

Higher Taxonomic Relationships among Extant Mammals Based on Morphology, with Selected Comparisons of Results from Molecular Data

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Received June 5, 1997; revised January 19, 1998

Until a few decades ago, phylogenetic relationships among placental orders were ambiguous and usually depicted to radiate as an unresolved "bush." Resolution of this bush by various workers has been progressing slowly, but with promising results corroborated by nondental, dental, and molecular characters. In this study we continue to seek resolution. A total of 258 nondental and 2 dental characters was analyzed by PAUP and MacClade on 39 vertebrate taxa (3 reptiles, 1 nonmammalian therapsid, and 35 mammals; 20 of the mammals are extant and 15 are extinct) to study higher taxonomic relationships with emphasis on Placentalia (Eutheria). About two-thirds of the characters are osteological, the rest concern soft tissues, including myological but excluding molecular characters (most are our data, the rest are from the literature). Cladistic analysis included all 39 taxa (fossil taxa help to evaluate polarities of characters) and all characters were given equal weight. Extant Mammalia are divided into Prototheria and Theria, the latter into Marsupialia and Placentalia. Placentalia comprises Xenarthra and Epitheria. Within Epitheria, Lipotyphla and Preptotheria (emended) are sister-taxa. Preptotherian taxa group into: ungulate-related taxa and various nonungulates. The former include Carnivora, Pholidota, Tubulidentata, Artiodactyla, Cetacea, Perissodactyla, Hyracoidea, Proboscidea, and Sirenia. A possible association to embrace Lagomorpha, Rodentia, Macroscelidea, Scandentia, Primates, Chiroptera, and Dermoptera is suggested. Significant differences between our findings and those of recent investigators include the dissociation of Pholidota from Xenarthra and the plesiomorphous position of Lipotyphla within Epitheria. Congruence between morphological and molecular results is closer than previously reported. © 1998 Academic Press

HISTORICAL ACCOUNT

Gregory (1910) is the best source on mammalian history and taxonomy for its time; prior publications on Mammalia were excellently summarized, with discussion of importance of characters in evaluating phylogenetic relationships. Selected works on mammalian phylogeny and taxonomy post-Gregory (1910) are: Sonntags (1925), Le Gros Clark and Sonntags (1926), Weber (1928), Simpson (1945), Thenius (1969), McKenna (1963, 1969, 1975), Szalay (1977), Goodman *et al.* (1985), Miyamoto and Goodman (1986), Novacek and Wyss (1986), Novacek *et al.* (1988), Shoshani (1986a), Rowe (1988), Czelusniak *et al.* (1990), Wible (1991), Honeycutt and Adkins (1993), Sarich (1993), Stucky and McKenna (1993), Luo (1994), Luo *et al.* (1995), MacPhee (1994), McKenna *et al.* (1997).

This study focuses on cladistic relationships within Placentalia (=Eutheria), although noneutherian mammals and sister-groups of Mammalia are included for comparison. We focus on Placentalia because there is consensus on the phylogenetic position of Monotremata and Marsupialia within extant Mammalia, yet there have been conflicting results on relationships of certain taxa and some unresolved polytomies within Placentalia. In particular, we investigated the phylogenetic positions of Pholidota, Carnivora, and Lipotyphla, and the cohesiveness of Anagalida (Lagomorpha, Rodentia, Macroscelidea) and Archonta (Chiroptera, Dermoptera, Primates, Scandentia). An overview of our methodology and stages of investigation is given in Table 1.

TAXA AND CHARACTERS STUDIED

Taxa

A total of 39 taxa was examined, divided as follows: 3 reptiles (*Chelydra*, *Sphenodon*, *Varanus*) 1 nonmamma-

TABLE 1

Stages of Investigation Followed in This Study

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- A. Major steps of investigation followed
1. Record characters in data matrix of morphological characters.
 - a. Define characters as clearly as possible.
 - b. Include characters from authors with whom we agree or disagree on their conclusions.
 - c. Include extinct and extant taxa, carefully choosing representatives of groups.
 2. Construct cladograms using PAUP (of Swofford, 1993) and MacClade (of Maddison and Maddison, 1992)—one for living taxa, and one for living and extinct mammalian taxa.
 3. Test phylogenetic hypotheses within Placentalia.
 4. Present one slightly modified strict consensus cladogram that best depicts interordinal relationships among living mammalian taxa, with bootstrap values (BV) and Bremer support values (BSV). Explanation in text.
- B. Assumptions
1. Extinct members of higher taxa generally incorporate the most plesiomorphic characters and help to establish morphocline polarities of characters.
 2. Evolutionary processes are not necessarily parsimonious, but must be treated as though parsimonious. Near parsimonious trees may be accommodated with corroborative evidence. There is no better way. Small departures from strict parsimony may be expected and may not be statistically significant.
- C. Hypotheses
- Mammalia, Theria, Placentalia, and Epitheria are monophyletic taxa. Within Epitheria, orders and higher categories are related in a defined branching pattern, not an unresolvable polytomy—specifics are briefly addressed in text.
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lian synapsid (*Cynognathus*), 20 extant mammals [may be considered 25 taxa if one splits Lipotyphla into 3, Carnivora into 2, Cetacea into 2, and Chiroptera into 2], and 15 extinct mammalian taxa (4 orders, 11 genera). Of these 39, we considered six taxa as outgroups (4 nonmammals, Monotremata, and Marsupialia), and Placentalia (33 taxa) as the ingroup. More than one outgroup were employed because the polarities (direction of evolution) and transformations (changes of character states of one character) of characters for the ingroup—Placentalia—are better defined. Also, one outgroup may give a false reading if it has derived conditions for certain key characters (details in Forey *et al.*, 1992).

For simplicity, marsupials and insectivores are treated as one taxon each (Marsupialia and Lipotyphla). McKenna *et al.* (1997) treated Marsupialia as composed of at least nine orders and Lipotyphla as three orders. Divisions within Marsupialia do not affect results in this study because Monotremata, Marsupialia, and four nonmammalian taxa are employed as outgroups of Placentalia. On the other hand, because of emphasis on placental mammals in this study, supposed polyphyly of Lipotyphla bears particular importance in testing hypotheses suggested by molecular

studies (e.g., that Chrysochloroidea is related to paenungulate taxa, see below). Characters examined for the present study do not allow testing the phylogenetic position of Chrysochloroidea; an expanded roster of characters is required.

Selection of taxa was heuristic. All living mammalian orders are represented, as well as extinct forms that are believed to be related to taxa of interest (e.g., ungulate-related) or whose phylogenetic position is uncertain (e.g., *Plesiorcycteropus* and *Eurotamandua*). In addition, the choice of taxa was dictated, in part, by the taxa studied by the authors whose hypotheses we are testing. In the case of polymorphic taxa, character codings were based on the earliest known representatives. For example, *Diacodexis pakistanensis*, the most primitive artiodactyl, had a clavicle (Thewissen and Hussain, 1990, pp. 41–44), whereas later artiodactyls do not have a clavicle—coding for this character for Artiodactyla as a monophyletic taxon was the plesiomorphic condition as in *Diacodexis* [other examples are given in Appendix 1; see character 114 = [72] on the humerus, entepicondylar foramen]. Whenever possible, at least three specimens for each taxon were examined. In many cases about 10 specimens, representing different families, ages, and sexes, were employed to record variations (details in Appendix 1). Additional specimens were sought when a character was in doubt (mostly because of polymorphism).

Characters

Characters examined fall into two major components, skeletal and soft tissue characters, summarized in Table 2. Description and coding of characters are extremely important for them (especially the latter) have direct influence on position of taxa on a cladogram. Sources are provided with listing of characters in Appendix 1. The data matrix (Appendix 2) for living and extinct taxa was derived from two main sources: Shoshani (1986b; mostly living forms) and other workers. We believe that employing characters from as many bodily systems as possible lessens the chance for convergence and/or parallelism to affect the results.

When uncertain about polarity of a character (based on our experience and/or the literature), the majority rule (over 50% of specimens, as was conducted by Domning, 1994) was employed, that is, the character state exhibited by most specimens was used as the primitive condition. When certain about the polarity of a character, we coded the primitive character state, even if it was not prevalent among specimens studied [additional comments on character coding, weighting, and evaluating are in the Introduction to Appendix 1 and in Shoshani *et al.*, 1996].

When searching for characters (other than those of Shoshani, 1986b), we tried to be objective and incorporated characters of other investigators. Whenever pos-

TABLE 2

**A Summary of Morphological Characters
Examined in This Study**

Components	No. of characters	Subtotals and totals
Skeletal tissues		
Skull (Cranium and Mandible)		
General: characters 1–51 + 253–256 ^a	55	
Foramina: characters 52–90	39	
Subtotal		94
Axial and appendicular skeletons		
Axial: characters 91–101	11	
Appendicular: characters 102–154	53	
Subtotal		64
Total		158
Soft tissues, others		
Integumentary system and derivatives: characters 155–157	3	
Muscular system: characters 158–206	49	
Circulatory system: character 207–209 + 257–258	5	
Digestive system: characters 210–216 + 259–260	9	
Respiratory system: character 217	1	
Urogenital system + chromosomes: characters 218–236 + 252	20	
Nervous system: characters 237–246 + 251	11	
Ecology, life history, other systems: characters 247–250	4	
Subtotal		102
Total		260 characters ^{b,c}

Note. Details in Appendix 1 on the Web site.

^a The second set of numbers after the “+” sign (253–256, 257–258, 259–260, 252, 251) represents characters added at a later date; they are included in the addendum following the 250 original characters.

^b Note that the validity of eight characters is uncertain [characters 23 = [C2] through 28 = [C7], and characters 238 = [S19] and 240 = [RF]]; see notes under characters 23 = [C2] and 238 = [S19]. To accommodate these uncertainties and to test what effect these characters would have on the overall results, tests with PAUP were conducted with and without them, either separate sets of characters or without all of them. Results obtained indicate that in all four tests (with 252, 254, 258, and 260 characters), the branching patterns among living mammalian taxa were identical for all runs; understandably, the length of the tree for each test was different.

^c One additional character [tentorium osseum or intracranial osseous lamina; number 261 = [St]] was employed at a late stage of this study and thus is not included in the analysis. For this and other reasons (see Appendix 1 and under *Ferae* in the text), a “#” is presented for *Ferae* instead of the bootstrap values (BV) and the Bremer support values (BSV) used for other nodes in Fig. 1.

sible, we consulted with the original authors and confirmed that we could use the characters as intended for phylogenetic analysis. By his own admission, Beard (1993) remarked on some of his characters that were questionable. We did not include these characters, but

did include 12 characters of Beard (1993) in our analysis (six are his; others were employed by other investigators). Of these, four [our numbers 111 = [B9], 115 = [B11], 148 = [B26], and 153 = [B28] in Appendix 1] were coded specifically to support sister-group relationship between Dermoptera and Primates. With a small data set (Beard used 29 characters), these characters would be significant and would support a Primates/Dermoptera close affinity. With a large body of data, however (260 characters in this study), Beard's hypothesis was “overpowered,” and Chiroptera, instead of Primates, is supported as the sister-group of Dermoptera.

CLADISTIC ANALYSIS

Computer Programs

Data matrices were analyzed with two computer programs: PAUP (Phylogenetic Analysis Using Parsimony, of Swofford, 1993) and MacClade (of Maddison and Maddison, 1992). We ran PAUP in two ways: one with living mammalian taxa only and one with all taxa, living and extinct. PAUP provides a single most parsimonious tree, or a number of equally parsimonious trees, from which a consensus tree is computed. MacClade enables an investigator to test alternative hypotheses with relatively little effort by removing one branch from its position (as obtained from PAUP) and joining it to another clade, but, if only one branch at a time is moved, local parsimony will be favored and more general but less obvious parsimony may be missed. Length of trees and consistency indices for the new topologies are given. Employing the parsimony principle, one can then decide between and among trees.

PAUP was run using heuristic search with ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) settings. Heuristic search was conducted with the options “general” and “stepwise addition.” The latter was conducted with these four options: “simple,” “closest,” “asis,” and “random” with 1000 replications. Except for the “stepwise addition, random” test, which took 15.5 h to run, all tests were executed in a few seconds. In some tests, a more parsimonious tree was found with the “stepwise addition, random” option than with other options. We employed the “standard” character option in which characters are unordered and unweighted, with reversals possible. Outgroups were not defined. Once a consensus tree was obtained, a list of synapomorphies and their consistency indices (CI) was obtained (“list of apomorphies” option). We also obtained bootstrap values (BV, confidence limits for each node; cf. Felsenstein, 1985; Appendix 3), choosing 1000 replications. Bremer support values, BSV (decay indices or strength of grouping of Goodman *et al.*, 1985, and Bremer, 1988; Appendix 4) were obtained from PAUP.

TABLE 3

Number of Mammalian Orders, Families, and Genera According to Five Classifications

Authority(ies)	Orders extant/ extinct	Families extant/ extinct	Genera extant/ extinct	Totals orders/ families/ genera
Gill (1872)	13/1	105/31	—	14/136/—
Gregory (1910)	17/8	—	—	25/—/—
Simpson (1945)	18/14	118/139	932/1,932	32/257/2,864
Wilson and Reeder (1993)	26/NA ^a	135/NA	1,135/NA	NA/NA/NA
McKenna <i>et al.</i> (1997) ^b	23/23	125/299	1,083/4,076	46/424/5,159

^a NA, not applicable.

^b McKenna *et al.* (1997) report on almost thrice as many families in over 100 years and about twice as many orders, families, and genera in about 50 years.

RESULTS AND DISCUSSION

Table 3 provides a summary of mammalian orders, families, and genera according to five classifications. Changes in numbers of taxa (orders, families, genera) among classifications are due not only to new discoveries, but also to different interpretations and synonymies. There are 46 mammalian higher taxa given the rank of order (23 extant and 23 extinct) in the McKenna *et al.* (1997) classification. Examples of 15 extinct taxa were included in PAUP analysis, yet we focus on results with living orders, mostly due to incomplete data for fossils.

We constructed two cladograms (one for living and one for living and extinct mammalian taxa) to compare the results and learn whether differences are due to missing data or change in polarities due to density of the data matrix. Overall, results from both runs for the strict consensus trees were similar, except that with the combined data Carnivora and Pholidota joined in a polytomy within Preptotheria, and Perissodactyla joined Eparctocyona. Discrepancies or equivocal results from both runs of PAUP are indicated on Fig. 1 by dashed lines (based also on 71 branch-swapping tests and relatively low BV and BSV).

Another criterion for helping to decide if a particular hypothesis should be accepted or rejected was through results obtained from branch-swapping (details in Appendix 5). For example, Novacek (1992, and previous papers) suggested that Xenarthra and Pholidota are sister-taxa. It costs 12 additional steps, however, to join Pholidota with Xenarthra in the strict consensus cladogram of living taxa. This is a high number of additional steps and it could have been even higher if not for the relatively high number of missing data ("—") in the character matrix [see, for example, assorted cells for characters 163 = {6m} through 200 = {F69}, and also characters 255[ep] and 256 = {Ra6}]. There are no set

"rules" as to how many numbers of steps are accepted or rejected for a particular hypothesis; each case should be evaluated independently, keeping in mind the relative amount of missing data. A dotted line and a question mark join Pholidota and Carnivora (see discussion under Ferae).

Of the 260 morphological characters presented in Appendices 1 and 2, and in Table 2, about 40% (104 characters) deal with soft tissues, ecology, life history, and other nonskeletal systems. This means that the 15 extinct mammalian taxa have missing data for these characters in addition to the missing data for other characters—a total of at least 50% missing data for the extinct taxa for the entire character matrix. Missing data is one good reason for a large number of equally parsimonious trees (we obtained 140 trees) leading to polytomous consensus solutions, and for low change in the score when conducting branch-swapping (see Appendix 5; Wilkinson, 1995; Shaffer *et al.*, 1997).

Synapomorphies for clades discussed below are given in the caption to Fig. 1; others are in Appendix 6. A classification based on this figure is provided in Table 4. Discussion begins with Mammalia and proceeds along the main axis of the cladogram (Fig. 1).

MAMMALIA

Prototheria (=Monotremata) and Theria Dichotomy

Much has been discussed in the literature about this dichotomy, with almost no disagreement (cf. Gregory, 1910; Simpson, 1945; McKenna, 1975).

Marsupialia and Placentalia (=Eutheria) Dichotomy

Marsupialia. Assuming that the relationships depicted in Fig. 1 are a plausible hypothesis with regard to the position of Marsupialia, then, in many aspects, living marsupials are quite different from what one would expect. For example, characters that are present in taxa studied and which appear as synapomorphies on this clade (there are 16 such synapomorphies, including the loss of the septomaxillary bone; cf. character 6 in Appendix 1) either evolved independently in Marsupialia and Placentalia, or ancestors of marsupials had the primitive condition and those studied have the derived condition. [We believe these derived conditions for marsupials could explain the low BV of 83% and BSV of 3 for Theria clade.] A third alternative is that relationships depicted in Fig. 1 are not valid. In this scenario, Marsupialia can be a sister-group either to Prototheria or to an undiscovered taxon.

Placentalia (=Eutheria). This taxon has been in formal classification since 1837 when Owen proposed it. Our results strongly support this clade with a BV of 97% and BSV of 8. Previous investigators (e.g., Gregory, 1910; Simpson, 1945; McKenna, 1975; Novacek and

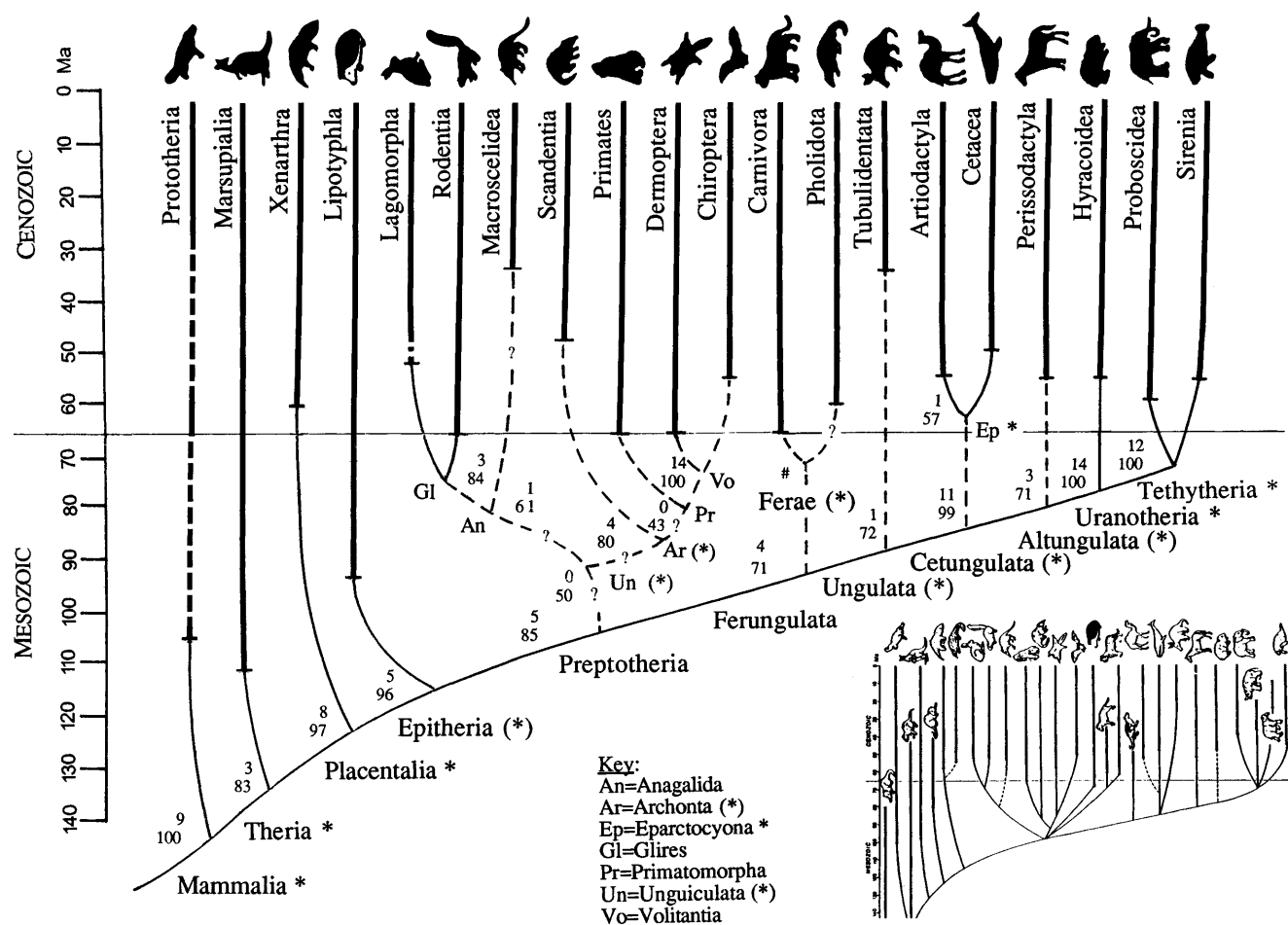


FIG. 1. A Mammalia cladogram for living taxa based on combined morphological evidence for living and extinct taxa. Outgroups include *Chelydra*, *Sphenodon*, *Varanus*, and *Cynognathus*. Heavy solid lines represent known fossil occurrences; cf. Appendix 7 after McKenna *et al.*, 1997 (gaps in the records are ignored; Ma = *Mega annum*, million years before present), updated after Archibald (1996) and Gheerbrant *et al.* (1996). Fine solid lines indicate suggested relationships. Dashed lines and question marks [?] indicate uncertain placement when a relationship is based on data from living taxa alone, or on combined data from extinct and extant taxa, based on branch-swapping tests, low BV and BSV, and incongruities between morphological and molecular results. An asterisk [*] indicates congruence and [(*)] indicates partial congruence with molecular data. The figure at bottom right is after Novacek (1992), and the enlarged figure is modified to incorporate our results, with the silhouettes of mammals used by Novacek for easy reference (significant differences between these figures include the positions of Lipotyphla and Pholidota). Tree length for the top figure is 664 steps (CI = 0.45); when we tested the hypothesis of Novacek (1992) against our data for living taxa, the score of the tree increased by 54 steps (this and other 70 branch-swapping tests are presented in Appendix 5). Numbers at nodes are BV for 1,000 replications (bottom) and BSV (top). A complete list of synapomorphies as obtained from PAUP is given in Appendix 6; here, we provide selected synapomorphies for mammalian clades. Some of these synapomorphies do not appear for certain taxa in previous literature. A "[?]" implies not so "good" a character as others (authorships for these characters are given in Appendix 1). Mammalia: character no. 2—quadrate-articular contact is not involved in the jaw joint articulation (manifested in presence of three middle ear ossicles), ch. 44—dentary is the largest or the only bone in the hemimandible, ch. 59—cribriform plate present; Theria: ch. 4—prefrontal and/or postfrontal absent, ch. 33—cochlea auris with at least one full turn, ch. 219—ovipary absent; Placentalia: ch. 67—optic foramen is separate, i.e., not confluent with the orbital fissure, ch. 75—foramen ovale located within alisphenoid, ch. 228—chorioallantoic placenta, ch. 254—os caruncula or "egg tooth" absent; Epitheria: ch. 130—fibula-femur contact absent, ch. 204—stylohyoid muscle is a derivative of posterior digastric, ch. 221—vagina's longitudinal divisions or traces of them absent, ch. 234—penis developed; Preptotheria: ch. 109—pars chondralis of the interclavicle absent, ch. 215—cloaca absent, ch. 237—encephalization quotient more than 0.21; Unguiculata: ch. 22—[?] tegmen tympani partly fused with tubal cartilage, ch. 103—[?] scapular spine only $\frac{2}{3}$ – $\frac{3}{4}$ of scapular length; Anagalida: ch. 72—[?] masticatory and buccinator foramen(ina) present, ch. 226—embryonic disc oriented toward mesometrial pole of uterus at time of implantation; Glires: ch. 11—premaxilla-frontal narrow contact present before or at anterior border of orbits, nasals long (not retracted), ch. 32—glenoid fossa elongate high with no postglenoid process, ch. 223—uterus duplex; Archonta: ch. 198—[?] flexor digitorum brevis manus absent, ch. 235—penis free and pendulous; Primatomorpha: ch. 121—shape of acetabulum is elliptical in outline, ch. 251—neurovisual character complex; Volitantes: ch. 24—fenestra rotundum of cochlea faces directly posteriorly, ch. 96—ribs flattened, ch. 156—patagium (including associated skeletal and muscular characters); Ferungulata: ch. 159—monoceps brachii, i.e., short head is reduced or absent, ch. 242—floculus of cerebellum vestigial or not visible in dorsal view, ch. 255—[?] enamel prism noncylindrical and not surrounded by interprismatic matrix (no data for Pholidota and Tubulidentata); Ferae: ch. 261—tentorium osseum well-developed, with possible parallelism in Tubulidentata (the use of "#" instead of BV and BSV is explained in Table 2), certain molecular data (see text); Ungulata: ch. 83—opening of stylomastoid foramen is dorsal to level of cheek

Wyss, 1986; Novacek *et al.*, 1988; Shoshani 1986a,b) reached a similar conclusion.

Xenarthra and Epitheria Dichotomy

Xenarthra. Much effort was invested in understanding xenarthran conservative features, as Eisenberg (1981, pp. 42–56) called them. Gregory (1910, p. 468) first depicted *Xenarthra* (“American Edentates”) as the earliest branch of placental mammals. Simpson (1945, pp. xii, 69) classified *Xenarthra* as a suborder of Edentata with seven other orders in the cohort Unguiculata. In 1975, McKenna reconfirmed Gregory’s (1910) hypothesis and placed *Xenarthra* as the sister-group to Epitheria within Placentalia. Many morphologists after McKenna (1975), e.g., Novacek (1986), Novacek and Wyss (1986), Shoshani (1986a,b), placed *Xenarthra* close to the base of Placentalia but associated with Pholidota. Admittedly, characters used by these workers were almost identical, thus similar results are not surprising. In this study, we reexamined most of the previously used characters, edited our data matrix, and added new characters based on our own observations and from the literature (e.g., Edgeworth, 1914; Slijper, 1946; Szalay, 1977; Zeller *et al.*, 1993; Gaudin *et al.*, 1996). Our results reaffirm the ancient position of *Xenarthra* within Placentalia as depicted in Fig. 1 and in the classification (Table 4).

Molecular evidence for *Xenarthra* being “one of the oldest offshoots of the eutherian stem, either as a separate branch or on a common base with Hyracoidea and Proboscidea,” comes from the alpha crystallin A chain data (de Jong *et al.*, 1985, p. 65). These authors also claimed that Pholidota and xenarthrans do not share any derived characters of alpha crystallin A sequences (*contra* McKenna, 1992). Pholidota, according to de Jong *et al.* (1985, p. 65), “can be most economically connected near a common carnivore-ungulate stem”; cf. McKenna (1987).

Epitheria (emended). Established by McKenna in 1975, Epitheria is supported by morphology and molecular aspects. The BV for this node is 96%, and BSV is 5. Many character polarities are plesiomorphic for *Xenarthra* and synapomorphic for Epitheria. Epitheria, thus, represents an independence from archaic Mesozoic mammalian characters still present in xenarthran

taxa. Samples of these synapomorphies for Epitheria are: first presence of a baculum (character 124), presence of stylohyoid muscle as a derivative of posterior digastric muscle (character 204), and true endothermy (character 248; see also caption to Fig. 1).

Lipotyphla (=Insectivora) and Preptotheria (Emended) Dichotomy

Lipotyphla (=Insectivora). In early stages of mammalian systematics, “Insectivora” included not only typical insectivore taxa but also members of families Tupaiidae and Ptilocercidae (now classified in order Scandentia) and Macroscelididae (now classified in order Macroscelidea). This “waste-basket” approach for “Insectivora” was practiced until recently (cf. discussions in Gregory, 1910; Simpson, 1945; Yates, 1984). A recap of the history of insectivore taxa is as follows. Haeckel (1866b) divided Insectivora into Lipotyphla (including Tenrecoidea, Chrysochloroidea, Erinaceoidea, and Soricoida) and Menotyphla (Macroscelidoidea and Tupaioida). Gill (1872) grouped Tenrecoidea and Chrysochloroidea in Zalambdodonta, and Erinaceoidea, Soricoida, Macroscelidoidea, and Tupaioida in Dilambdodonta (cf. Simpson, 1945, p. 176; Hill, 1972, pp. 11, 14). Lipotyphlan insectivores, according to Gregory (1910), were part of a branch including Chiroptera, Dermoptera, Scandentia, and Primates. Simpson (1945) classified all six superfamilies in one order, Insectivora. Recognizing that Macroscelidoidea and/or Tupaioida are distinct from other insectivorans began when Butler (1956) designated macroscelidids as an order—Macroscelidea. This ordinal recognition was followed by many authors, e.g., McKenna (1975), Yates (1984), Novacek (1986), and will be in this paper. Lipotyphla as an earlier offshoot of Epitheria is manifested by primitive characters such as presence of cloaca and occasional presence of pars chondralis of the interclavicle (details in Appendix 1).

Preptotheria (emended). In the McKenna *et al.* (1997) classification of Mammalia, Preptotheria includes these major clades: Anagalida, Ferae, Lipotyphla, Archonta, and Ungulata. In this study, Preptotheria is modified to include members of Unguiculata and Ferungulata. Departure of members of Preptotheria (as defined here) from insectivore stock is mani-

teeth, ch. 129—[?] rounded or approximately ball-shape patella (flattish and/or elongate in Hyracoidea), ch. 137—[?] distal phalanges spatulate (non-spatulate in earliest Artiodactyla), ch. 158—accessorius pedes (=quadratus plantae) extremely reduced or absent; Cetungulata: ch. 154—calcaneal peroneal tubercle indistinguishable or absent (no data for Cetacea for this and other characters for this node), ch. 162—common calcaneal tendon = “hamstring” for tendo Achillis absent, ch. 168—semi- and presemimembranosus muscles fused almost to insertion, ch. 205—iliocostalis and longissimus muscles are fused; Eparctocyon: ch. 134—pes paraxonic, i.e., digits III and IV are subequal, ch. 185—lumbricales muscles reduced or absent, ch. 253—incus crus breve is longer than crus longum; Altungulata: ch. 3—petrosal and basioccipital contact absent, ch. 108—clavicle (even as vestigial or cartilage) absent, ch. 151—astragalar head with short neck, or neck absent with flat head, ch. 236—penial glandular fossa present; Uranotheria: ch. 12—anterior border of orbit shifted anteriorly relative to cheek teeth, opening of infraorbital canal forward of orbit, ch. 140—taxeopody, ch. 173—ceratohyoideus absent, ch. 225—reduced, free yolk sac (in later stages of development), associated with zonary placenta; Tethytheria: ch. 20—zygoma thick and laterally expanded, ch. 182—digastricus originates on stylohyal, ch. 207—heart is bifid (with two apices).

TABLE 4

**Simplified, Nonranked Classification of Recent Mammalia Based on Morphological Evidence Presented Here,
with Reference to Molecular Evidence^a**

Mammalia Linnaeus, 1758
Prototheria Gill, 1872
Monotremata Bonaparte, 1838
Theria Parker and Haswell, 1897
Marsupialia Illiger, 1811 (=Metatheria Huxley, 1880)
Placentalia Owen, 1837 (=Eutheria Gill, 1872)
Xenarthra Cope, 1889 (=Edentata Cuvier, 1798)
Epitheria McKenna, 1975 (emended)
Lipotyphla Haeckel, 1866a (=Insectivora Bowdich, 1821) ^b
Preptotheria McKenna, 1975 (emended)
Unguiculata Linnaeus, 1766 (emended after Simpson's 1945) ^c
Anagalida Szalay and McKenna, 1971
Macroscelidea Butler, 1956 ^c
Glires Linnaeus, 1758
Rodentia Bowdich, 1821
Lagomorpha Brandt, 1855
Archonta Gregory, 1910 ^{c,d}
Scandentia Wagner, 1855
Primates Linnaeus, 1758 ^c
Volitantia Illiger, 1811
Dermoptera Illiger, 1811
Chiroptera Blumenbach, 1779
Ferungulata Simpson, 1945 (emended)
Ferae Linnaeus, 1758 (emended)
Carnivora Bowdich, 1821 ^c
Pholidota Weber, 1904 ^c
Ungulata Linnaeus, 1766 (emended)
Tubulidentata Huxley, 1872
Cetungulata Irwin and Wilson, 1993 (emended) ^e
Eparctocyona McKenna, 1975 ^f
Artiodactyla Owen, 1848
Cetacea Brisson, 1762
Altungulata Prothero and Schoch, 1989 ^g
Perissodactyla Owen, 1848
Uranotheria (=Paenungulata Simpson, 1945, in part) McKenna <i>et al.</i> , 1997
Hyracoidea Huxley, 1869
Tethytheria McKenna, 1975
Proboscidea Illiger, 1811
Sirenia Illiger, 1811

Note. Taxa are nested to facilitate correspondence with branching on Fig. 1 (authorships here and elsewhere in the text are not included in the References unless they are cited elsewhere in the text or notes below).

^a We incorporated portions of McKenna *et al.*'s (1997) classification, employing the total group and stem group concepts.

^b Lipotyphla includes Chrysochloridea, Erinaceomorpha, and Soricomorpha (including Soricoidae and Tenrecoidea; McKenna *et al.*, 1997). Erinaceomorpha and Soricomorpha are more closely related to each other than either is to Chrysochloridea.

^c Phylogenetic position uncertain.

^d This provisional arrangement of the taxa in this clade is a concept first proposed by Linnaeus (1758) who included in Primates the genera *Homo*, *Simia*, *Lemur* [including the lemuroids and *Galeopithecus* (= *Cynocephalus*)], and *Vespertilio* (see text for discussion of this hypothesis).

^e Irwin and Wilson (1993, p. 264) employed the concept of Cetungulata (they used "cetungulate") to include Cetacea, Artiodactyla, and Perissodactyla. Here, this taxon is emended; cf. Thewissen (1994, p. 175) who used Cetungulata. Cetungulata of Irwin and Wilson, 1993, is an actual, but not necessarily legal, junior objective synonym of Pycnoderma (thick skinned) of Haeckel, 1866a, p. cxlv. Haeckel used the term for Linnaeus' ungulates plus whales. The International Code of Zoological Nomenclature does not rule in this regard, but since Haeckel's Pycnoderma has not been applied in formal classification and Cetungulata has been, we employ Cetungulata.

^f Eparctocyona, as a total group, can include the crown group Cetartiodactyla (after Montgelard *et al.*, 1997, p. 556) for the living Cetacea and Artiodactyla, their latest common ancestor, plus the descendants of that ancestor (Jefferies, 1979, p. 443).

^g Thewissen and Domning (1992, p. 498) preferred the term "Pantomesaxonia" of Franz, 1924, over "Altungulata"; cf. discussion in Prothero (1993, p. 177). Here, we follow the scheme of McKenna *et al.* (1997).

fested by an encephalization quotient of more than 0.21 (character 237) and absence of the cloaca (character 215; see also caption to Fig. 1).

Unguiculata and Ferungulata Dichotomy

Unguiculata (emended). Unguiculata of Linnaeus, 1766 (emended after Simpson 1945), includes Anagalida [Macroscelidea and Glires (Rodentia and Lagomorpha)] and Archonta [Scandentia and Primatomorpha [Primates and Volitantia (Chiroptera and Dermoptera)]]. This clade is weakly supported by a BV of 50% and BSV of 0 (cf. Fig. 1). There are two characters in support of Unguiculata: (character 22) with CI = 0.5 and (character 103) with CI = 1.0. If we test an equally parsimonious alternative hypothesis where Anagalida and Archonta are separated, such that Archonta joins Ferungulata, the eight synapomorphies assigned for this clade are very weak, with a consistency index ranging from 0.2 to 0.4. For this reason, we chose the tree on which Anagalida and Archonta are united with dashed lines and question marks.

Anagalida. Relationships within this clade are not universally accepted. For example, Macroscelidea, according to molecular studies (e.g., de Jong *et al.*, 1993; Porter *et al.*, 1996; some results of Shoshani 1986b), is closely related to paenungulates (here uranotheres, after McKenna *et al.*, 1997) taxa. [It is of interest that representatives of Macroscelidea, Pholidota, and Ungulata have eyes open at birth and their neonates are usually precocial, character 249 = [S5].] It costs 30 steps to join Macroscelidea to Uranotheria. Thus, based on available evidence, this hypothesis is strongly contradicted.

Glires. Like a pendulum, acceptance or rejection of Glires—to include Rodentia and Lagomorpha—shifts in either direction, depending on available evidence. Discussions and data to corroborate or contradict this hypothesis can be found in: Gregory (1910), Simpson (1945), McKenna (1975), Novacek (1986), Novacek and Wyss (1986), Shoshani (1986a, b), Li *et al.* (1987), Li and Ting (1993). In summarizing some of the characters uniting members of Glires, Gregory (1910, pp. 325–326) wrote: “The Duplicidentata (Weber, 1904, p. 493) possess many deep seated characters in common with the Simplicidentata, such as: . . .”

Archonta. First established by Gregory (1910), members of Archonta include Scandentia, Primates, Dermoptera, and Chiroptera, but relationships among them are controversial (cf. Pettigrew, 1991, Simmons, 1993, Miyamoto, 1996, and references within). Simpson (1945) classified Tupaioidea within Primates; Tupaioidea now is recognized as a separate order (e.g., Luckett, 1980, pp. 22–23). Beard (1993) included Dermoptera within Primates, a concept followed by McKenna *et al.* (1997), although there is weak molecular evidence (Bailey *et al.*, 1992; Porter *et al.*, 1996). Here, we provide a

provisional arrangement within Archonta, a concept first proposed by Linnaeus (1758); cf. footnote *d* in Table 4.

Primatomorpha Beard, 1991 (emended). Beard's (1993, p. 145) Primatomorpha includes five families of extinct taxa, Dermoptera, and Primates. Here, we extend Primatomorpha to include Chiroptera. There is no molecular evidence in support of Primatomorpha as presented here (cf. Stanhope *et al.*, 1993, and Miyamoto, 1996), and the morphological evidence is weak (see caption to Fig. 1). Nonetheless, results from living taxa, as well as combined data from living and extinct taxa, depict Primates as a sister-taxon to Volitantia. When Primates are forced to join Scandentia with living data, there is a change of five steps in the score of the tree, whereas, with combined data, it costs one additional step; but when a polytomy [Primates, Scandentia, and Volitantia] is sought, the score of the tree is raised by five additional steps. For this reason, Primates are joined with a dashed line to Volitantia, with a BV of 43% and BSV of 0. Tests conducted to evaluate parallelism or reversals within Primatomorpha for 260 characters reveal that, when employing ACCTRAN optimization that favors reversals over convergence, there are 11 characters assigned for this node [two of which have a CI of 1.0, four of 0.5, and the rest are below 0.5]. When employing DELTRAN optimization that favors convergence over reversals, there are nine characters for the same node, five of which are the same as were obtained from ACCTRAN. These results convey the complexity of some of the characters and the intricate details employed in decision making about which assumption (e.g., ACCTRAN vs DELTRAN) to choose, for they carry much weight; cf. Simmons (1993).

Volitantia Illiger, 1811. This clade is strongly supported (BV of 100% and BSV of 14). Note, however, that characters supporting Volitantia may be adaptive to volant and glissant locomotion, thus parallelism/convergence may be inevitable; cf., e.g., Van Valen, 1979, and notes under Archonta above.

Ferungulata Simpson, 1945 (emended). Except for Cetacea, which is included in our ferungulate classification, all taxa are similar to those of Simpson's (1945) living and extinct forms. Our study confirms that Ferungulata is a relatively stable clade with a BV of 71% and BSV of 4 (cf. Fig. 1). Simpson's 1945 classification implies that his Ferae (Creodonta and Carnivora) is the most plesiomorphous taxon within Ferungulata, followed by ungulate taxa; this position seems to have some credence, see below.

Ferae and Ungulata Dichotomy

Ferae Linnaeus, 1758 (emended): Carnivora. Gregory (1910) depicted Creodonta as ancestral to modern Carnivora and this entire branch as a sister to Artiodactyla. Simpson (1945) effectively listed Carnivora as a

plesiomorphous member of Ferungulata, a cohort that also includes ungulates. The position of Carnivora after Simpson's work varied from related to Insectivora (e.g., Novacek, 1986), to Pholidota (Shoshani, 1986a, b; de Jong *et al.*, 1993), to Primates (Shoshani, 1986a, b), or to Ungulata (McKenna, *et al.*, 1997). Our results suggest that Carnivora's phylogenetic position may be sought within ungulate-related mammals as proposed by Gregory (1910) and Simpson (1945). Starck (1967, p. 546) and MacPhee (1994, p. 78) reported that Carnivora and Pholidota share the presence of a well-developed ossified tentorium and Wyss and Flynn (1993, p. 33) added that Creodonta also possesses this character. Emry (1970, p. 471) observed that *Patriomanis*, a late Eocene pholidotan, has a bony tentorium but it is not so developed as in *Manis*. We confirm these observations and add that Tubulidentata also possess an ossified tentorium similar to that in Pholidota.

Pholidota. Often associated with edentate mammals during the 19th century (e.g., Smith, 1897, 1899) and into the 20th century (e.g., Novacek, 1986; Shoshani, 1986a), pholidotans were given ordinal status in 1904 by Weber. Gregory (1910, p. 100) classified Pholidota within Edentata. Simpson (1945, pp. xi, xii) put them within Unguiculata, together with Insectivora, Dermoptera, Chiroptera, Primates, and Edentata (=Xenarthra). Departures from these hypotheses are those of Shoshani (1986a, p. 228; based on immunodiffusion results), and de Jong *et al.* (1993, p. 9, based on a new interpretation of alpha lens crystallin results) who placed Pholidota with Carnivora. In this study, if we consider living taxa only, Pholidota (with weak support) turns out to be a sister-group to Ungulata, whereas if all taxa are analyzed, Pholidota is depicted in a polytomy within Preptotheria.

Having weak morphological evidence of the position of Pholidota within Mammalia, we tentatively accept that, based on molecular data noted above and the possible sharing synapomorphy of the ossified tentorium, Pholidota and Carnivora are closely related. McKenna (1987) conducted extensive reanalysis of de Jong *et al.* (1985) alpha lens crystallin sequences and observed that two pangolins, *Manis* and *Phataginus*, and a sloth bear, *Melursus*, share a synapomorphy—tyrosine instead of phenylalanine at position 74. With this regard, McKenna (1987, p. 72) noted that "... living pangolins and their fossil palaeonodont allies of the early Caenozoic of the Northern Hemisphere originated from early pantolestid-like 'insectivores' (Rose, 1978) that were themselves closely related to early carnivorans and Cretaceous palaeoryctoids, but special relationship to *Melursus* verges on the incredible [a possible convergence because it also occurs in the opossum]." These results possibly suggest that pantolestids, as early members of Ferae, had some of the carnivore genes that are still expressed in pholidotans. In a more recent analysis of the same data, McKenna

(1992, pp. 353–354) noted that "... pangolins can be tied weakly to the edentates. ..." In this paper, our justification of placing Carnivora with Pholidota in Ferae is weak.

Ungulata Linnaeus, 1766 (Emended)

Tubulidentata. Much has been written about the phylogenetic position of this mammalian order (e.g., Broom, 1909a, b; Gregory, 1910; Le Gros Clark and Sonntag, 1926; Simpson, 1945; Patterson, 1978; Thewissen, 1985; Shoshani, 1986a, b, 1993; Novacek *et al.*, 1988), but there has been no clear decision as to its affinities, although the consensus is that it belongs to ungulate stock. Our study confirms Tubulidentata's position within Ungulata, but with a relatively weak support—BV of 72% and BSV of 1 (cf. Fig. 1).

Cetungulata Irwin and Wilson, 1993 (Emended):

Eparctocyona and Altungulata Dichotomy

Eparctocyona McKenna, 1975. As a total group that embraces the stem group and crown group, Eparctocyona can accommodate representatives of living Cetacea and Artiodactyla as well as extinct taxa included in McKenna *et al.* (1997). Artiodactyla and Cetacea join as sister-taxa in analysis of data matrices—that of living taxa and that of combined data of living and extinct mammals. Despite the weak BV for this clade (57%), and the BSV of 1, Cetacea is joined to Artiodactyla with fine solid lines because there is no discrepancy between results from living taxa and from living and extinct taxa, and there is corroborating evidence from molecular data. The resultant clade is joined to the main axis of the cladogram with dashed line because with combined data of living and extinct mammals, Perissodactyla joins Cetartiodactyla (after Montgelard *et al.*, 1997); see note [f] in Table 4. Note, however, that it costs one additional step to join Cetacea to Altungulata with data of living taxa and up to 12 additional steps to separate Cetacea from Artiodactyla with data of living and extinct taxa. One of the earliest molecular, immunodiffusion results to suggest a relationship between Artiodactyla and Cetacea is that of Shoshani (1986b, p. 197), who depicted *Delphinapterus* between *Suina* and *Hippopotamus*. Other molecular studies that corroborated a cetartiodactyl clade include Sarich (1993) and Czelusniak *et al.* (1990).

Altungulata Prothero and Schoch, 1989. Exact relationships within this clade are not yet generally agreed upon, but its contents appear to be accepted by most morphological studies (e.g., Prothero *et al.*, 1988; Fischer and Tassy, 1993; Thewissen and Domning, 1992). Fischer and Tassy (1993), however, favored Perissodactyla-Hyracoidea affinity, a hypothesis that would raise the score of the strict consensus tree from living or combined data by 14–20 steps. This hypothesis is not accepted here. Perissodactyla was retained as a sister-

taxon to *Uranotheria*, even though, in the tree from combined data for living and extinct taxa, *Perissodactyla* was a sister-taxon to *Eparctocyona* (cf. Graur *et al.*, 1997 for molecular result). Of the 15 characters from the combined data that support *Perissodactyla*-*Eparctocyona*, the only three with CI = 1.0 are myological characters in the foot region for which we have no evidence for the extinct forms. Also, based on results from living taxa, it costs three additional steps to join *Perissodactyla* with *Eparctocyona*. The BV for *Altungulata* is 71% and the BSV is 3.

Uranotheria (= *Paenungulata*, in part) McKenna *et al.*, 1997. Except for the work of Fischer (e.g., Fischer, 1989) who resurrected 18th century thoughts of *Perissodactyla*-*Hyracoidea* affinity, all other studies—morphological and molecular (cf. Czelusniak *et al.*, 1990; Novacek *et al.*, 1988; Shoshani, 1993)—support the relationships depicted in Fig. 1.

Tethytheria McKenna, 1975. Currently, this is a universally accepted taxon based on morphological and molecular studies (e.g., McKenna *et al.*, 1997; Sarich 1993).

MORPHOLOGY VS MOLECULES

Comparison between results obtained from morphology and molecules shows that within *Mammalia* there are several cases of correspondence. These include relationships and/or position of *Theria*, *Placentalia*, *Eparctocyona*, and *Uranotheria* (*Tethytheria* included); cf. “*” in Fig. 1. Partial correspondence between morphology and molecules has been reported for seven clades; cf. “(*)” in Fig. 1. Miyamoto (1996) discussed relationships within *Archonta* and noted noncongruent results between morphology and molecules; the latter includes the “New” group (Miyamoto, 1996) which encompasses *Rodentia*, *Lagomorpha*, *Dermoptera*, *Primates*, and *Scandentia* (a part of *Unguiculata* used here). Observations and comparisons among morphological and molecular approaches and results were made by Shoshani (1986a), Honeycutt and Adkins (1993), and Shoshani *et al.* (1996, p. 122; cf. Graur *et al.*, 1997).

CONCLUSIONS

Extinct taxa are important to establish polarities of characters. Nondental characters proved useful in evaluating the phylogenetic positions of mammalian taxa that either lack teeth or have modified dentition in adult stages in the taxa we studied (e.g., *Monotremata*, *Xenarthra*, *Pholidota*, *Tubulidentata*, *Bibymalagasias*, and *Eurotamandua*). In some instances, understanding the ontogenetic and phylogenetic history of even one bone helps to elucidate relationships among taxa, which otherwise remain obscure [cf. characters 39 = [O1] and 40 = [40.1] in Appendix 1, with regard to the

interparietal and supraoccipital bones]. *Mammalia*, *Theria*, *Placentalia* (= *Eutheria*), and *Epitheria* are monophyletic taxa. Within *Epitheria*, higher categories are related in a branching pattern (not a “bush”) as follows: *Lipotyphla* is the first (plesiomorphous) branch within *Epitheria*. The remaining 16 orders seem to cluster into two groups: (1) Those without affinity to ungulates, including *Lagomorpha*, *Rodentia*, *Macroscelidea*, *Scandentia*, *Primates*, *Dermoptera*, and *Chiroptera*; (2) Those with affinity to ungulates, including *Carnivora*, *Pholidota*, *Tubulidentata*, *Artiodactyla*, *Cetacea*, *Perissodactyla*, *Hyracoidea*, *Proboscidea*, and *Sirenia*. Living representatives of *Pholidota* (four genera) and *Tubulidentata* (only one genus) are too specialized and may affect their systematic position.

Support for relationships depicted in Fig. 1 comes from data from both living and extinct mammals. Among extinct forms, relationships are not well resolved. Nonetheless, cladograms incorporating extinct taxa helped resolve some questions among living forms (see examples above for *Pholidota*, *Eparctocyona*, and *Perissodactyla*).

Overall, the classification of McKenna *et al.* (1997) and the one presented here are similar. Their classification differs from that which is presented in Table 4 in these points: *Lipotyphla* is within *Preptotheria*, *Primates* and *Dermoptera* are sister-taxa, and the dissociation of *Archonta* and *Anagalida*. Notable differences between results presented here and those of most other investigators include the separation of *Pholidota* from *Xenarthra* and the ancient position of *Lipotyphla* within *Epitheria*.

It is possible that the currently held view of *Lipotyphla* (= *Insectivora*), i.e., the union of *Soricomorpha*, *Erinaceomorpha*, and *Chrysochloridea*, is not valid, and this group may be polyphyletic. Correspondence between results from morphology and molecules for *Placentalia* includes these clades: *Epitheria* (in part), portions of *Unguiculata* (*Rodentia*, *Lagomorpha*, *Dermoptera*, *Euprimates*, and *Scandentia*), *Ferae* (in part), *Ungulata* (in part), *Cetungulata* (in part), *Eparctocyona*, *Altungulata* (in part), *Uranotheria*, and *Tethytheria*. Since there is only one phylogenetic history of mammalian taxa, incongruent results between morphology and molecules should be interpreted as challenges for future investigators (see comments at end of Appendix 1).

ACKNOWLEDGMENTS

Museum staffs where specimens were examined (including about 25 museums and other localities, some of which are listed in Shoshani (1986b), pp. 559–560) are acknowledged for their help with collections. Individuals who helped us in various ways include: Susan K. Bell, Edward M. Golenberg, Morris Goodman, Jann S. Grimes, Eleanor C. Marsac, Jin Meng, Michael Nedbal, Scott L. Page, Jules L. Pierce, Kenneth D. Rose, J. G. M. (Hans) Thewissen, and Michael S.

Woodford. Singled out is Susan K. Bell for her continued support in this study. Other acknowledgments are given in Appendix 1.

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