any of the outgroups to the Pilosa.

84) Postglenoid foramen reduced absent—Engel- mann (1978, 1983) suggested that the reduction or absence of the postglenoid foramen is a synapomorphy of pilosans. The foramen is clearly present in all the edentate outgroups (with the exception of Metachironomys; Patterson et al., 1992), and clearly is absent among the Vermilingua. Among sloths, however, the distribution of this feature is less straightforward. The foramen is very well developed in the Pleistocene taxon Megatherium, but in its sister genus, the Pliocene Erethrotherium, as well as in earlier Miocice sloth gen- era, there are a number of well-developed vascular foramina in the rutuse area immediately posterior to the glenoid fossa. Sometimes one of these foramina is distinctly larger than the others, and thus might be considered a distinct "postglenoid foramen." The my- lodontid sloths Cynotherium, Scelotherium, and Catagonus, as well as the megalonychid genus Megal- oxyce, possess a clear postglenoid foramen, but in each case this foramen, though isolated, is rather small. Al- though I suspect that the presence of a well-developed postglenoid foramen might be primitive for sloths, I will provisionally follow Engelmann in considering the postglenoid foramen to be reduced or absent in pilosans, with all sloths but Megatherium either lacking the foramen entirely or retaining it in a reduced state.

Three characters, in addition to the features listed above, may serve to characterize the Pilosa. The first of these, a contrast between enontympanic and mastoid (31), is also found among palaeotornids, and hence may be a synapomorphy at a more inclusive level with- in Edentata. However, the character state assignment for glyptodontans is unknown, and in dasyuropods and the early euphractan Prozacharia (in contrast to later euphractan taxa), the entotympanic is not well devel- oped posteriorly and does not contact the mastoid. It is difficult to determine polarity for the two states of character. In dasyuropods and euphractans, the dor- sal incaul facet of the maierus is much larger than the ventral facet, while in the maierus is much smaller. In pilosans, the two facets are subequal. The morphology of the maierus in palaeotornids and glyptodontans is unknown, while the incudal facet of pholidota are often quite poorly differentiated and of variable size relative to one another (i.e., in some species the facets are subequal, e.g., Mansus australis, M. tembercius; in others, the dorsal facet is larger; e.g., M. tembercius, M. tembercius). Because cingulates are designated as the "second," and presumably more primitive, out- group to the Tardigrada, the unequal incaul facets of the maierus characterizes these forms are rather arbitrarily assumed to represent the primitive condi- tion. The final character, glenoid located at or above the level of the supercifles mastoid (75), is characteristic not only of pilosans, but also of dasyuropods, euphrac- tans, and Metachirocyotes. In Palaeotornis, glyptodi- tons, and pholidota, the glenoid is situated ventral to the supercifles meatus. If pholidota and palaeo- stenops are employed as outgroups, the more dorsal position of the glenoid is optimized as a convergence among Metachirocyotes, the Dasyaya, and the Pilosa. If these taxa are not considered in outgroup compar- isons, the ventrally situated glenoid becomes an au- tomorphy of the Glyptodontidae.

Note 3: Vermilingua (Figs. 3.2.)—While monophyly of the Cingulata and Pilosa has been constrained prior to each of the present analyses, monophyly of the Ver- mingua and Tardigrada has not. Therefore, the pres- ent study provides a test of the monophyly of each of the latter taxa. The results of the present analysis sup- port the monophyly of the Vermilingua with as many as eight unequivocal synapomorphies, four of which are unique to this group (40, 60, 62, 69). Five addi- tional characters provide equivocal support for the clade (Appendix 3).

48) Entotympanic reduced—Patterson et al. (1992) note that the entotympanic of the Vermilingua with as many as eight unequivocal synapomorphies, four of which are unique to this group (40, 60, 62, 69). Five addi- tional characters provide equivocal support for the clade (Appendix 3).
omically—It is almost universally the case among mammals that the eustachian tube exits the antero-medial corner of the tympanic cavity to open into the nasopharynx. However, the secondary palate of antemtes extends posteriorly almost to the level of the posterior lacrimal foramen. This has brought the choanae and nasopharynx to a position posterior to the tympanic cavity, and has caused a concomitant shift in the position of the opening for the eustachian tube. In all antemtes this opening lies at the postero-medial corner of the tympanic cavity.

62) Eustachian tube directed posteroventrally—The orientation of the eustachian tube has been altered by its shift to a more posterior position in the nasopharynx. Primitively, the eustachian tube is directed ventrally and somewhat medially and anteriorly. In antemtes, it is directed strongly posteroventrally. It is worth noting that pholvidens cataphus, a condition somewhat intermediate between antemtes on the one hand and other xenarthrans as well as thersians (as well as thersian) on the other. In pangolins, the eustachian tube emerges last anterior to the mid-portion of the tympanic cavity, and from there courses anterolaterally through the nasopharynx (Winge, 1941).

69) Arteria diploatica magna enters sidewall of braincase.—In both polacanthodonts and xenarthrans the occipital artery travels within a groove or canal in the mastoid, near the petrosquamous suture, leading eventually to a so-called "mastoid foramen" at or near that suture (Patterson et al., 1972). This foramen is an opening for the arteria diploatica magna into the braincase. Angulates are unique among xenarthrans, however, in that the arteria diploatica magna branches off from the occipital artery and runs along the lateral wall of the braincase, entering the braincase through a foramen located on the suture between the parietal and squamosal (Hyrtl, 1854; Buggé, 1979; Wible, 1984).

Note 4: Tardigrada (Figs. 2, 4)—The morphophy of the Tardigrada is one of the most strongly supported results of the present analysis. The ear region of thyrsos is very distinctive, and this node on the cladogram is supported by eight unequivocal synapomorphies, five of which are unique (4, 23, 33, 66, 78). Another eight equivocal characters represent potential synapomorphies, four unique to thyrsos (19, 28, 51, 59; see Appendix 3).

4) Posterior crus of tympanic attached to squamosal-mastoid bridge.—In other xenarthrans the posterior crus of the tympanic attaches not only to the squamosal and mastoid, but to the tympanohyal as well. In thyrsos, however, a thin bridge of bone, formed either by squamosal, mastoid, or by both bones (the sutural relations
in this area are unclear in animals old enough to possess this bony bridge), separates the posterior crus from the tympanohyal.

16) Length of entotympanic greater than tympanic—Because of the extreme reduction of the entotympanic in anteaters, and its poor development posteriorly in dasyuspods and early eutherpods, the length of the entotympanic is less than or equal to that of the tympanic in these groups. However, in sloths the entotympanic is well developed posteriorly and forms a continuous crest with the paroccipital process. Therefore, the length of the entotympanic in sloths is typically much greater than that of the tympanic.

23) Entotympanic lateral surface flat ventrally, hollow dorsally—The entosymphysis is a thin bone in palaeanodonts, cingulates, and verminilus. In the former two taxa it is a laterally concave plate which descends from the ventral surface of the petrosal to form the medial wall of the tympanic cavity. It then arches ventrolaterally to participate in the floor of the cavity as well. In sloths, however, the morphology of the lateral surface of the entotympanic has an unusual configuration. It is hollowed out dorsally, arching under the ventral surface of the petrosal to participate in the floor of the tympanic cavity; but, ventrally, it forms a flat vertical surface which serves as the site of its attachment to the tympanic (see Fig. 6).

32) Mastoid exposed in depression between exoccipital and nuchal crest—In all xenarthrans, as in palaeanodonts but in contrast to pholidotes, the mastoid has a wide exposure on the posterior lateral surface of the skull (Piatnitz and others, 1992, contra Oppel and Wysa, 1996). However, in some dasyuspods and in all sloths, this mastoid exposure bears an unusual configuration. The bulge of the mastoid exposure lies in a dorsovertebrally elongate depression situated between two crests on the posterior lateral corner of the skull. One of these crests is the nuchal crest, which is continuous ventrally with the mastoid process; the second is a crest formed by the exoccipital which connects dorsally with the nuchal crest and ventrally forms the paroccipital process.

33) Mastoid with weak lateral exposure—In palaeanodonts, cingulates, and anteaters, the mastoid has a very broad lateral exposure. This is the case even in those dasyuspods in which a mastoid depression, as described above, is present. Among basal members of the Teguidae, however, the nuchal crest and mastoid process project posteriorly to such an extent that they effectively conceal the mastoid when the skull is viewed from the side.

58) Stylomastoid canal directed posteroventrally—As noted above in the discussion of the Cohort Edentata, in primitive ruminants, as well as in palaeanodonts, most cingulates, and verminilus, the facial nerve emerges from the tympanic cavity in a canal or groove which courses posteroventrally beneath the tympanohyal. However, a derived condition is found in pangolins, in which the stylomastoid groove runs directly posteriorly. Similarly, in Bradypus and other basal tardigrades, the stylomastoid cartilaginous first runs posteroventrally, but then turns and enters via the stylomastoid foramen as a posteroventrally directed groove travelling just medial to the mastoid process. Often, this groove appears to connect with the groove for the occipital artery, running within the mastoid depression immediately internal to the nuchal crest. The position of this character is somewhat variable, and may even vary among the tree in a one or two cases depending upon the resolution of the trichotomy at node 5.

68) Internal carotid artery sulcus saddle-shaped—In palaeanodonts, dasyuspods, and the anteater Cyclopes, the internal carotid artery runs in a bony sulcus (or, in the case of the latter taxon, an enclosed canal) medial to the tympanic cavity. This sulcus slopes anteroventrally from the posterior lacrimal foramen to the carotid foramen (in the former two clades) or to the median lacrimal foramen (in the latter taxon). A similar sulcus is present in sloths, but it does not assume a uniform anterodorsal slope. Rather, its posterior portion is inclined anterodorsally (often times quite steeply) and its anterior part slopes anterodorsally to form a saddle-shaped sulcus.

78) Glenoid with medial shelf—Naples (1987) has noted that, in the ground sloth Nothrotheriops and the tree sloth Bradypus, the medial translation of the dentary condyle in the glenoid is restricted by a raised, anteroposteriorly directed ridge formed at or near the sulcus between the squamosal and pterygoid bones. Contrary to the findings of Naples (1987), Webb (1985) has reported the presence of a similar crest in the tree sloth Choloepus, as well as in ground sloths of the family Megalonychidae (sensu Engelmann, 1985). The present study has found the distribution of this feature to be much wider among tardigrades than is indicated by either Naples (1987) or Webb (1985). A similar crest is present at or near the sulcus between the squamosal and pterygoid in all tardigrade taxa examined. The crest is an extension of the entotympanic process, and runs anteroposteriorly mediolaterally to the glenoid and just lateral to the foramen ovoid.

Four additional features may appear at this node and are unique to tardigrades, although optimization procedures leave their position somewhat ambiguous. The entosymphysis of sloths is a vertical plate attaching dorsally to the lateral portion of petrosal, and bearing a horizontal mediolateral expansion which lies above the course of the internal carotid artery (19). In contrast, the entosymphysis in dasyuspods and palaeanodonts is a more mediolaterally situated vertical plate without a mediolateral expansion (note that this character, which is unique to tardigrades, cannot be scored for the highly reduced entosymphysis of anteaters). The sloth entotympanic possesses a lateral process which contacts the tympanohyal (28). A contact between the two bones is also present in palaeanodonts, extant eutherpods, and pyrethopteriosteans, although not in the form of a distinct process. The tympanohyal of tardigrades is directed ventrally and somewhat posteriorly (51), unlike the condition in anteaters and cingulates, in which the tympanohyal is directed ventrally (in the case of R. furmr (or b) bearing the process of the incurved groove for i (or b) in a situationally similar gesture.)

This connect (the character paralingualis, which is not attributable for the anter.). Bradypus — the branch is its basal point of autapomorphy (in many as for example, the 'brach 82) in this synapomorphy (character). 82 is not usable to the characters (note that the process of the synapomorphy (character)

Node 5 (Fig. 3) of the features are not well resolved so far. in the absence of data (so more juvenile taxa are included in this analysis. In more advanced states they represent differences between Bradypus, this character can be resolved by as many as many synapomorphies as possible.)

22) Entotympanic anastomosis with the entosymphysis (in some cingulata) (1989), the entotympanic (as in anteriorly.)

In upper slightly the width of the tympanohyal.
which the tympanohyal deviates sharply from the vertical in either the lateral direction (in the case of the former) or both the lateral and medial direction (in the case of the latter). Lastly, slots possess a groove leading from sylomastoid foramen that connects to the groove for the occipital artery, linking the ventrally situated sylomastoid foramen to the distant, dorsally situated foramen for the arteria diploietica magna (58). This connection is not present in any other edentates (the character is not applicable in the case of vermiculinae, which lack the typical postquamosal foramen for the arteria diploietica magna).

Bradyopus - The auditory region of the living three-toed sloth is very unusual among atroglands, as both the basal position in the cladogram and its large number of autapomorphies (9 unequivocal autapomorphies and as many as six which are equivocal attempts. Interestingly, the presence of several autapomorphies (5701, 8372) in this genus and the absence of several of the synapomorphies which characterize all other sloths (see characters 52, 53, 56, 81 at node 5) might be attributable to the neotenic retention, in the adult, of juvenile features present in immature specimens of other sloths (see character 53 below, as well as discussion of vagina processus hyoideus; Patterson et al., 1992). Also of interest are the many derived characters found both in Bradyopus and the megatheriids (1111, 1311, 2411, 6410, 6312, 6300, and the ambiguous characters 1011 and 311, of which nearly half are features of the well-developed tympanic bone of these two taxa. Several of these characters are unequivocal Bradyopus and megatheriids (or nearly so), and in preliminary analyses implicated Bradyopus as the sister group to megatheriids (Braun, 1990), but note that the Santacrucian megatheriid Pliopithecus was not utilized in the earlier analyses. The presence of a rough-walled epimastic nymph in Bradyopus and some of its relatives (Patterson et al., 1992, 1993) to link Bradyopus and megatheriids, was deleted from the final analysis in the present study, because it was present only in the sloth genus Bradyopus and Erethizonidium and in myrmecophagid anteaters, and was not useful for diagnosing more inclusive clades. As mentioned above, several of the features which support the monophyly of a clad including all sloths except Bradyopus may simply be the result of extreme retention of a more juvenile morphology. However, even if one were to ignore these features on the assumption that they represent autapomorphic neotenic reversals in Bradyopus, this node is still relatively well supported as similarly as five unequivocal and one equivocal synapomorphies (Appendix 3).

22) Eotyotympanic widened posteriorly. — In Bradyopus, vermiculinae, and some cingulates, the width of the eotyotympanic is fairly uniform throughout its length in some cingulates, e.g., Procynodon (Patterson et al., 1989), the eotyotympanic is actually somewhat widened anteriorly. In most sloths, however, the eotyotympanic tapers slightly toward the front, whereas posteriorly the width of the bone increases sharply just anterior to the stylohyal fossa (see below) due to the presence of the lateral process which extends out to contact the tympanohyal.

46) Small lateral exposure of the fenesträ cochlearis. — In pholidotans and cingulates the fenesträ cochlearis is broadly exposed in lateral view. Although the lateral exposure of the round window is less well developed in vermiculinae and Bradyopus, the lateral edge of the fenestra lies well in advance of the medial edge in ventral view. In basal sloths, the fenestra cochlearis is not well exposed laterally, and its lateral edge is either slightly or not at all anterior to the medial edge in ventral view. This character is rather labile within the Tardigrada. It reverses itself on three separate occasions (nodes 15 and 20, Pliopithecus), and may shift its position on the tree depending on the resolution of the basal trichotomy at node 5.

52) Tympanohyal widened distally. — In pholidotans and cingulates, the tympanohyal is a slender, rod-like element of relatively uniform width throughout its length. Among tardigrades, however, the tympanohyal is markedly expanded distally, widening to form a large portion of the articulans fossa for the stylohyal (see below). Bradyopus is the only sloth which lacks such a distal expansion of the tympanohyal. However, the lack of an expanded tympanohyal in Bradyopus may represent a neotenic retention of a juvenile feature, as the stylohyal fossa in other sloths tends to develop fairly late in ontogeny (Patterson et al., 1992, pers. obs.).

The stylohyal fossa present — As described by Patterson et al. (1992), sloths are characterized by the possession of a large fossa at the distal end of a process typically formed by the tympanohyal, mastoid, enotympanic, and exoccipital bones (but see description of Schizoatherium; Patterson et al., 1992). This fossa serves as an articualr facet between the skull and the stylohyal. To my knowledge such a fossa is not found in any other group of mammals. The only structure that comes close to resembling the stylohyal fossa among other edentates is a small, circular pit found in some eucharctans. This pit is formed in the mastoid region and is a surface exposure of the tympanohyal, where the stylohyal attaches to the skull. The stylohyal fossa is not present in Bradyopus, which instead possesses a depression formed at the tip of the tympanohyal, the vagina processus hyoidei, which serves as a site of attachment for the stylohyal. However, examination of juvenile specimens of other sloth genera (Patterson et al., 1992, pers. obs.) has shown that the stylohyal fossa of adults develops from a juvenile condition very similar to the vagina processus hyoidei of Bradyopus. This raises the distinct possibility that the presence of the vagina in adults of Bradyopus represents a neotenic retention of a more general juvenile condition.

56) Stylohyal articulation faces ventrally. — Both the stylohyal pit of some eucharctans and the vagina processus hyoideus of Bradyopus face almost directly posteriorly. The stylohyal fossa of other basal sloths, on the other hand, is directed primarily ventrally (as well
as slightly posteriorly, and slightly medially or laterally. In various more derived tardigrade groups the stylolythic fossa may develop a strong lateral exposure (node 17; Hapaloplis, Planhori, Chlopos新华社). 81) Posterior surface of the pleurodont ridge—The area immediately posterior to the pleurodont fossa has a relatively smooth surface in all the taxa which have been employed as outgroups to the Tardigrada in the present analysis. Similarly in Bradypus, this region is fairly smooth (although this may again represent a retention of a juvenile feature). In other basal stylol taxa, however, this area becomes quite rugose, and is usually perforated by numerous vascular foramina, often including (as stated above, see node 2) the postpleural foramen/foramina.

Node 5 is characterized by a basal trichotomy among the Santacrucian genera Pelalyodon and Schizommotherium and all remaining stylolths. In trees in which all character states are weighted equally, all three resolutions of this trichotomy are equally parsimonious. In trees in which all characters are weighted equally, only two of the three possible resolutions are represented in the shortest trees. The two resolutions which are supported in this latter instance are a sister-group relationship between the two Santacrucian genera, and a tree in which Schizommotherium is the sister group to a clade including Pelalyodon and all other stylolths. The former grouping is supported by (5), the medially unexpanded tympanic of the two Microrn genera, the latter by the shared possession, in Pelalyodon and higher stylolths, of (15), a stylolythic articulation formed by mas- toid, entotympanic, and exoccipital as well as tympano-typhal.

Node 6 (Fig. 2)—This node, which unites the Santacrucian genera Hapaloplis and Euchelavogloss with retaining stylolths, is one of the more weakly supported nodes in the cladogram. Only one unambiguous character supports the monophyly of this clade in all trees, which is the presence of two additional inequivocal characters, depending on the resolution of the trichotomy at node 5, and as many as five additional equivocal features (Appendix 3). In preliminary analyses, Hapaloplis and Euchelavogloss were found to group with their fellow Santacrucian genera Pelalyodon and Schizommotherium (Gaudin, 1992).

The rugose tympanic in almost all members of the various tardigrade outgroups, the external surface of the tympanic is relatively smooth. A smooth tympanic is also variably present in Bradypus (although usually in younger individuals; Patterson et al., 1992), as well as in the Santacrucian forms Pelalyodon and Schizommotherium. However, the external surface of the tympanic in Hapaloplis is roughened, especially toward its outer margins. A similarly rugose tympanic is found among other stylolths traditionally placed in the superfam-ily Nothotheriinae, as well as in the Megalotheriidae and some members of the family Megalonychidae (see node 14). This character is the only unequivocal synapomorphy of this clade found in all three most parsimonious trees.

26) Entotympanic forms medial and lateral wall of internal carotid sulcus—As in Bradypus and dasyopod-ids, the entotympanic of Hapaloplis and Euchelavogloss forms not only the lateral wall and roof of the internal carotid artery, but the medial wall as well. This medial wall takes the form of a ridge extending ventrally from the medially expanded portion of the entotympanic and running parallel to the lateral, platy-like portion of the bone. This medial ridge is present in all stylolths which occupy a position above this node in the cladogram, with the exception of the genera at nodes 16 and 22.

39) Pterygoid with lateral groove (Fig. 4)—In Hapaloplis a wide groove runs along the posteroarterial surface of the descending lamina of the pterygoid and enters the tympanic cavity through a broad opening lying dorsal to the eustachian tube and ven- tral to the sulcus magellensis and fossa glaseri (Pa- tterson et al., 1992). This groove is also present in other stylolths, including Euchelavogloss, Bradypus, nothotheri- inae, and megatheriines. Its function is unknown, al- though Patterson et al. (1992) have speculated that it may represent the attachment site for the tensor veli palatini muscle. This character and character 26 are equivocal only in trees in which Pelalyodon and Schizom- otherium form a clade.

Node 7 (Fig. 2)—The monophyly of a clade including both Hapaloplis and Euchelavogloss is weakly supported by two unambiguous and one ambiguous characters. The first of the unambiguous characters is a unique feature among edentates (36), in which the lateral tip of the mastoid process is perforated by a small oval foramen that opens into a small, posteriorly directed groove ending at the posterior edge of the nuchal crest. This foramen is presumably vascular in nature. The other unambiguous character that supports this node is (61), eustachian tube emerges between the entotympanic and tympanic bones only, a feature con- vergent on the condition in dasyopodids.

Node 8—"Eustardigrada" (Fig. 2)—This clade is pro- visionally termed the Eustardigrada, fot it contains all the well known Pleistocene stiloliths, including the type genus Bradypus and the genera Nothotherium, Dasyopygus, Megalonychus, and their close relatives, as well as all members of the families Megalotheriidae and Mylodon- daceae. The presence of this group is supported by four unequivocal synapomorphies, two of which (48, 59) are unique to this clade, as well as one addi- tional equivocal feature.

29) Entotympanic with strong participation in tym- panic cavity floor—The dorsal hollow in the lateral surface of the entotympanic, which is a unique feature of the Tardigrada (see node 4), is much more strongly developed in nothotheriines, megatheriids, and most mylodontids than in Bradypus tardigrades or in megalony- chids (see node 14). This allows the entotympanic a greater participation in the floor of the tympanic cavity, so that it forms roughly the same proportion of the floor as the entotympanic of palaeanodonts and dasy- pods.
48) Internal auditory meatus deep, undivided.—The morphology of the internal auditory meatus is unique among eustardiagride sloths. The meatus is not a shallow fossa perforata but a very large foramen, as is typical for other edentates and for early thran mammals (MacIntyre, 1972; Wible, 1990), but is an undivided canal penetrating deep into the medial side of the petrosal. In fact, the bar of bone dividing the course of the auditory nerve from that of the facial nerve is not visible in medial view in any fossil eustardiagride sloth, with the sole exception of Acrotriconus, in which it is recessed within a deep hollow.

59) Stylohyoid foramen connected to ventral opening of canal for occlusal artery by strong groove.—As described above (node 4), sloths are characterized by an open groove which connects the ventrally situated stylohyoid foramen to the dorsally placed foramen for the arteria diploatica magna. In most eutardiagride sloths, however, the occipital artery is at least partially enclosed in a bony canal (see node 10). The ventral opening to this canal is much closer to the stylohyoid foramen than is the opening for the arteria diploatica magna. It typically lies posterior and slightly dorsal to the stylohyoid foramen. Various modifications to this arrangement appear repeatedly within this clade (see Notritheriini, Pilopinae, Megalonychidae, Pseudopeneceratium; nodes 9, 12, 15, 18, 22).

In addition, the Eustardiagridea may be distinguished from most basal sloth taxa on the basis of an ambiguous character (30) involving the position of the medial expansion of the eustardiagrine relative to the basi- ceranium. As described for node 4, the entotympanic of sloths usually takes on the shape of a laterally situated vertical plate with a medial expansion lying above the internal carotid artery. In most basil tardigrades, this medial expansion lies near the level of the basi- ceranium. In the Santacruziacrus genus Eucolobopit and the eutardiagride sloths, this medial expansion is well above the root of the basi- ceranium.

Node 9: Subfamily Notritheriinae (Fig. 2) — As traditionally defined, this taxon would include not only Plio-Pleistocene genera, but also the Miocene Santa- cruziana genera discussed above. The results of the pres- ent analysis indicate that the subfamily so defined rep- resents a paraphyletic taxon. I therefore suggest that the name Notritheriinae is more appropriately used to refer only to the Plio-Pleistocene forms, represented in the present study by the Pleocene genus Pronothri- therium and the Pleistocene Notritheriops. (Note that the "subfamily" distinction here is somewhat meaningless, as the notritherines lie outside the three traditional ground sloths families in this analysis. A familial distinction for this group might be more appropriate.) However, even this restricted definition of notritherines might be questioned on the basis of 

14) Fissura Glasteri opens into squamosal groove — The fissura Glasteri is present in all sloths, opening between the sulcus malleolaris of the tympanic and the squamosal near the pterygo-squamosal suture. The fissura Glasteri of notritherines is separated from the squamosal suture by a secondary suture (node 14) and of Bradypus, in that it opens into a distinct groove in the squamosal which passes medial to the enotympanic process and terminates at the foramen ovale. Such a groove is weakly indicated in some speci mens of Myrmecophaga, but is otherwise not present in other sloths or in any edentate outgroup taxa.

54) Stylohyal fossa oval — The stylohyal fossa of most sloths, including the basal taxa, is circular in shape. However, in a few derived forms, including nothroti- 

eres (see also Acracricus, Octoedotherium; node 18), the fossa elongates anteroposteriorly and takes on a more oval shape.

85) Root of zygoma directed anteriorly.—In almost all edentate taxa the root of the zygoma extends anteriorly and somewhat laterally from the side wall of the braincase. In glyptodonts and certain sloths (node 14), the zygoma becomes oriented more laterally in connection with the mediolateral expansion of the gleno- 

oid. In nothrotiheres, however, the zygoma is oriented in the opposite direction, extending almost directly anteriorly from the side wall of the braincase. This an- teroposterior orientation of the zygomatic root is also developed in Bradypus and in certain megatheriids (node 12).

The morphol ogy of the nothrotiheres is further sup- ported by one ambiguous character (69) that is unique to nothrotiheres. In both Notritheriini and Proto- 

ohippotheres, the occipital artery is encased in a bony 

channel which perforates the mastoid process, entering the occiput ventrally from the mastoid depression and emerging dorsally on the side of the braincase. Pre- sumably, the artery dips diplotica magna exits the brain- 

case fold within this canal.

Node 10 (Fig. 2) — The monophyly of this node, which groups together members of the three traditional fam- 
ilies of ground sloths (Megalonychidae, Megalonychinae, and Myiodontidae) to the exclusion of sloths from the subfamily Notritheriinae, is diagnosed by three un- equivocal and three equivocal synapomorphies. Of the three unequivocal synapomorphies at this node, one (50) represents a reversal to the primitive edentate con- dition, while the character state assignments for an- other (74) are unknown in more than half of the sloth genera examined, suggesting that the monophyly of these taxa rests on weak evidence at best.

27) Entotympanic curves above tympanic anteri- orly.—As described above, in basal tardigrades the lat- 

teral portion of the entotympanic takes the form of a vertical plate along most of its length. Towards the an- terior end of this plate, however, the dorsal portion of the plate begins to bend laterally, and so comes to lie above the eustachian tube and the tympanic, forming a small part of the roof of the tympanic cavity. Among sloths of this clade, as well as in members of the genus Eucolobopit, this lateral curvature of the anterior por-
tion of the entonypamic is absent, and the entonypamic does not participate in the tympansic cavity roof.

74. Angle between mammillar head and neck of mammillar less than 180° — The mammillar of euphractan aramidales, verminiquas, and the basal tardigrade genera Bradypus and Notrothriopotes are all characterized by a mammillation which is roughly in line with the neck of the bone in lateral view (Patterson et al., 1992). In dasypodid aramidales and in this clade, the angle between the mammillation and neck of the mammillar is typically much less than 180°, ranging from 110-130°.

Other features which may serve to diagnose this node include the ambiguous synapomorphies (963) and 711(1). The former character, in which the occipital artery is completely enclosed within a bony canal, with the dorsal opening for the artery diplagnosta magna located within the canal and hidden from external view, differs from that character state described at node 9 in that the canal does not perforate the mastoid process, but rather travels along within or just posterior to the nuchal crest. Character 71, in which the head of the mammillar is parallel-sided in dorsal view, was described by Segal (1976) as characterizing all pilosans except Cyclopes. Patterson et al. (1952) noted that the parallel-sided mammillar head, while present in other anteaters and in Bradypus, is not characteristic of the genus Notrothriopotes. Since the condition of the mammillar is unknown in other basal tardigrades, this feature is considered convergent between myrmecophagines, Bradypus, and the clade represented at node 10.

Node 11: Megatheriidae (Fig. 2).—While noting the marked similarity between Planopos and the other sloths from the Santa Cruz Formation, Scott (1903-1904) suggested that this genus (along with the closely related form Protatherium) may be allied to the Megatheriidae based on its large size, possession of an odontoid process on the astragali, and a dorsoventrally elongate pubis and ischium. The present analysis provides tentative support for the common ancestry of Planopos and the Plio-Pleistocene megatheriids, in the form of three unambiguous ear region synapomorphies.

7) Styloform process of tympanic absent — In almost all other edentates, a small styloform process is at least variably present at the anterioventral corner of the tympanic bone. Indeed, this process is also present in some, but not all, specimens of the megatherid Eremotherium which I had the opportunity to examine. The complete absence of such a process in the megatheriids Planopos and Megatherium and its convergent loss in the mylodontid 'Leotodon' may be due to the small number of specimens available for examination in each of these taxa. However, the absence of this process is provisionally accepted as a synapomorphy of megatheriids, which is secondarily reacquired in some individuals of Eremotherium.

10) Tympanic-pterygoid contact — The presence of a distinct contact between these two bones represents a convergence between Bradypus and megatheriids; in both, it is attributable to the prae medial and lateral expansion of the tympanic bone. Hypertrophy of the pterygoid is responsible for the convergent appearance of this character among vertebrata; a tympanic-pterygoid contact is also consistently acquired in the sloth genera Acratus and Glisochtherium/Paramylodon.

24) Entonypamic directed anteroposteriorly — In almost all edentates, the entonypamic extends anteroposteriorly, medially from the tympanicotub and border of the posterior lacerate foramen to the eustachian tube and medial lacerate foramen. Its shift to a more anteroposterior alignment (with a presumably corresponding lateral shift in the position of the latter two openings) in megatheriids is unusual, and represents yet another convergence with Bradypus, as well as with the Pleisto- cene megalonychid Megalonyx.

Node 12: Megatheriinae (Fig. 2).—Although the association of the Myconoe genus Planopos with later mega- theriids may remain somewhat tentative, there is little doubt as to the monophyly of the Plio-Pleisto- cene megatheriids, a morphologically homogeneous group represented in the present analysis by the southern South American genus Megatherium and the more widespread, northerly genus Eremotherium, known from deposits in northern South America, Central America, and southern North America (Hoffstetter: 1952; Gazin, 1956). Monophyly is supported by no less than 11 unambiguous auditory region characters, five of which are convergent on the living tree sloth Bradypus.

The latter five include characters 3(1), 11(2), 13(1), 64(0), and 85(0). Character 11, in which the tympanic bone forms a posterior extension to the glenoid fossa, is a feature unique to Bradypus and megatheriines. Char- acter 13, an ossified external auditory meatus, is a character known elsewhere among edentates only from the Paleonodonata and euphractan aramidales. In addi- tion to these five characters, the Megatheriinae can be diagnosed by one unique feature, (76), the presence of a hemispherically-shaped glenoid fossa; one nearly unique feature, (6), an anteroposteriorly elongate tym-panic (present only in the anteaner genus Cyclopes among other edentates), and two reversals to a more primitive condition, characters 8(1) and 170(1).

Node 13 (Fig. 2).—In contrast to the phylogenies of Patterson and Pascual (1968, 1972) and Patterson et al. (1992), the present analysis does not support the monophyly of the Megalonychidae, defined as a clade including megalonychids and megatheriids (the latter incorporating the subfamily Notrothriopinae) to the exclusion of mylodontids. Rather, the megalonychids and mylodontids are allied as a monophyletic clade diagnosed by six unequivocal synapomorphies (Ap- pendix 3), with both the Megatheriidae proper and the Notrothriopinae excluded from this grouping.

37) Nuchal and exoccipital crest converge distally — In conguaculates and all of the more basal tardigrade taxa, the nuchal and exoccipital crests which delimit the mastoid depression run essentially parallel in posterior view. However, in basal members of both the Megap- paretetes and otophylacaus, with cental surface flat, and surfaces in the
distant (i.e. ventral) extremities. It is worth noting that, within both families, the crests are modified so that they appear to diverge distally in some taxa (see Chelopus; note 19).

38) Parocarcipal process well-developed—In basal tardigrades the parocarcipal process tends to be rather poorly developed, with only a slight participation in the formation of the stylohalyostomatous fossa (and in some juvenile individuals with no participation in the fossa; see description of Hapalognus in Patterson et al. (1992). However, in all megalanochydids and mylodontids, the parocarcipal process is a well developed crest with a substantial participation in the stylohalyxal fossa. Indeed, as in the character above, there is a parallel further hypertrophy of the process within both families (see nodes 15, 18).

70) Foramen magnum venous sinus present—Patterson et al. (1992) describe a large groove occurring in sloths of this clade which connects the internal opening of the posterior lacerate foramen to the foramen magnum. The groove is present in the extant tree sloth Choloepus, in which Patterson et al. (1992) claim the groove marks the course of a large venous sinus (although it is unclear whether Patterson and Segall performed the necessary dissections to confirm this). The groove is lost in Glossotherium/Paramylodon and appears to be convergently acquired in the genus Nothotherium.

82) Glenoid well separated from porus acousticus—As in Nothotherium, the glenoid fossa in both megalanochydids and mylodontids is displaced far anterior to its primitive position just anterior the porus acousticus. This unusual anterior migration of the glenoid relative to the ear region is known elsewhere among edentates only in the Pholidota and the pygmy anteater Cyclopes.

Node 14: Megalanochydidae (Figs. 2, S)—The monopoly of a megalanochydid clade which excludes nothotheres and includes the extant two-toed sloth Choloepus is perhaps one of the most surprising conclusions of Bryan Patterson’s systematic work on the Xenarthra (Patterson and Pascual, 1968, 1972; Patterson et al., 1992). As discussed by Patterson et al. (1992), it is also the most strongly supported of his conclusions. The monopoly of this clade is also strongly supported in the present analysis, diagnosed by seven unequivocal and two equivocal characters (Appendix 3).

29) Entotympanic with weak participation in tympanic cavity floor—In a reversal from the condition characteristic of the Eutardigrada (node 8), megalanochydids reduce the prominence of the dorsal hollow of the entotympanic, and concomitantly reduce the extent of entotympanic participation in the floor of the tympanic cavity. The entotympanic plays only a minor part in formation of the floor in Megalanoxys and Megalocnus, while in Acratocnus and Choloepus, the lateral surface of the entotympanic is almost completely flat, and only the posterior portion of the bone participates in the tympanic cavity floor.

64) Posterior lacerate foramen circular—As is evident from Appendix 3, the shape of the posterior lacerate foramen is somewhat labile among edentates, changing up to five times on the shortest tree. Nevertheless, the evidence from pholidotans, cingulates, verminilugus, and basal tardigrades strongly suggests that an oval posterior lacerate foramen is primitive for edentates as a whole, and that the circular foramen characterizing megalanochydids, as well as palaeoedonts, megatheres, Bradypus, and Pseudopropotherium, is a derived feature evolved independently in each of these clades.

75) Glenoid ventral to superficies melatus—The difficulties of assigning polarity to this character within the Edentata are noted in the above discussion of characters diagnosing the Plisosa (node 2). While it remains unclear whether or not the ventral position of the glenoid (as found in pholidotans, glyptodonts, and some palaeoedonts) is primitive for all edentates, it is abundantly clear that such a position is derived within the Tardigrada and constitutes a unique feature of the megalanochydid sloths. Indeed, the glenoid fossa of this family is highly distinctive, as attested to by the fact that five of the nine characters diagnosing this node are characteristics associated with the glenoid.

76) Glenoid widened mediolaterally—The glenoid fossa of megalanochydids differs from that of other sloths and resembles that of glyptodonts and palaeoedonts in being extremely narrow anteroposteriorly and very wide mediolaterally. The fossa takes on an almost rectangular shape in Megalanoxys and Megalocnus, a shape reminiscent of glyptodonts, whereas in Acratocnus and Choloepus the fossa is more crescentic, resembling more closely the glenoid of the palaeoedonts.

85) Root of zygoma directed laterally—The zygomatic root of megalanochydids resembles neither the anterolaterally-directed root of primitive edentates, nor the anteroposterior-directed zygomatic root of certain sloths (Bradypus; nodes 9, 12), but rather the laterally-oriented zygomatic root of glyptodonts. This re-orientation of the zygomatic root, which corresponds to the transverse widening of the glenoid, is unique to these two groups of edentates, with the possible exception of the Santacrucian sloth genus Eucholeopus, which, as noted by Scott (1903–1904), may show an incipient lateral re-orientation of the zygomatic root (although it is not coded as such in the present analysis).

Node 15 (Fig. 2)—As in the phylogenetic hypotheses of Hirschfeld and Webb (1968), Engelmann (1985), and Webb and Perrigo (1985), the present analysis supports the monophyly of the Pleistocene sloths from the Greater Antilles. However, unlike these hypotheses, but in accord with the phylogeny of Patterson et al. (1992), the present study also supports the inclusion of Choloepus in this group. Node 15 is diagnosed by three unequivocal and two equivocal synapomorphies (Appendix 3).

Node 16 (Figs. 2, S)—Patterson et al. (1992) noted...
that the group of Puerto Rican sloths and the auditory characters vary between the two genera. However, parts of the stapedial and tympanic cavities are more primitive in both genera, and the bulla and tympanic cavity remain compact. The sulcus is also present in both genera.

9) Sulcus of the stapedial and tympanic cavities. The sulcus tends to be more developed in the anterior part of the tympanum, forming a more distinct sulcus in the posterior part.

25) Dorsum and Chorda tympani. The dorsal process is reduced in most species, particularly in the anterior part of the tympanum, forming a rather flat area.

26) Glenoid fossa. The glenoid fossa is slightly deeper in the anterior part of the tympanum, and the articular surface is closer to the stapedial process. The co-ossification between the squamosal and the tympanic bone is more complete in some species.

The equidistant centrum is covered by the tympanic bone, covering the centrum and the tympanic cavity.

FIGURE 5. Ventral view of the posterior portion of the skull in: A. Choloepus hoffmani, FMNH 30739 (left side only); and B. Acratospilus odontognathus, AMNH 17722. Characters and character states as in Figure 3 (drawings reprinted, with permission, from Patterson et al., 1992).
that the ground sloth *Acaractes*, from the Pleistocene of Puerto Rico, exhibits remarkable similarity to *Cholo-
dus* in many features of its cranial (and postcranial) anatomy, but the resemblance is especially marked in the auditory anatomy of these two taxa. There are ten characters which indicate a close common ancestry between these two genera (Appendix 3). Only three of these characters are unambiguously assigned to this node. However, this fact may be attributed in large part to gaps in our knowledge of the auditory anatomy of *Megaloceros*. The hypothesized sister-genus to *Astra-
cerus* and *Choloerus* none of the *Megaloceros* spec-
ies examined preserves more than fragmentary re-
mains of the tympanic and ototympanic. More than half of the ten characters at this node are reversals to a more primitive condition, indicative of the fact that, at both genera, the degree of ossification of the auditory bulla and its surrounding elements is reduced with respect to that of closer related forms.

9) Sulcus and crista tympanica reduced—This is one of two characters which are unique to these two genera of sloths (the other being character 20; see below). The sulcus and crista tympanica, which are located on the inside of the tympanic ring and mark the attachment site of the tympanic membrane, are well developed in all other edentates. In *Acractes* and *Choloerus*, how-
ever, the crista takes the form of a low ridge and the sulcus is barely indicated.

23) Dorsal edge of ototympanic flat—In *Acract-
nes* and *Choloerus* the ototympanic is considerably reduced, lacking for the most part of the malleohyoid, and indeed other sloths in general. This reduction is es-
specially marked anteriorly, where the ototympanic forms a very narrow carina. As a result, it does not curve dorsally with the ventral surface of the pro-
antomium, as in other sloths (even in those basal forms in which such a curve is weakly developed), but rather forms a nearly flat dorsal edge.

82) Glenoid separated from porous acousticus—Along with the reduction of the tympanic and ototym-
picanic, these taxa exhibit a reversal in the position of the glenoid relative to the porous acousticus. As dis-
cussed above at node 13, megalonychids and mylo-
donids in general can be distinguished from other sloths by the anterior displacement of the glenoid. Patterson et al. (1992) point out that the glenoid is situated much closer to the porous in *Acractes* than in *Megaloceros* and *Megalotis*, and that in *Choloerus* the glenoid is even closer to the porous. In fact, in *Choloerus*, as in basal tardigrades, the glenoid is only narrowly sepa-
rated from the porous by the entoligoid process.

The equivalent characters assigned to this node also provide evidence for the reduction of the ototympanic and tympanic in *Acractes* and *Choloerus*. The lateral plate of the ototympanic becomes very thin and sharp-
edged ventrally (20), a feature unique to these two taxa, and the lateral surface of the ototympanic becomes flat (23). Because of the anterior reduction of the ototym-
picanic, the median lacerate foramen is only par-
tially covered in *Choloerus* (15) and is fully open in

ventral view in *Acractes*. The reduction of the me-
dial expansion of the ototympanic means that the ototympanic no longer participates in the medial wall of the internal carotid sulcus (26).

Node 17: *Myloodontidae* (Figs. 2, 6, 7)—Although Patterson et al. (1992) use the morphological differ-
cence of this family, they provide little character support for the monophyly of the group. In the present analysis, however, this is one of the more robust nodes of the entire cladogram. There are 13 characters which serve to diagnose the monophyly of this family (Appendix 2), 10 of which are unambiguous, and three of which (45, 58, 83) are unique among xenarthrans.

5) Tympanic medial expansion absent—As at node 16 above, a reduction in ossification of the auditory bulla occurs in myloodontids. However, here it is the tympanic that is reduced, taking on a simple, unex-
panded, ring-like morphology in all taxa for which it is known.

12) Auditory bulla partially ossified—Consistent with the reduction of the myloodontid tympanic, the tympanic floor incorporates a substantial membranous component to its walls. As the tympanic is still typi-
cally in contact with the ototympanic at some point, the membranous component remains small, transient-
tng the condition in cingulates and the Santa Cruzian genus Schizoherium.

33) Mastoid with strong lateral exposure—As de-
scribed above, tadpole-like as a whole are characterized by a small lateral exposure of the mastoid. Mylo-
donid and mephalopsids show an increase in size of the exoccipital and paroccipital crests, which leads in the latter group to an increase in lateral exposure of the mastoid, as the edge of the mastoid depression is pulled out posteriorly and ventrally. The mastoid does not exhibit a greater lateral exposure in any megalonychid but *Choloerus*, because all other megalonychids have a coincident increase in the size of the mastoid process, which serves to obscure the mastoid in lateral view.

43) Epitympanic sinus absent—The primitive state for this character among Xenarthra as a whole is some-
what uncertain. It is present in pholodons, palaean-
donts, and euphractan armidillios, but absent in all other cingulates. However, almost all pilosilanos possess a well, developed epitympanic sinus, and the presence of such a sinus is clearly primitive among sloths. The absence of such a sinus among myloodontids distinguishes them from other sloths in this regard.

45) Fossa incudis lies in posteriorcomial epitympanic recess—The fossa incudis of myloodontids lies within the epitympanic recess, as it does in all edentates. How-
ever, the epitympanic recess is somewhat more later-
ally expansive in mylopondontidae. This is typical of eden-
tates. As a result, the fossa incudis is restricted to the postcomial corner of the recess, alongside the lateral wall of the crista facialis. In all other edentates, with the sole exception of *Palaeanodon*, the fossa incudis occupies the entire ventral portion of the postcomial wall of the epitympanic recess.

56) Stylohyal articulation faces ventrolaterally—As
described above, the stylohyal fossa of most basal taxa is directed almost directly ventrally (see node 5). However, in a number of tardigrade taxa, including the mylodontids, as well as the genera *Hapalognathus*, Plan separates, and *Chelognathus*, the fossa is directed not only ventr  
ally and slightly posteriorly, but also strongly later ally, rendering the fossa clearly visible in lateral view.  
38) Stylohyal canal directed ventrolaterally. The stylohyal canal is usually in mylodontids  
in that it opens into a canal running almost directly laterally, across the anterior faces of the tympanic cavity and the mastoid, which projects ventrally to form large por  
tions of the stylohyal fossa. In other sloths discussed above, this canal runs either posterolaterally or directly pos  
teriory.  
62) Eustachian tube directed anteriorly—Patterson et al. (1992) note a distinction between mylodontid and "megalonychoid" (i.e., megatheriid and megolen -ycho) sloths in the course taken by the eustachian tube after emerging from the tympanic cavity. The eustachian tube of "megalonychoids" follows a fairly prim  
tive course, exiting between enostympanic and tym  
panic and travelling ventrally as well as somewhat medially and anteriorly. Among mylodontids, however,  
the eustachian tube takes a much less ventrally oriented and much more strongly anteriorly oriented course, crossing the base of the pterygoid lamina in a broad, fairly well-defined groove. This strong assessor orien  
tation of the eustachian tube is much like that char  
acteristic of glyptodontans, although in the latter group the tube passes well dorsal to the small pterygoid bone.  
83) Entoglenoid process weak, oppressed to de  
sending lamina of pterygoid—The entoglenoid pro  
cess of mylodontids is weakly developed, much like the entoglenoid of *Bradypus* and some megatheriids. The mylodontid entoglenoid process differs from that of the latter taxa in that it is not a free standing ridge. Rather, it is a clearly identifiable ridge which runs along the inside of the descending lamina of the pterygoid from the antennomandibular corner of the tympanic cavity to the lateral edge of the foramen ovale. An entoglenoid of this particular architecture is unique to mylodontid sloths.  
There is one ambiguous character, 81(1), that is unique to mylodontid sloths (and to the Pleistoce  
genus *Nothrotheriops*), wherein the area immediately posterior to the glenoid is traversed by longitudinal grooves and ridges.
Node 18: Scelidotheriinae (Fig. 2)—Patterson et al. (1992) point out the extreme similarity in the auditory regions of Catonax and Scelidotherium, describing the two as the same species. Indeed, Scelidotherium has no autapomorphic characters taken from this matrix which are not also shared by Catonax, whereas Catonax has but a single autapomorphy. The monophyly of the two genera is supported by four unequivocal and one equivocal character (Appendix 3). The unequivocal synapomorphies include character (59), stylomastoid foramen connected to ventral opening of canal for occipital artery by a weak groove. The scelidothere condition resembles that of other eutherians, except that the groove which connects the ventral opening of the occipital artery canal to the stylomastoid foramen weakens considerably as it curves around the lateral surface of the tympanohyal and mastoid projections at the base of the stylohyal fossa.

Node 19: Mylodontinae (Fig. 2)—As discussed in Patterson et al. (1992), the contents of this subfamily are somewhat controversial, and its membership as defined in the present study must be considered provisional. The support for the monophyly of this group is weak, in large measure because there are so many missing data for the early mylodontids Pseudopropothetrum, from the "Frijianó" of La Venta, Colombia, and Oxiodontotherium, the earliest sloth for which well preserved cranial material is known, from the DeSeadan of Patagonia. This node is diagnosed by only two synapomorphies, both of which are unequivocally assigned to the node. One of these, character (47; Fig. 7), fenestra cochlearia with a medial groove, is unique.

FIGURE 7. Stereophotographs of perrosal and middle ear cavity in; A, Hapalops elongatus, FMNH P13138, shown in ventral view; and B, Mylodon darwini, FMNH P14288, shown in lateral view. Characters and character states as in Figure 3.
to mylodontines. In all these taxa a sharply defined, narrow groove exits the medial corner of the teardrop-shaped fenestra and travels across the posterior surface of the promonomitrum and beneath the enotympotic, terminating before reaching the medial edge of the petrosal. In several genera (e.g., Glossothorium, Lestodon, Mylodon), the groove terminates at a small foramen in the ventral surface of the petrosal. The function of the groove and the foramen at times occurs at its medial extremity is unknown.

The genus Pseudopheoatherium is excluded from a clade including all other mylodontines (node 20) by two unequivocal characters (Appendix 3). A clade including the genera Mylodon, Lestodon, Glossothorium, and Paramyloodont (node 21) is weakly supported by one unambiguous and five ambiguous synapomorphies (Appendix 3).

Node 22 (Fig. 2)—The union of the genera Lestodon, Glossothorium, and Paramyloodon into a clade is at odds with several recent phylogenies of the Mylodontidae (Engelsmann, 1985; Hirschfeld, 1985; Webb, 1989), and may be attributable to the restriction of the present analysis to characters taken from the auditory region. Engelsmann (1985) has discussed the problem of whether the genera Glossothorium and Paramyloodon are distinct or represent one highly variable genus. The detailed examination of all relevant specimens which would be required to decide the issue is beyond the scope of the present study. For the purposes of this analysis, Glossothorium and Paramyloodon are lumped together as a single, highly variable OTU. The node is diagnosed by eight unambiguous synapomorphies, all but two of which have their root in the tremendous reduction in the size of the enotympotic in these taxa. In all specimens of Paramyloodon examined, and at least some specimens of Glossothorium, the enotympotic is a short, blocky mass of bone situated on the ventral surface of the promonomitrum, and extending only slightly forward of the anterior edge of the stylotal fossa. In Lestodon (Klauber, 1931a; Guth, 1961) and perhaps some specimens of Glossothorium, the enotympotic extends somewhat further anteriorly, as far as the midpoint of the promonomitrum. Characters 42 and 59 are the only two characters assigned to this node which are not obviously related to the reduction of the enotympotic. The condition of the latter feature in these sloths is virtually identical to that described for the Scelidotheriinae (node 18), but is optimized on this tree as an apomorphic that has been convergently acquired.

DISCUSSION

Although the present analysis of ear region features yields only two or three most parsimonious trees, depending on the weighting scheme utilized, the consistency indices of these trees are somewhat lower than expected, given the size of the matrix (expected value for 26 taxa, CI = 0.472; Sanderson and Donoghue, 1989; note that the CI = 0.405 resulting from the present analysis is much greater than would be expected from a random data set. CI = 0.140; Klassen et al., 1991). Given the high degree of homoplasy in the data matrix, I have employed several additional tests to ascertain the robusticity of the phylogenetic pattern illustrated in Fig. 2. Two separate tests have been performed in this regard. In the first, PAUP has been directed to save trees longer than the most parsimonious. These trees are generated using the global best swap algorithm. Only one of the weighting schemes, that in which character states are weighted equally, has been employed. Otherwise, the constraints and initial settings are identical to those of the previous analyses. Strict consensus trees have been generated for all trees of one step, two steps, three steps, and four steps longer than the most parsimonious.

There are 24 trees one step longer than the most parsimonious, 104 trees that are two steps longer, 385 trees that are three steps longer, and 1,240 that are four steps longer. A strict consensus tree was generated for each of these sets of trees. The inclusion of a single additional step results in a consensus tree with a number of significant changes from the most parsimonious tree. Among these is a loss of resolution of the relationships among mylodontids, so that most mylodontids fall into an unresolved multichotomy at node 17. In addition, nodes 9 and 10 collapse into a multichotomy, as do the four basal Santacrucian genera. Fewer changes result from the addition of two or three steps; however, nodes 11 (Placopterus plus megatheres) and 15 (the West Indian sloth clade) collapse in these consensus trees. The consensus of trees which are four steps longer than the shortest tree shows the most fundamental change. These changes include the collapse of the Eutardigradi, (node 8) and the collapse of node 13 joining the Megalonychidae to the Mylodontidae. However, the monophyly of the Megalotragulidae, the Megalonychidae, and Mylodontidae remains intact, as does the position of Bradypus as the sister taxon to all other sloths.

In addition to examining trees which are slightly longer than the shortest tree, the robusticity of the relationships depicted in Figure 2 has been evaluated by comparison with other specific phylogenetic hypotheses. In this second test, PAUP has been constrained to produce trees in accord with various hypotheses, hypothesized relationships, so that the length of these trees might be compared with the most parsimonious, given the current data set.

First, PAUP was constrained to produce the shortest tree in which both the Pilosa as a whole and the Bradypoda, podidae in particular are monophyletic. A shortest tree results, in which Bradypus joins Choloepus in its position nested deep within the Megalonychidae. This tree is 23 steps longer than the shortest tree as depicted in Figure 2.

Next, PAUP was constrained to produce a tree similar to that given in the conclusions section of Pat-erson et al. (1992), in which the Pilosa, Mylodontidae, and Megalonychidae (the latter including the two ex- tant genera) are constrained to be monophyletic. Seven
shortest trees result. In the consensus of these trees, *Chloepus* occupies its usual position within a monophyletic Megalonychidae. *Bradypus* is pulled up from its basal position in Figure 2 to a place within the Megaherididae of Figure 2, so that *Bradypus* and the megatherines form the sister group of the Santacrucian megatherian *Platymyotis*. This consensus tree is 12 steps longer than the tree depicted in Figure 2.

Finally, in accordance with the preliminary conclusions of Auffenberg (1990), PAUP was constrained to produce a tree in which *Bradypus* and the Megatheriidae form a monophyletic group. This results in a single most parsimonious tree, with *Bradypus* and the megatheres arranged as described in the above paragraph. This tree is only seven steps longer than the most parsimonious tree shown in Figure 2.

The results of these two tests, in conjunction with the results of the analyses detailed in the results section above, indicate that there are a number of well supported phylogenetic hypotheses which might be proposed on the basis of this data set, and a number of hypotheses proposed by other investigators which lack strong support.

The present study is in accord with those of Gutt (1961), Patterson and Pascual (1968, 1972), Webb (1985), and Patterson et al. (1992) in its strong support of a diphyletic origin for the modern tree sloths. A monophyletic arrangement of Bradypodidae in the sense of more traditional classifications (Winge, 1941; Simpson, 1945; Hoffstetter, 1938; Romer, 1966) requires an additional 23 steps as compared with the tree favored in the present analysis. The present analysis leaves some doubt as to the position of *Bradypus* within sloths as a whole. It is placed as the sister to the Macroscelididae and all other tarsiroids in the shortest tree, and in trees as many as four steps longer than the shortest. However, as was pointed out in the results section, its placement here may be at least partially ascribed to its nec
tonic retention of a number of juvenile features of the sloth auditory region. Moreover, there are a number of untested derived resemblances between Bradypus and megatherine sloths, such that only seven additional steps are required to unite the two taxa in a monophyletic sense, and accord with White's (1993a) preliminary cladistic analysis based on postcranial fea
tures). While elucidation of the relationships of *Bradypus* awaits further character informative from other parts of the cranial and postcranial anatomy, the pos
tion of *Chloepus* is quite firmly supported by ear region characters. *Chloepus* is nested well within the megalonychids in all trees generated in the present analysis, even in the tree in which Bradypodidae were constrained to be monophyletic. In trees up to three steps longer than the shortest, it forms the sister group to the Puerto Rican ground sloth, *Acratocnus*, a position which is supported in the shortest tree by 10 characters, of which most are features of the tympanic and en
tosynaptic. It shares another five characters with other West Indian sloths, and another nine characters with all other megalonychids (most of the latter nine are

characteristics of the geisleroid fousa; Webb, 1985, con
siders these resemblances of the geisleroid to be primiti
ve, in part because of his lumping of features of the geisler and dentary clypeus into a single character, and in part because of his use of myolodontids as an outgroup). Whatever the position of *Bradypus*, it is highly unlikely that it can be united with *Chloepus* as a derived member of the Megalonychidae. Thus, this analysis strongly favors a separate origin for the two extant genera.

The present analysis also strongly contradicts the monophyly of the Megalonychidae (Megatheriidae + Megalonychidae), as proposed most notably by Pat
terson and Pascual (1968, 1972) and Patterson et al. (1992), but also by Winge (1941) and Romer (1966). The shortest tree in which both the Mylodontidae and Megalonychidae are monophyletic is 12 steps longer than the shortest tree depicted in Figure 2. As has been noted in the conclusions of Patterson et al. (1992), it is clear, on the basis of craniodental anatomy, that the Mylodontidae is much more distinct from the Me
gaherididae and Megalonychidae (however these two families are defined) than the latter families are from each other. It is not clear, however, whether the re
semblances between megatherids and myolodontids are primitive or derived. The present analysis would appear to indicate that these similarities are primitive.}

Kampen (1905). Klauow (1931a, b), and Patterson et al. (1992) have all noted the resemblance of the slender tympanic ring of myolodontids to that of other primitive eutherians, and used this as a basis for inferring that the family must occupy a primitive position relative to other sloths. However, analysis of outgroups to the Tardigrada demonstrates that the expanded tympanic of *Bradypus*, *Hapalopus*, nathrotherines, megatherids, and some megalonychids is much more similar to that of the anisotremes, the dasydopids, the palenodontids, and even the pholidolestes than is the unexpanded tym
panic ring of the myolodontids. The suggestion that the unexpanded tympanic and incompletely ossified au
ditory bulla of *Megalonyx* represents a reduced condition in a primomely fully ossified condition may seem unusual (indeed, I am unaware of any other group of mammals in which it is thought that an unossified bulla proceeds from a primitively ossified condition; howe
ver, see Novacek's (1977) comments on the cartilag
inous entosympaticum of *Dipylus* and the carnivoran *Nandina*). Patterson et al. (1992) have proposed a similar reduction in the auditory bulla within mega
lonychidae, however, and the current data set suggests that a similar loss of the ossified bulla has occurred on at least five separate occasion within the Xenarthra: in myolodontids, *Acratocnus* (with further reduction in *Chloepus*), *Schismotherium*, glyptodontians, and *Dau
ypus* (Novacek, 1977). The functional implications of such bone loss in the walls of the tympanic cavity are unknown, as I am unaware of any study which ad
resses the acoustical properties of membranous vs. osseous bullae.

While the current data set would seem to contradict
both the concept of a monophyletic Megalonychoidea and a monophyletic Bradypoda, it does seem to indicate support for Engelmann's (1978, 1985) resurrection of a dichotomous split within Xenarthra into Chingulata and Pilosa. It is interesting to note here that, while the monophyly of both of these two clades is diagnosed by a number of auditory region characters, the present analysis, much like that of Jansa et al. (1992), does not generate strong support for the monophyly of the order as a whole on the basis of features of the ear region. All edentates are relatively similar to one another in the morphology of their ear regions, but the broadest distinctions within Edentata appear occur not between xenarthrans and omnivores, but rather between pholidolates and other edentes. There are relatively few characters which distinguish the ear region of xenarthrans as a whole from the ear region of palaeonotothids.

Within the Pilosa, the Tardigrada and Vermilingua form two of the strongest nodes in the entire analysis, with the former diagnosed by as many as 16 synapomorphies and the latter by as many as 12. Many of these synapomorphies are unique to these clades, e.g., the expanded parasympathetic contribution to the tympanic cavity in anteaters, and the peculiar medially expanded entotympanic and styloloph fossa of sloths. The morphological distinctiveness of the auditory regions in these lineages is perhaps not surprising, given the distinctiveness of the overall morphologies and ecologies of the three major xenarthran lineages.

Among tardigrades, the "nothotherine" genera from the early to middle Miocene Santa Cruz fauna occupy a basal position in the cladogram (except, of course, for Bradypus). Such a position is in accord with the supposed primitive nature both of these animals and of the Santa Cruz fauna as a whole (at least as regards xenarthrans). Scott (1903-1904) felt that the ancestors of all three Plio-Pleistocene sloth families could be found in this fauna. He believed these three families showed only incipient separation from one another in the fauna. However, Scott's allocation of Hapalops and the family Nothoheriae to the subfamily Nothoherinae (Simpson, 1945; Hoffstetter, 1951; Patterson et al., 1992). Indeed, the Nothoheriaceae in the traditional sense is suggested to be, as in Engelmann's (1985) cladogram, a paraphyletic stem group, but a stem group not for megatherians only, as in Engelmann's phylogeny, but for all tardigrades (excluding Bradypus). The present analysis lends some support to a monophyletic Notho-

otheriaceae in a more restricted sense, i.e., including only the Plio-Pleistocene members of the group, represented here by Prosorhytidium and Nothotheriops (though this "subfamily" cannot be assigned to any of the three traditional ground sloth families). However, this node is very weakly supported, and collapses in a consensus tree with the inclusion of trees only one step longer than the shortest. The addition of character information from other portions of the skull and postcra-
nium will in all probability support the union of at least the Plio-Pleistocene members of this group (see, e.g., the discussion of the unusual morphology of the vomer in these forms in Patterson et al., 1992), but it is less obvious whether or not such information might eventually support the inclusion of the earlier Mio-
cen taxa.

The term "Eutardigrada" is provisionally suggested for the clade including all megatheriids, megalo-

nychids, and mylodontids, as well as nothothereines in the restricted sense. The monophyly of such a grouping is fairly well supported, and does not break down until four steps are added to the shortest tree. However, the position of megatheriids as being more closely related to mylodontids and mylodonids than are the theo-

nothereines is less robust, and disappears with the ad-

dition of only a single step to the shortest tree. The monophyly of a family Megatheriidae which includes the Miocene Santacruzan genus Planopus is another interesting, though weakly supported result of the pres-
ent analysis. Although Scott (1903-1904) suggested a link between the Miocene form and late Plio-
Pleis-

tocene genera in his original description of Planopus, he felt the genus sufficiently distinct from late Pliocene forms to retain it in a separate family Planopodidae. He was fol-

lowed by Winge (1941), and most later workers have included Planopus and its close relatives as a subfamily of the Megatheriidae (Simpson, 1945; Hoffstetter, 1951; Patterson and Pascual, 1968, 1972; Paula Couto, 1979). The three unanimous synapomorphies which diagnose megalonychids in the present analysis support such an arrangement.

The union of the families Megalonychidae and Mylo-
dontidae into a single monophyletic clade is a novel result of the present study. This node is fairly well supported, collapsing in the consensus tree only after four additional steps are added to the shortest tree. As noted above, mylodontids are superficially much more similar to megatheriids than to mylodonids, but the present analysis suggests that the characters utilized by Patterson and Pascual (1968, 1972), Patterson et al. (1992) to unite the megalonychids and megatheriids may well be primitive for all tardigrades. Clearly, this new arrangement of the major tardigrade subfamilies is a result of the inclusion into the clade of other portions of the skull and postcranial skeleton before it can be accepted on anything more than a provisional basis.

Although the union of megalonychids and mylo-
dontids into a single clade may be questioned, the pres-
ent analysis provides strong support for the monophyly of each family. As noted in reference to the position of Choloepus, the glenoid fossa of the Megalonychidae is highly distinctive, and serves as the primary means to diagnose this group as monophyletic in all trees which have been generated over the course of this anal-

ysis. The division of the family into a mainland North American clade and a West Indian clade, although only weakly supported by this data (the node collapses with the addition of only two steps to the shortest tree), is
in accord with the proposed relationships of Engelmann (1985) and Webb and Perrigo (1985). However, the latter authors do not provide any character which might serve to diagnose the clade. In contrast to these works, Choleopus is placed family within the West Indian clade in the present study. Engelmann (1985) did not include Choleopus within the megalonychids, and Webb and Perrigo (1985) placed the modern genus as the sister-taxon to all other megalonychids. The position of Choleopus in the present study is consistent with that in the phylogeny of Patterson et al. (1992), who first noted the strong similarity in the auditory region of the two-toed sloth to that of the Puerto Rican genus Acrathrodon.

The node defining the base of the family Mylodontidae is one of the strongest in the entire cladogram (rivaling in this regard the Tardigrada and Vermilinguas). It is diagnosed by as many as 13 synapomorphies. The strength of this node reflects the morphological distinctiveness of this family in its auditory region anatomy. Patterson et al. (1992), although recognizing (along with many other authors) the distinctiveness of this family relative to other sloths, were able to provide only a few derived characters of the ear region to support this clade. While the present study has been successful in demonstrating the monophyly of this group, it has been less successful in sorting out relationships within the group. Almost all resolved infrafamily relationships collapse with the addition of a single step. The poor resolution of these relationships is perhaps not surprising given the degree of disagreement that exists over the arrangement of these taxa in previously published phylogenies. Most authors agree on division of the Plio-Pleistocene forms into the subfamilies Mylodontinae and Scelotherinae. The position of the latter, more poorly preserved Miocene and Oligocene taxa is problematic. The mid-Miocene "Frisian" genus Pseudomegatherium was excluded from both subfamilies by Engelmann (1985), whereas Webb (1989) considered it to be closely related to mylodontines and leiodontines than to scelotherines. The early to middle Miocene South American genera Nematherium and Analimbranchus have been placed either within the Mylodontinae (Simpson, 1945; Paula Couto, 1979), within the Scelotherinae (Patterson and Pascual, 1968, 1972; Engelmann, 1985; Hirschfeld, 1985), or outside of both subfamilies (Hoffstetter, 1958). The Oligocene genera Orobolodon and Ocotodontotherium have been included within the Mylodontinae (Patterson and Pascual, 1968, 1972; Hirschfeld, 1985; Patterson et al., 1992), but have also been excluded from both the scelotherines and mylodontines (Engelmann, 1985), and even from all other sloths (Hoffstetter, 1958; Paula Couto, 1979). The latter arrangement is based on the histology of the cheek teeth and the dubious presence of an armadillo-like carapace in these two genera. The present analysis supports the hypotheses of Webb (1989), Patterson and Pascual (1968, 1972), and Paterson et al. (1992) in considering the Miocene genus Pseudomegatherium and the Oligocene genus Octo-
todontherium to be more closely related to the Plio-
Pleistocene members of the Mylodontinae than to the Scelotherinae.

The purpose of the present study was to investigate the relationships among the four traditional tardigrade families in a detailed and rigorous cladistic fashion, as well as to provide additional information on the evolu-
tion of the auditory region in xeranthurans and other edentates in general. It has provided new characters of the auditory region which may serve to diagnose the Pholidota, Palaeonadonida, Xenarthra, Pilosa and Cin-
gulata. The data matrix has yielded a robust phylo-
genetic pattern despite the rather high degree of ho-
mosyly which would appear to characterize this re-
gion of the tardigrade skull. The results of this analysis strongly support the monophyly of the Tardigrada as a whole, as well as the monophyly of two of its cons-
tituent families, the Melegonychidae and Mylodon-
tidae. In addition, the analysis provides new evidence against a monophyletic origin of the so-called "me-
galonychoid" sloths and for a diphyletic origin of the extant "bradypodid" tree sloth genera. This diphyletic origin for tree sloths may indeed represent one of the most remarkable examples of convergent evolution known among mammals.

This study also supports several traditional group-
ings of sloths, including the monophyly of a family Megatheriidae which would include the genera Plio-
Planops, the monophyly of the Plio-Pleistocene mem-
ers of the subfamily Notothriherinae, and the sepa-
ratization of megalonychids sloths into West Indian and mainland North American clades. It also suggests a number of novel arrangements, including the place-
ment of Bradypus as the sister group to all other sloths, the paraphyletic arrangement of several South American "nothixoneres" near the base of the tardigrade tree, the monophyly of a so-called "Guatigrade" taxon which would include megatheriids, megalonychids, mylo-
dontids, and Plio-Pleistocene nothriherines, and the union of the families Megalonychidae and Mylodon-
tidae into a monophyletic group. The analysis was largely unsuccessful, however, in convincingly sorting out relationships among the South American taxa at the base of the tree or within the Mylodontidae.

In conclusion, it should be emphasized that all the relationships proposed in the present study are based solely on information taken from the bony anatomy of the auditory region in the taxa examined. The de-
cision to concentrate on this region of the skull was based on a belief that this portion of cranial anato-
my holds more potential for yielding significant phy-
genetic information than other regions of the cra-
rium and postcranium. The ear region was selected because the previous work of Patterson et al. (1992) showed the anatomy of this region to be a fruitful area of study for addressing questions of relationship in the group at hand. The information gathered from the ear region needs to be expanded upon in both its taxo-
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Listing of Characters and Character States

(Characters marked with a single asterisk (*) are multistate, those marked with two asterisks (**) are multistate and dis-
placed.)

1. Tympolc external surface: (0) smooth; (1) rugose.

2. Tympone directed: (0) anteromedially; (1) anteropro-

terally; (2) anteroventrally; (3) posteroventrally.

3. Tympone attachment: (0) loose dorsal attachment; (1) fused dorsally.

4. Attachment of posterior crus of tympanic: (0) squa-

round, tympanohyal and mastoid; (1) squamous; mastoid bridge.

5. Median suture of tympanic: (0) absent; (1) present.

6. Shape of tympanic: (0) elongate dorsoventrally; (1) circular; (2) elongate anteroventrally.

7. Gill-length: (0) absent; (1) present.

8. Recessus meatus: (0) absent; (1) present.

9. Saloon and crista tympanica: (0) prominent; (1) re-
duced.

10. Tympanic/petroydoid contact: (0) absent; (1) present.

11. Sinus tympanicus: posteros lateral wall of genal fossa: (0) no; (1) yes.

12. Auditory bullae: (0) bullae completely ossified or nearly so, membranous bulla absent or rudimentary, en-

totympanic and tympanic attached along entire length, petrosal hidden in vertical view; (1) membranous bul-

APPENDIX 1

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(1) laterally situated vertical plate with horizontal medial expansion dorsally.
20. Enostylosis: (20) thickened interpubic plate: (0) inclined mediolat erally; (1) very thin.
21. Ventral edge of entostylosic: (0) flat in lateral view; (1) extended into anterostylosic process.
22. Entostylosic width: (0) fairly uniform throughout its length; (1) widened posteriorly.
23. Entostylosic lateral surface: (0) concave; (1) flat verti cal surface ventrally with deep dorsal hollow; (2) nodular and exostial crests (in anterior portion).
24. Entostylosic direct: (0) anteromedially; (1) antero- posterorly; (2) antero-laterally.
25. Dorsal edge of entostylosic: (0) strong concave cur vature in lateral view, with dorsal projection at an terior end; (1) weakly curved, without dorsal projec tion; (2) flat, or nearly so.
26. Entostylosic participation in sulcus for internal cal cid artery: (0) forms lateral wall of sulcus; (1) forms lateral wall and at least part of the roof; (2) forms lateral wall, roof, and has medial ridge forming at least part of the medial wall.
27. Lateral process of entostylosic extending above ant erior portion of tympanic: (0) absent; (1) present.
28. Entostylosic lateral extension contacting tympanoh yal: (0) absent; (1) present.
29. Entostylosic participation in tympanic cavity floor: (0) rudimentary or absent; (1) weak participation in medial portion of floor; (2) strong, forming almost entire medial half of floor.
30. Position of medial expansion of entostylosic: (0) dor sal to floor of basioccipital; (1) at level of basioccipital.
31. Entostylosic/mastoid contact: (0) absent; (1) present.
32. Mastoid depression: (0) absent; (1) present.
33. Mastoid lateral exposure: (0) weak; (1) strong (Mat thew, 1918; Novacek and Wyss, 1986).
34. Depth of mastoid depression: (0) narrow, fairly deep; (1) broadened, shallow.
35. Mastoid process: (0) rudimentary or absent; (1) well- developed; (2) greatly enlarged.
36. Mastoid process foramen: (0) absent; (1) present.
37. Nurhal and exostialium: (0) globose; (1) dorsover tically elongate, flat anteriorly and globose posteriorly; (2) anteroposteriorly elongate, flat anteriorly and globose posteriorly.
38. Processus crista facialis: (0) small, reduced plate; (1) large, concave plate; (2) large, rugose bone mass; (3) enormous, exposed external to tympanic cavity.
39. Epitympanic sinus: (0) absent; (1) present (Emery, 1970; Novacek, 1986).
40. Stapedius fossa: (0) circular, situated directly posterior to fenestra ovalis; (1) anteroposteriorly elongate, bounded by strong ventral ridge, situated lateral to fenestra ovalis in ventral view.
41. Fossa incudis: (0) situated in anteromedial corner of wide epitympanic recess; (1) occupies entire poster oventral wall of epitympanic recess.
42. Lateral exposure of fenestra cochleae: (0) small; (1) well-developed.
43. Medial groove of fenestra cochleae: (0) rudimentary or absent; (1) well-developed.
44. Internal auditory meatus: (0) shallow fossa perforated by large foramina; (1) deep, undivided canal.
45. Direction of internal auditory meatus: (0) medial; (1) posteromedial.
46. Position of subarcuate fossa relative to internal auditory meatus: (0) posterodorsal; (1) dorsal.
47. Direction of tympanolabyrinthic canal: (0) initially posterolateral, then turns distally and runs posteromedial; (1) posterolateral distally; (2) strongly ventral distally.
48. Width of tympanolateral: (0) roughly uniform along ent ire length; (1) greatly widened distally.
49. Stylohyal fossa: (0) absent; (1) present.
50. Shape of stylohyal fossa: (0) circular; (1) oval.
51. Stylohyal articulation elements: (0) mostly tympanoh yal; (1) tympanohyal, mastoid, entostylosic, and parapostiolar process of exoccipital.
52. Direction of tympanic articulation: (0) ventral; (1) ven trolateral; (2) posterior.
53. Position of stylomastoideum foramen relative to tympanohyal/stylohyal fossa: (0) posterolateral; (1) lateral or anterolateral; (2) directly anterior.
54. Direction of stylomastoideum canal: (0) dorsal; (1) pos teroventral; (2) posteroverentral; (3) ventrolateral.
55. Connection of stylomastoideum foramen and foramina for occipital a. / d. diploica magna: (0) no connection; (1) stylomastoideum foramen connected to widely separated foramina for a diploica magna via open groove for occipital a.; (2) stylomastoideum foramen connected to nearby ventral opening of canal for occipital a. by weak groove; (3) stylomastoideum foramen connected to nearby ventral opening of canal for occipital a. by strong groove; (4) stylomastoideum foramen and ventral opening of canal for occipital a. open into same fossa.
56. Position of sustentaculum: (0) anteromedial corner of tympanic cavity; (1) posteromedial corner.
57. Elements in sustentaculum tube opening: (0) entostylosic and tympanic; (1) entostylosic, tympanic, and pterygoid; (2) tympanic, pterygoid, and basioccipital-basi sphenoideal.
58. Direction of eustachian tube: (0) posteroverentral; (1) ventral; (2) anterior.
59. Size of the posterior lacerate foramen: (0) small; (1) greatly enlarged (Matthew, 1918; Novacek, 1986).
60. Posterior lacerate foramen foramen inlaid below and behind entostylosic and periotic: (0) no; (1) yes (Englemann, 1978, 1985).
61. Posterior lacerate foramen relative to condylar foramen: (0) close; (1) well-separated.
62. Internal carotic artery foramen (within entostylosic or between entostylosic and basioccipital): (0) absent; (1) present.
63. Slope of internal carotic artery sulcus: (0) anterodorsal; (1) saddle-shaped, first anterolateral then antero dorsal.
64. Grooves, canals, and foramina of occipital a. and a.
diplotecta magna (0)/; diplotecta magis travels along sidewall of braincase, where it enters cranial cavity; (1) occipital a. travels in open groove near periotic-squamous suture; a. diplotecta magna branches off dorsally to enter foramen leading into braincase; (2) occipital a. travels without partially closed canal; (3) occipital artery completely enclosed within canal; (4) canal for occipital a. short, perforates mastoid process dorsoventrally.

70. Fortesque magnum venus sinus: (0) absent; (1) present.
71. Shape of maxillar head in dorsal view: (0) rounded; (1) parallel-sided (Segall, 1976).
72. Size of dorsal and ventral incudal facets of malleus in lateral view: (0) dorsal > ventral; (1) dorsal subequal.
73. Lamina and anterior process of malleus: (0) small; (1) enlarged.
74. Angle between manubrium and neck of malleus: (0) much less than 180° (ca. 110° to 130°); (1) near 180°.
75. Glenoid position relative to superficial meatus (the latter defined by Pastron et al. (1992:5) as “the groove on the ventral surface of the squamous lateral and dorsal to the tympanum”); (0) glenoid as or above meatus; (1) glenoid ventral.

*76. Shape of glenoid: (0) elongate anteroposteriorly; (1) hemispherical; (2) widened mediolaterally (Niehr, 1944; Naples, 1982, 1987; Webb, 1983).
*77. Glenoid inclination: (0) posertordorsal; (1) horizontal; (2) anterodorsal (Naples, 1982).
78. Glenoidal medial shelf: (0) absent; (1) present (Naples, 1987).
79. Glenoidal lateral shelf: (0) absent; (1) present (Naples, 1987).
80. Glenoid posterior shelf: (0) absent; (1) present.

**61. Position surface of glenoid: (0) smooth; (1) grooved; (2) rugose.
**62. Position of glenoid relative to porus acusticus: (0) just anterior; (1) separate; (2) well-separated.
**63. Ensiform process: (0) rudimentary or absent; (1) weakly developed, depressed against lateral side of descending lamina of parrygoid; (2) weakly developed but free-standing; (3) well-developed.
84. Postglenoid foramen: (0) reduced or absent; (1) present (Hoffstetter, 1958; Engelnmann, 1978, 1985).
*85. Direction of root of zygoma: (0) anterior; (1) antero-lateral; (2) lateral.
APPENDIX 2

Data Matrix
(The symbol "?" represents missing information or a symbol of question; the number "0" is used in cases where a character is not applicable to a given taxon. The following symbols are used to represent character states in polymorphic taxa: a = (0, 1); b = (1, 2); c = (0, 1); d = (1, 3); e = (2, 3).*

10 20 30 40 50 60 70 80

Pholidota
0101 0210 0001 0000 0200 0200 0200 0200
Palaeonodon
0111 0211 0211 0100 0211 0001 0001 0001
Atelocynoidea
0111 0211 0211 0100 0211 0001 0001 0001
Glyptodontidae
0000 0211 0000 0100 0201 0100 0011 0011
Euphracta
0211 0101 0211 0211 0000 0100 0200 0000
Dasyopodidae
0111 0211 0211 0100 0211 0001 0001 0001
Cyclopes
0111 0211 0211 0100 0211 0001 0001 0001
Myocastorphanes
0111 0211 0211 0100 0211 0001 0001 0001
Octodontidae
0011 0000 0000 0100 0211 0100 0211 0100
Pseudagriotheriidae
0001 0211 0100 0211 0100 0211 0100 0211
Lestrodont
0001 0000 0000 0000 0211 0100 0211 0100
Glossotheriidae/Para.
0011 0211 0000 0100 0211 0100 0211 0100
Catonyx
0000 0100 0211 0211 0211 0211 0211 0211
Sclerotheriidae
0000 0100 0211 0211 0211 0211 0211 0211
Mylodon
0000 0100 0211 0211 0211 0211 0211 0211
Chasmaporthetes
0000 0100 0211 0211 0211 0211 0211 0211
Lacromeryx
0000 0100 0211 0211 0211 0211 0211 0211
Conotherium
0000 0100 0211 0211 0211 0211 0211 0211
Notothoristes
0000 0100 0211 0211 0211 0211 0211 0211
Euchilotheres
0000 0100 0211 0211 0211 0211 0211 0211
Hapalops
0000 0100 0211 0211 0211 0211 0211 0211
Phalangers
0000 0100 0211 0211 0211 0211 0211 0211
Eremotherium
0000 0100 0211 0211 0211 0211 0211 0211
Megalotherium
0000 0100 0211 0211 0211 0211 0211 0211
Sclerotherium
0000 0100 0211 0211 0211 0211 0211 0211
Pelecyodon
0000 0100 0211 0211 0211 0211 0211 0211

*Presumed primitive states for polymorphic taxa given constraints and initial settings for PAUP analysis as described in Materials and Methods section above, and utilizing a weighting scheme in which all character states are weighted equally.

Pholidota: (7) a = 1; (38) a = 0; (44) a = 0; (61) b = 1; (71) a = 0; (73) a = 0.
Glyptodontida: (82) c = 0.
Euphracta: (53) a = 0.
Dasyopodidae: (5) a = 1; (7) a = 1; (12) b = 1; (28) a = 0; (31) a = 0; (69) d = 1.
Cyclopes: (7) a = 1.
Myocastorphanes: (1) a = 0; (7) a = 1; (14) a = 0; (78) a = 0; (83) a = 0.
Octodontidae: (43) a = 0; (7) a = 1; (77) b = 2; (22) a = 1; (50) a = 1; (69) e = 3.
Pseudagriotheriidae: (15) c = 2; (67) a = 1.
Glossotheriidae/Para.: (67) a = 1.
Hapalops: (12) b = 1 or 2; (16) c = 2; (35) a = 1; (54) a = 0; (67) a = 1.
Notothoristes: (33) a = 0; (38) b = 2; (60) a = 1.
APPENDIX 3. Distribution of apomorphies on consensus trees in Figure 2. (Equivalal characters in italics, character reversals marked with *) Those characters in which optimality varies with the specific taxa employed in outgroup comparison (see Node 7) have been omitted. Characters marked by **(T)** vary in their pattern of character state optimization on the cladogram, depending on how the tri-chotomy at node 5 is resolved.

Node 1. Cingulata: 12(1) (conv. Schizorhynchum, Chelon- par, node 17); 28(2) (conv. Megaalonus, Megaalonusa); 42(9); 65(0) (conv. Palaeaodonata.)

Glyptodontidae: 20(0) (conv. Cyclonex, Chelonpar, node 21); 56(3) (conv. Pelvozoum, Schizorhynchum, Chelonpar, node 17); 8(0) (conv. node 5); 12(2) (conv. Chelonpar, node 23); 28(9) (conv. Node 3, Nothorothis, Megaluro- num, node 13); 57(0) (conv. Philodius, Brasyptus, 6(2) (conv. node 17); 76(2) (conv. Palaeaodonata, node 14); 80(5) (conv. Palaeaodonata, node 13); 85(0) (conv. node 14).

Dasyproctida: 21(1) (conv. node 5); 29(2) (conv. Palaeaodonata, node 8).

Dasyproctidae: 15(2) (conv. Palaeaodonata, node 3, Pronoth- rohum, node 10); 29(2) (conv. Bradypus, node 6); 32(3) (conv. node 4); 42(0) (conv. Cyclonex, node 23); 73(1) (conv. Myrmmorphaginaceae, node 14, 21); 74(0) (conv. node 10).

Euphractia: 2(2) (conv. Schizorhynchum, node 18); 3(1) (conv. Palaeaodonata, node 3, Brasyptus, node 12, Me- galonon, 15(1) (conv. Palaeaodonata, Brasyptus, node 12); 16(1) (conv. node 12, 12); 17(2) (conv. node 5); **40(0)** (conv. Bradypus, Nothorothis, Megalonusa, Chelonpar, 58(0); 69(2) (conv. node 12, Megalonusa, Pericloeprepterygium).

Node 2. Piérola: 1(1) (conv. Palaeaodonata, 59(1) (conv. node 10, Myxodon, Leptodon, 63(1) (conv. Palaeaodon- at, 72(1)); 79(1); 84(0); 0 (conv. Metaschismus).

Node 3. Vermilingua: 3(1) (conv. Palaeaodonata, Euphractia, Brasyptus, node 12); 10(1) (conv. Bradypus, node 11, Astrapenthus, Glossotheriun, 15(2) (conv. Palaeaodonata, Dasyproctidae, Pronothrohum, node 10); 18(0) (conv. Philodiusa, Brasyptus, Philodius, 3(1) (conv. Glyptodontina, Noth- rothis, Megalonusa, node 14); 40(3); 51(2); 37(1) (conv. Palaeaodonata, 60(1); 62(0); 69(0).

Mesomorphaginaceae: 29(1) (conv. Palaeaodonata, node 4); 29(0) (conv. Palaeaodonata, node 22); 61(2) (conv. node 23); 71(1); 73(1) (conv. Philodiusa, Brasyptus, node 19); 73(0) (conv. Dasy- proctidae, node 24, 21).

Cyclonex: 20(0) (conv. Glyptodontina, Chelonpar, node 21); 60(0) (conv. node 12); 42(0) (conv. Dasyproctidae, node 22); 66(1) (conv. Metaschismus, node 15, 17); 82(0) (conv. Philodiusa, Nothorothis, node 13).

Node 4. Tardigrada: 4(1); 6(2) (conv. Palaeaodonata, 17(1) (conv. Chelonpar, 19(1); 23(1); 36(2) (conv. node 16, 22); 28(1) (conv. Palaeaodonata, Myrmmorphaginaceae, 31(2) (conv. Dasyproctidae, 33(0); 51(2); 75(1) (conv. Philodiusa, Brasyptus, node 5); 58(1) (conv. node 15); 68(3); 78(1); 70(1).

Bradypus: 8(1) (conv. Palaeaodonata, Euphractia, node 3, 12, 42(0) (conv. node 3, 11, Astrapenthus, Glossotherium, 11(1) (conv. node 12); 32(1) (conv. Pal- eaodonata, Euphractia, node 12); 41(1) (conv. node 9, 24(2) (conv. node 11, Megaalonusa, 26(2) (conv. Da- sypodidae, node 6); 36(1) (conv. node 6); **40(0)** (conv.