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The Phylogenetic Resolving Power of Discrete Dental Morphology Among Extant Hedgehogs and the Implications for Their Fossil Record

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ABSTRACT

Discrete dental morphology among members of the extant Erinaceidae (Mammalia; Lipotyphla) is comprehensively reviewed in order to ascertain its phylogenetic resolving power. This analysis responds to the need to better understand the nature of the characters—discrete dental morphology—most commonly used to diagnose erinaceid fossil taxa, and reconstruct their evolutionary histories. This investigation attempts to set the parameters for a phylogenetic analysis of both fossil and living erinaceids.

The first phase of this investigation reviews 246 descriptive discrete dental transformation series—the majority of which were gathered primarily from the literature and are (or have been) considered apomorphies at various taxonomic levels within the family Erinaceidae. These characters were reviewed across 10 species of hedgehogs: a minimum of two species per extant genus (excluding the rare species), of which all are represented by series of individuals. The data were compiled and analyzed for each individual for inter- and intraspecific variation (including asymmetry), and its possible covariation with sex, relative age (based on tooth eruption and wear stage), and geographic location.

The second phase tests the phylogenetic resolving power of the discrete dental transformation series when considered as the sole body of evidence for hypotheses of evolutionary relationships. The discovered phylogenies of parsimony analyses of the discrete dental data are compared to previous hypotheses of relationships based on all known morphological evidence.

Results suggest that dental variation is intemperant both inter- and intraspecifically within the Erinaceidae and cannot unequivocally be attributed to any one of the variables considered (see above); and, more specifically, the phylogenetic resolving power of the dental data (across the considered taxa) is contingent on the inclusion of other data (i.e., cranial and postcranial material). Consequently, the applicability of this character set to the erinaceid fossil record as the sole source of evidence for phylogenetic inference is challenged.

INTRODUCTION

This study investigates the appropriateness of using the dental morphology of hedgehogs (Mammalia; Lipotyphla; Erinaceidae) as the sole character suite for positing phylogenetic relationships in living and in fossil taxa. More specifically, it is designed to ascertain the extent of inter- and intraspecific dental variation among the living members of this group, and to determine whether interspecific variation can be correlated to the age, sex, and/or geographic locality of the reviewed individuals. The phylogenetic resolving power of these data across the extant taxa will then be explored under the tenets of the parsimony principle. Subsequently, the applicability of these data as the sole source of evidence for inferring evolutionary relationships among the fossil taxa will be reevaluated.

OVERVIEW

Historically, the reliance upon discrete dental data as evidence for positing phylogenetic relationships has been incongruous between the extant and fossil erinaceid taxa. That is, fossil taxa are predominantly represented by teeth, either isolated or in incomplete jaws and maxillary bone. Consequently, many fossil species are diagnosed and their phylogenetic histories reconstructed based almost exclusively on presumed discrete dental apomorphies (de Blainville, 1840; Matthew, 1903; Koerner, 1940; Hürzeler, 1944; Simpson, 1945; Butler, 1948, 1956a, 1956b, 1972, 1988; Crusafont et al., 1955; Friant, 1961; Van Valen, 1967; McKenna and Holton, 1967; Rich and Rich, 1971; Rich and Rasmussen, 1973; Gilbert, 1975; Krishtalka, 1976; Schwartz and Krishtalka, 1976; Krishtalka and West, 1977; Stevens, 1977; Black et al., 1980; Munthe and West, 1980; Engesser, 1972, 1979, 1980, ; Rich, 1981; Novacek, 1985; Novacek et al., 1985; see appendix 1). Phylogenies of the extant taxa, however, are based on comprehensive morphological data sets that include pelage, cranial, and dental characters (Corbet, 1974, 1988; Frost et al., 1991; Storch and Qiu, 1991; Gould, 1995), as well as molecular and morphometric ones (Ruedi et al., 1994; Ruedi and Fumagalli, 1996; Robbins and Setzer, 1985). Consequently, the disparate treatment of the extant and fossil taxa has resulted in partitioned data sets: (1) dental characters that have been considered only for fossil taxa; and (2) more comprehensive characters that are applicable only to the extant forms as a result of poor preservation in fossil taxa. A survey of the literature indicates there is very little character overlap between data sets (see appendix 1 citations).

Polymorphism of discrete dental characters has been reported in many of the extant hedgehogs (Woodward, 1896; Brockie, 1964; Van Valen, 1967; Harrison and Bates, 1985; Poduschka and Poduschka, 1986), the most extreme being complete absences of individual teeth which seem to occur fairly frequently both inter- and intraspecifically, as well as within individuals (Van Valen, 1967). These observations suggest that plasticity of these characters may occur more commonly, and possibly more globally (i.e., across all taxonomic levels), than was previously believed. A cursory review of the literature turned up 31 citations on tooth anomalies within bats, rodents, cervids, carnivores, and other lipotyphlans (Palmer, 1937; Hall, 1940; Hooper, 1946; Kurten, 1953, 1982; Hooper, 1957; Jones, 1957; Setzer, 1957; Meester, 1959; Van Valen, 1967; Haft, 1963; Martin, 1968; Wallace, 1968; Choate, 1969; Ziegler, 1971; Fish and Whitaker, 1971; Janossy and Schmidt, 1975; Smith, 1977; Dippenaar, 1978; Woloszyn, 1978; Hall and Yalden, 1978; Nadachowski, 1978; Krausman, 1978; Beaver et al., 1982; Woods, et. al., 1982; French, 1985; Hillson, 1986; Davis, 1987; Barnosky, 1990; Jernvall, 1995; Clarke, 1997; Bell and Repenning, 1999).

Unlike many other morphological characters, dental phenotype is not only a result of intrinsic (genetic and developmental) factors, it is a result of universal extrinsic factors that affect all teeth—tooth wear. Individual tooth wear patterns are a result of function (e.g., occlusal wear), diet (e.g., geographic location and/or individual preference), and sometimes idiopathic chewing behavior. Without a better understanding of the nature and frequency of dental variation, reliance on the phylogenetic resolving power of these data can seriously compromise any attempt to reconstruct a phylogeny at all levels of analysis. For example, within the Erinaceidae, the purported dental apomorphies outnumber the most recent complete (nondental) morphological data set (Gould, 1995) for the extant taxa by 2.5 to 1 (appendix 1), and the named fossil taxa comprise approximately 75% of the all the combined taxa at the generic level (McKenna and Bell, 1997), of which 75% are represented solely by teeth (Gould, 1995). If certain character states for a given transformation series were actually records of ontogenetic stages or discovered to be globally homoplastic (i.e., inter- and intraspecifically), hypotheses of the phylogenetic relationships of many of the fossil taxa would be rendered suspect.

Although this study focuses principally on one group of organisms and a particular data set (i.e., dental characters), the ubiquitous problem of paleontology is a paucity of material. Missing data is not an unexpected problem regardless of the taxonomic group under study or whether extant or extinct (Nixon, 1996). However, unlike the case with living taxa, the available data for many fossils is compromised by selective preservation, and often only one type of datum is commonly preserved (e.g., vertebrae of snakes or sauropods; teeth of sharks or mammals; skull caps of pachycephlosaurs). As mentioned above, this phenomenon complicates the problem of missing data: Not only does operational missing data (i.e., missing cells in the data matrix) need to be addressed subsequent to a phylogenetic analysis (see Platnick et al., 1991; Maddison, 1993; Nixon and Carpenter, 1996), but also the ramifications of the inherent missing data (i.e., the complete lack of other character sets). The effects of operational missing data can be tracked using diagnostic parsimony programs (e.g., MacClade, Clados, NONA); however, comprehensive absences of entire systems of an organism, such as skeletal or soft tissue material, pose a much more pervasive problem. It seems judicious, therefore, to test the reliability of monotypic data for establishing phylogeny. That is, how much confidence can we expect to have in a phylogeny or a proposed classification that is based exclusively on one type of data, or simply, on one small aspect of the organism?

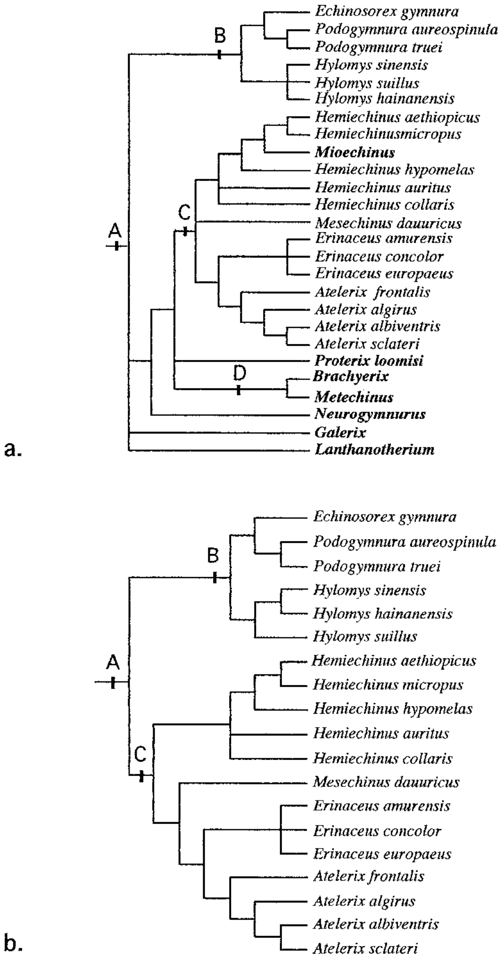

Fig. 1. (**a**) Gould's (1995) Adams tree, fossils are indicated in bold (**b**) Frost et al.'s (1991) single most parsimonious tree. A = Erinaceidae; B = Hylomyinae; C = Erinaceinae; D = Brachyericinae.

CURRENT TAXONOMY OF THE ERINACEIDAE

The Erinaceidae are a well-established monophyletic group (see fig. 1, stem A; Frost et al., 1991; Gould, 1995). There are approximately 19–23 reported living species, and over 30 recognized fossil genera (McKenna and Bell, 1997). A recent phylogenetic analysis of both fossil and extant taxa indicates that this lineage may extend as far back as the late Cretaceous (Gould, 1995), making this group one of the oldest surviving lineages of placental mammals.

Hypotheses of the historical relationships within the Erinaceidae are based almost exclusively on morphological data (Butler, 1948, 1988; Rich, 1981; Novacek, 1985; Frost et al., 1991; Gould, 1995; McKenna and Bell, 1997), although recently, molecular data have been employed in phylogenetic reconstructions of more inclusive groups (Ruedi et al., 1994; Ruedi and Fumagalli, 1996; Filippucci and Simson, 1996; Surin et al., 1997), and one morphometric-based phylogeny has been proposed for the living genera (Robbins and Setzer, 1985). Thus far, however, these data sets used to infer phylogeny have remained distinct, a practice that has resulted in incongruent hypotheses of relationships (see phylogenies proposed by Butler, 1948, 1988; Rich, 1981; Robbins and Setzer, 1985; Frost et al., 1991). Recent efforts to reconcile some of the disparate data sets (Ruedi et al., 1994; Gould, 1995, 1997) yielded, not surprisingly, conflicting results with all previous hypothesis of relationships that are based solely on partitioned data sets.

In the most recently proposed classification of all the known erinaceids (McKenna and Bell, 1997), four subfamilies are recognized (fig. 1), two of which include all extant members of the family: (1) the Hylomyinae (moonrats, or gymnures; stem B) of Malaysia and Indonesia, whose fossil record is currently challenged (Gould, 1995); and (2) the Erinaceinae (spiny hedgehogs, stem C), a group distributed throughout Europe, Asia, and Africa, whose fossil members are known from all three of these regions as well as North America. The remaining two subfamilies, the Brachyericinae (fig. 1b, stem D) and Tupaiodontinae (not shown in fig. 1), are exclusively composed of fossil taxa from both North America and Asia.

DISCRETE DENTAL DATA ANALYSES

METHODS AND JUSTIFICATION

CHARACTERS REVIEWED AND SOURCES OF DIFFICULTY: As mentioned in the Introduction, many of the fossil taxa are represented only by isolated teeth and jaws. The majority of the characters reviewed in this analysis (see appendix 1) were gathered primarily from the paleontological literature. In addition, some new characters and character states were added from personal observations made during the course of this analysis (appendix 1; see the following discussion).

All character states were compiled into a total of 246 transformation series. In many cases, the states within a given transformation series were so numerous and complex that it was more practical to handle them as a series of multiple binary transformations. Those cited transformation series that presented interpretive problems (e.g., relative size, relative position) are discussed below. It should be noted that the sequence in which the character states are listed in a given transformation series does not imply transformation additivity or polarity. Moreover, this phase of the analysis does not attempt to posit phylogenetic relationships: Outgroup comparison, and subsequent hypotheses of character polarity and directionality are addressed in the second phase (see Phylogenetic Analysis below).

Dental nomenclature follows that of Rich (1981); refer to figure 2. In general, because the nomenclature is fairly consistent across the Erinaceomorpha, the majority of the literature-based apomorphies are self-explanatory (refer to fig. 2) and need no discussion. The characters pertaining to the molars are illustrated in figures 2a, b, an idealization of the occlusal surfaces of upper and lower tribosphenic molars (following Salay, 1969 and Rich, 1981). Stereo photographs of occlusal surfaces of representatives of each genus reviewed in this analysis are presented in figures 3–7.

Interpretation difficulties are almost exclusively confined to those transformation series that attempt to characterize size and shape in a nominal (i.e., noncontinuous) fashion. For example, ‘‘the hypocone is larger than the protocone’’ (Storch and Qiu, 1991)—it is unclear whether the size ‘‘larger’’ refers to the height of the cusps, or the *gross* size (volume) of the cusps, or both. At first glance, this may seem trivial, but many fossil taxa, such as those that are represented only by dental material, are described and diagnosed based on such character states (appendix 1).

Herein I have tried to accurately define the size parameters to which I refer, however, there still remains the problem of visualizing size without the aid of controlled measurements (e.g., employing the use of calipers).

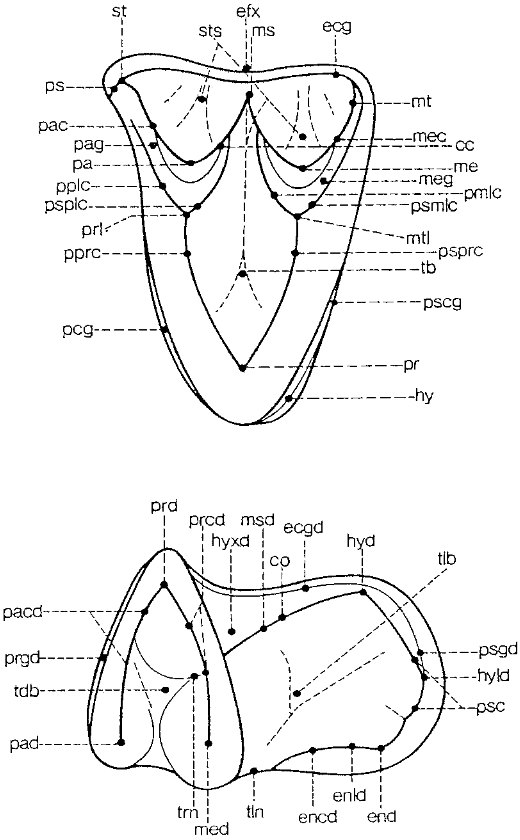

Fig. 2. Occlusal view of idealized tribosphenic molars: (**a**) first upper molar; (**b**) first lower molar (taken from Rich, 1981). Abbreviations: cc = centrocrista (to include postparacrista and premetacrista); co = cristid obliqua; ecg = ectocingulum; ecgd = ectocingulid; efx = ectoflexus; encd = entocristid; enld = entoconulid; end = entoconid; hy = hypocone; hyd = hypoconid; hyld = hypoconulid; hyxd = hypoflexid; me = metacone; mec = metacrista (or postmetacrista); med = metaconid; meg = metacingulum; ms = mesostyle; msd = mesoconid; mt = metastyle; mtl = metaconule; pa = paracone; pac = paracrista (or preparacrista); pacd = postparacrista; pad = paraconid; pag = paracingulum; pcg = precingulum; pmlc = premetaconule crista; pplc = preparaconule crista; pprc = preprotocrista; pr = protocone; prcd = protocristid; prd = protoconid; prl = paraconule; prgd = precingulid; ps = parastyle; psc = postcrista; pscg = postcingulum; psgd = postcingulid; psmlc = postmetaconule crista; psplc = postparaconule crista; psprc = postprotocrista; st = stylocone; sts = stylar shelf; tb = trigon basin; tdb = trigonid basin; tlb = talonid basin; tln = talonid notch; trn = trigonid notch.

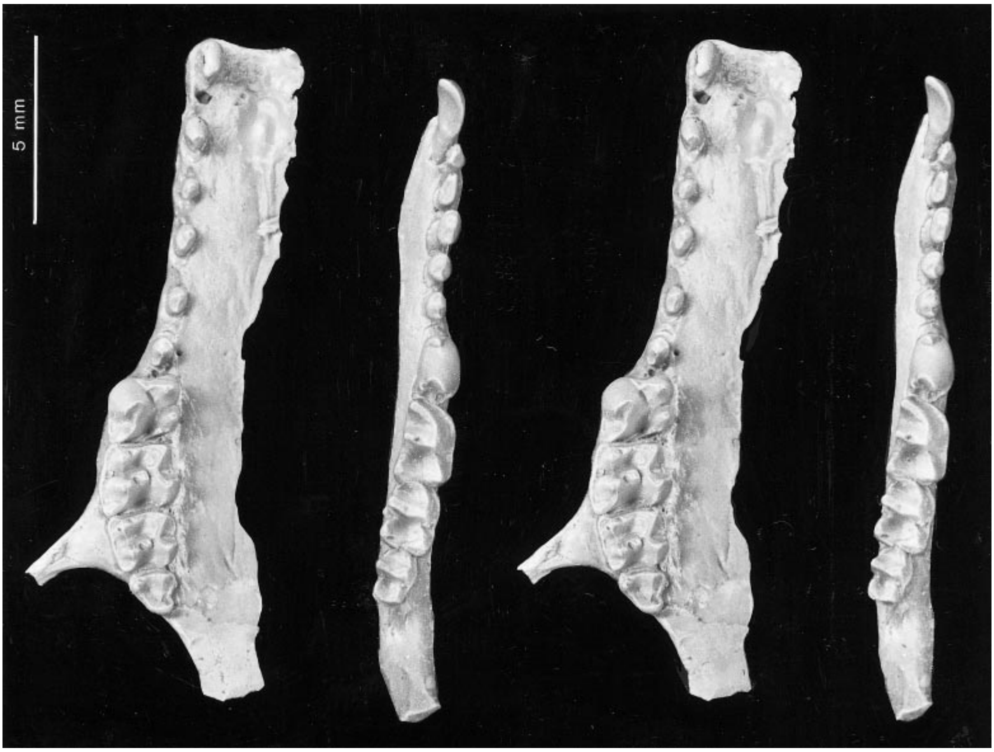

Fig. 3. *Echinosorex gymnura* (AMNH 115519) upper and lower jaw.

This difficulty became apparent on many occasions when I, along with W. R. Downs, reviewed the same specimen with considerably different impressions. Orientation is partly responsible for the variant interpretations: When the tooth is in situ (i.e., in the jaw), it does not sit on a level plane, therefore the heights of the cusps appear different depending on whether they are viewed labially or lingually. Because of the sheer magnitude of the number of specimens reviewed in this analysis (227), along with the varying size and fragility of the specimens, taking measurements for every cusp was precluded. Instead, the specimens (skull and jaws) were placed so that the occlusal surfaces were on approximately the same plane (a natural position) and the relative heights of the cusps were recorded.

Other ambiguous characters concern cusp position illustrated, for example, in the statement ‘‘the paracone is lingual to the metacone’’ (Koerner, 1940). As with size, descriptions of cusp position depend on which part of the cusp is referred to: the base or the apex. In many cases, especially the protocone and protoconid, the cusp is somewhat crescentic in shape (see figs. 3–7), and thus the apex extends lingually beyond the base of the cusp. The apex of the protocone, however, becomes more aligned with its base with progressive wear (personal obs.). I have thus tried to standardize these relative-position characters by referring to only the base of the cusp. These revised positional definitions may not be in accord with the original intention of the author(s) who first observed and noted these characters (appendix 1), nevertheless, the base of the cusp is much less susceptible to wear, making its position less likely to be compromised.

Equally difficult to interpret is what constitutes a character or character state in the mind’s eye of another investigator. Is an enamel ‘‘bead’’ on the labial side of the tooth equivalent to the presence of a labial cingulum? Or is a mediolateral crest extension of the protoconid on the p4 considered a distinct

Fig. 4. *Hylomys sinenesis* (AMNH 10106) upper and lower jaw.

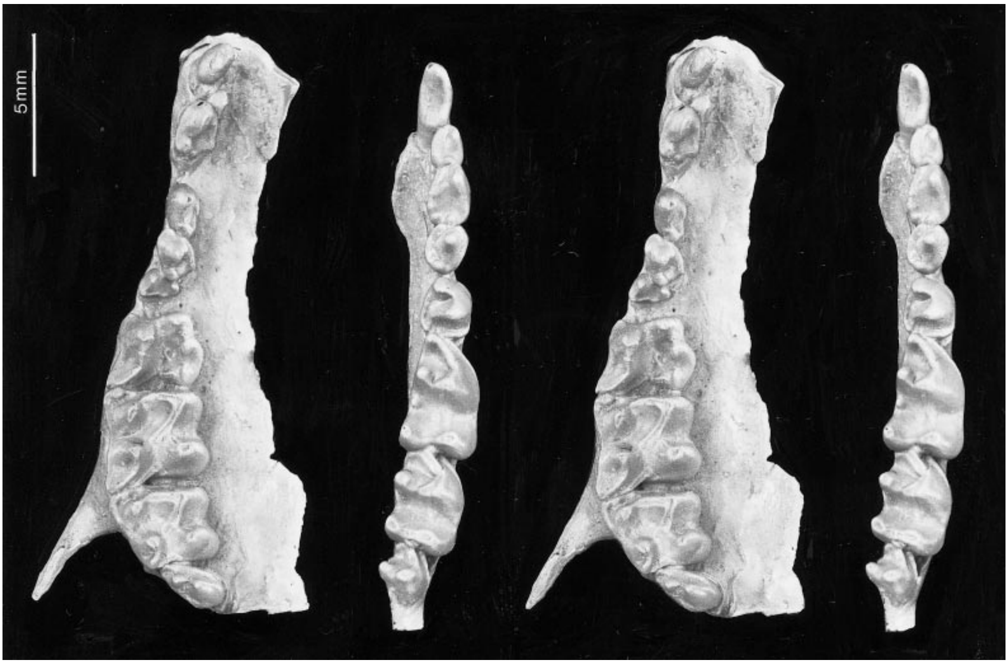

Fig. 5. *Atelerix albiventris* (AMNH 165804) upper and lower jaw.

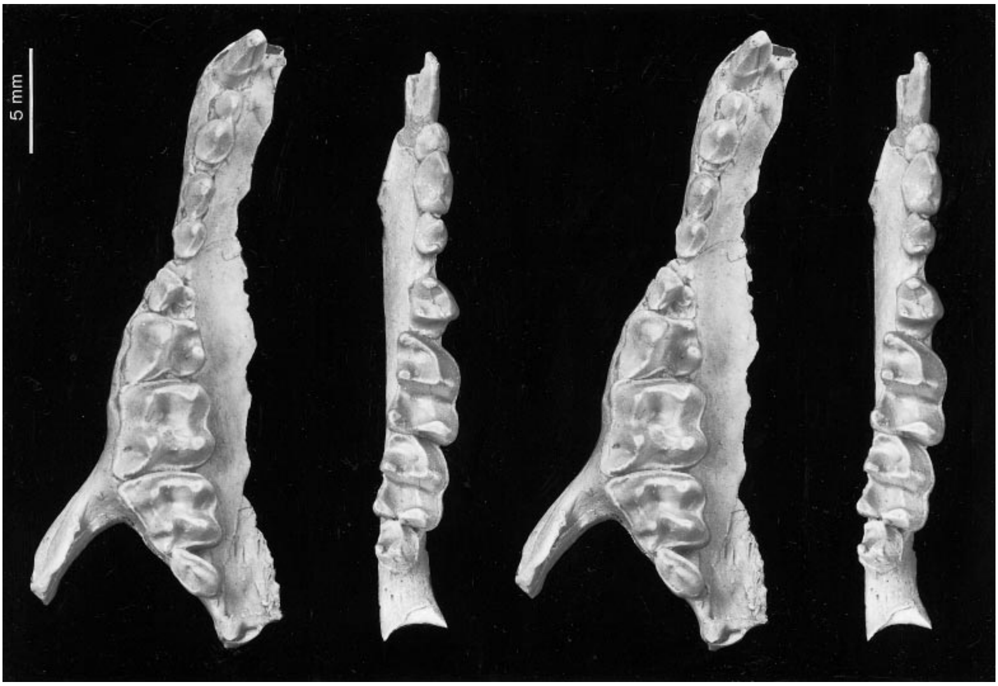

Fig. 6. *Erinaceus europeaus* (AMNH 70611) upper and lower jaw.

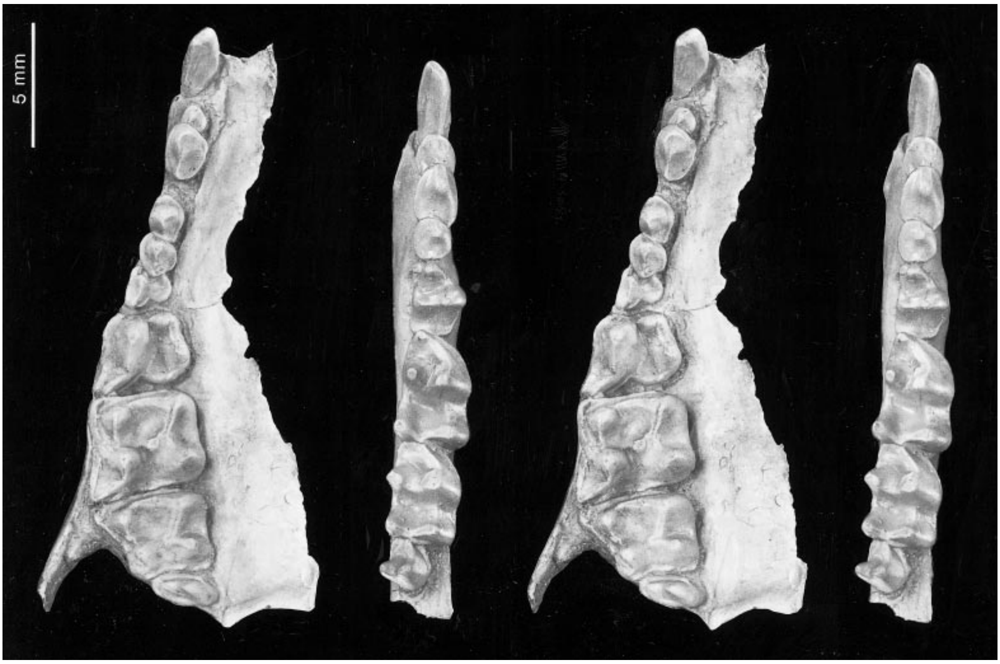

Fig. 7. *Hemiechinus auritus* (AMNH 85309) upper and lower jaw.

cusp (i.e., paraconid)? Fortunately, there are just a few examples where observer interpretation varies greatly. I have tried to adhere as closely as possible to the literal definitions of the characters reviewed (e.g., a labial enamel bead is not a cingulum, nor is a crest considered a distinct cusp). In some cases, I found it necessary to introduce new transformation series to accommodate commonly expressed character states (e.g., cuspules) that could not be accommodated comfortably in an already cited transformation series. I did not include those anomalous character states (e.g., double apex on the p4 paraconule) that were unlikely to have any potential for phylogenetic inference, since they are all individually specific, but it should be noted that such variation occurs.

The most pervasive difficulty in the analysis is apprehending the effects of wear on discrete dental characters. As discussed in the Introduction, wear is a consequence of many factors and processes, which ultimately results in the alteration of discrete dental characters at differing rates on an animal's full complement of teeth, both deciduous and permanent. These ontogenetic differences may be easy to apprehend as the effects of wear in a large sample. In those cases where only a few specimens are readily available (or even exist), however, this type of ambiguity could lead to unconscious character-state inference on the part of the investigator (Nixon, 1996).

Lastly, sample size itself may also pose problems: 25 individuals per taxon may not be a large enough sample to detect interspecific polymorphism, let alone the covariances with ontogenetic stages considered in the analysis.

SCORING OF CHARACTERS: All individuals (see appendix 2) included in this analysis were personally reviewed and appropriately scored for the listed transformation series (appendix 1). The maximum number of multistates within a given transformation series is 5 (i.e., 0–4). Due to asymmetry, however, character coding is not as straightforward as 0→4. The fashion in which the asymmetrical data were recorded was designed to clearly indicate ''morphographic distribution'' of the polymorphism in a single individual. For example, states in the left and right teeth described as [2,1] would mean the right tooth has state 2, and the left tooth has state 1. Because most statistical packages cannot accommodate entries with commas, necessitating recoding for final analysis, coding of asymmetry starts with 5 and ends with 14. Coding is as follows:

[0, 1] or [1, 0] 5; [0, 2] or [2, 0] 6; [0, 3] or [3, 0] 7; [0, 4] or [4, 0] 8; [1, 2] or [2, 1] 9; [1, 3] or [3, 1] 10; [1, 4] or [4, 1] 11; [2, 3] or [3, 2] 12; [2, 4] or [4, 2] 13; [3, 4] or [4, 3] 14.

Although many of these combinations of asymmetrical polymorphism do not exist in the taxon-specific matrices, it was more efficient to recode all the possibilities through a linear editing function approach of the statistical package in which the data were collected (see below) than to accomplish this task by hand.

A result of this coding method is the acute loss of asymmetry distribution (e.g., [1, 3] or [3, 1] 10). Because this analysis seeks only to acknowledge that dental asymmetry exists among erinaceids, without exploring its nature, the loss of distributional information on asymmetry is considered insignificant. The raw data are preserved in Gould (1997; appendices 9–18).

As with virtually any other data set, missing values are present. In those cases where observation of a character state was unequivocally compromised by wear, the cell was left blank. Also, for those transformation series that were not applicable to the taxon being reviewed, the cells were also left blank. I did not code these data differently from other missing data, because operationally they are treated the same in a phylogenetic analysis that employs the parsimony principle (Maddison, 1993; Nixon et al., 1994; Nixon, 1996).

TAXA REVIEWED: Of the 19 extant phylogenetic species currently recognized (fig. 1b), 10 were considered in this analysis (appendix 2). Many of the living erinaceids are surprisingly rare in North American collections, which constrained the sampling criteria accordingly. The optimal sampling parameters were as follows: (1) all specimens had to be accessible for personal review; (2) each taxon had to be represented by an ideal of 25 individuals and a minimum of 10, and the sampling constrained, if possible, to one geographic population; and finally, (3) each genus had to be represented by at least 2 species. Criterion no. 2 may violate classical sampling criteria in that the sample size may be insufficient to clearly apprehend variation (Sokal and Rohlf, 1995), either due to a paucity of specimens, or to a biased sampling within a population. Nevertheless, when dealing with the vertebrate fossil record, such parameters quickly become irrelevant in the face of inadequate sample sizes (e.g., one, or two specimens). Therefore, a small sample size of living taxa does not seem to be operationally any different than that of the fossil record, and in fact, a sample of 25 individuals per taxon is rare.

The limited sample size of this analysis also results from the need for personal review. As mentioned, North American collections of erinaceids are limited, the majority of which are located at the Smithsonian Natural History Museum and the American Museum of Natural History. Thus, taxa chosen were predetermined by their availability in these two collections. Of the 7 recognized living genera (following Frost et al., 1991; fig. 1b), 5 were sampled. Due to the rarity of *Podogymnura* (Hylomyinae, 2 species recognized) and *Mesechinus dauuricus* (Erinaceinae, monospecific genus) in these collections (fewer than 6 specimens per taxon were available), they were omitted from this analysis. *Echinosorex* (fig. 3), currently considered a monospecific taxon (*E. gymnura*) following Corbet (1988) and Frost et al. (1991), is the only taxon that is represented by more than 25 individuals (32 were reviewed). This exception to the maximum sample size exceeds the target sample size of 25 individuals from (presumably) one population from western Malaysia, and 5 individuals from the island of Borneo, which previously had been considered a separate (sub)species, *E. gymnura albus* (Corbet, 1988). Given the availability of these specimens and the nature of this project (inter- and intraspecific variation), the addition of these specimens seemed appropriate.

The following genera were analyzed: *Hylomys* (fig. 4), *Atelerix* (fig. 5), and *Erinaceus* (fig. 6) each represented by 2 species; and *Hemiechinus* (fig. 7), represented by 3 species. Three hemiechinines were analyzed to ensure the inclusion of at least one taxon that was previously considered to be *Paraechinus* (Rich and Rich, 1971; Rich, 1981; Corbet, 1988; Frost et al., 1991). Twenty-five individuals of the species *Hylomys suillus, Erinaceus amurensis, Atelerix algirus,* and *Hemiechinus hypomelas* were not available for review, and therefore, smaller sample sizes had to be accepted: 16, 11, 24, and 24, respectively.

OTHER DATA COLLECTED: Data regarding the relative age, sex, and geographic localities of each individual (see appendix 2; see also Gould, 1997, appendices 9–18) have also been compiled; they constitute the variables against which discrete dental variation was tested for covariance.

The relative age categories—juvenile, mature adult, worn teeth—are representative of wear stages, as there is no question that wear is principally a function of the age of an individual (Brockie, 1959; Skoudlín, 1976, 1981; Gregory, 1976; Kahmann and Vesmanis, 1977; Vasilenko, 1988). The identification of juveniles is straightforward; it is based on the presence of deciduous teeth. The remaining two age categories are based on the following definitions: [category: worn teeth] those specimens identified as old run the gamut from having teeth worn to the roots to teeth worn just to the point where identification of certain discrete characters becomes murky (e.g., metaconule, cristae); [category: mature adult] all remaining individuals that do not have deciduous teeth or morphology that is clearly compromised by wear. These categories may seem arbitrary or imprecise, but to estimate the age of a hedgehog accurately is no simple task. Previous investigations regarding age estimation among erinaceines suggest that the only reliable methods are: (1) measuring the relative dry weight of eye lenses, which increases with age (Morris, 1969, 1970, 1971); (2) noting the stage of epiphyseal fusion (Morris, 1971; Reeve, 1981; Dickman, 1988); (3) determining the number of periosteal growth lines in the lower jaw (Kristoffersson, 1971; Kratochvíl, 1975; Dickman, 1988); and (4) observing dental wear stage (Brockie, 1959; Skoudlín, 1976, 1981; Gregory, 1976; Kahmann and Vesmanis, 1977; Vasilenko, 1988).

TABLE 1

Results of Covariant Analyses

The percentages of polymorphic and asymmetric characters are calculated from the maximum of 246 transformation series minus those characters not applicable (Missing) to each taxon. The transformation series that covaried with sexual dimorphism, deciduous dentition, wear stage, and geographic locality are calculated based on the number of polymorphic transformation series per taxon.

				Covariance			
Taxon (sample size)	Missing	Polymorphic	Asymmetric	Sexual dimorph.	Deciduous dentition	Wear stage	Geographic locality
Echinosorex gymnura (32)	6	103 (43.1%)	48 (20%)	0	0	3 (2.9%)	1 (0.04%)
Hylomys sinensis (25)	20	77 (34.2%)	82 (36.4%)	0	0	0	0
Hylomys suillus (16)	18	67 (29.3%)	63 (28.0%)	0	1 (1.5%)	6 (8.9%)	0
Atelerix albiventris (25)	34	94 (44.5%)	84 (39.8%)	0	0	6 (6.4%)	0
Atelerix algirus (21)	28	80 (36.9%)	32 (14.7%)	0	0	4 (5.0%)	0
Erinaceus amurensis (11)	25	55 (25.0%)	9 (4.1%)	0	1 (1.8%)	6 (10.9%)	0
Erinaceus europaeus (24)	37	70 (33.7%)	60 (28.8%)	0	0	1 (1.4%)	0
Hemiechinus aethiopicus (25)	30	95 (44.2%)	66 (30.7%)	0	0	3 (3.2%)	0
Hemiechinus auritus (25)	30	66 (30.7%)	27 (12.4%)	0	2 (3.0%)	6 (9.1%)	0
Hemiechinus hypomelas (19)	28	75 (34.6%)	48 (24.5%)	0	0	11 (14.7%)	0

Given the lack of access to fresh eye lenses and postcranial material for review of epiphyseal fusion and of permission to take thin sections from hundreds of specimens for age determination, wear stage was deemed acceptable for estimating age.

Admittedly, using a second age variable would have increased the rigor in this analysis. However, an early analysis of cranial suture closure (basioccipital and premaxillary-maxillary-palatine) demonstrated that these sutures close at approximately the same time very early on in ontogeny (personal obs.; Gould, 1997), thus, they would not have provided any additional information regarding the age of an individual.

The other variables—sex and geographic locality—were determined from specimen tags.

ANALYSES CONDUCTED: Data were initially collected in MicroSoft Excel 4.0 for the Macintosh. It was then subsequently transposed and imported into both StatView 4.1, and a promotional version of (SAS) JMP for the Macintosh. The vast majority of all of the discrete dental data analyses (DDA) were conducted using StatView 4.1. All taxon data matrices (Gould, 1997, appendices 9–18) were first reviewed for intraspecific variation, as well as asymmetry within a transformation series (DDA 1). The data were analyzed by generating frequency tables for each transformation series across all the taxa (Gould, 1997, appendices 9–18). The results have been compiled in one table (appendix 3) for a global overview of variation. Identified interspecific polymorphism was then analyzed for covariance with sexual dimorphism (DDA 2), deciduous dentition and wear stage (DDA 3), and geographic locality (DDA 4). Bar chart cell plots were employed to visualize the distribution of the data, and their covariation with the variables noted (see appendix 4 for examples).

RESULTS OF DISCRETE DENTAL ANALYSES

Discussion of the results of each analysis is as follows: only those transformation series that *decidedly* covaried with the three variables considered—sex, relative age, and geographic locality—are herein discussed and illustrated. Table 1 is a compilation of the overall results of this analysis, and appendix 3 is a comprehensive table of frequency of all the taxa and transformation series that have been reviewed in this study.

Decidedly implies that the results were not equivocal. That is, the frequency distributions did not require any ad hoc hypothesis to explain conflicting results. For example, in fig. 8a, the distribution of I2 posterior cuspules is illustrated. In the juvenile, one condition is observed—present—whereas in the

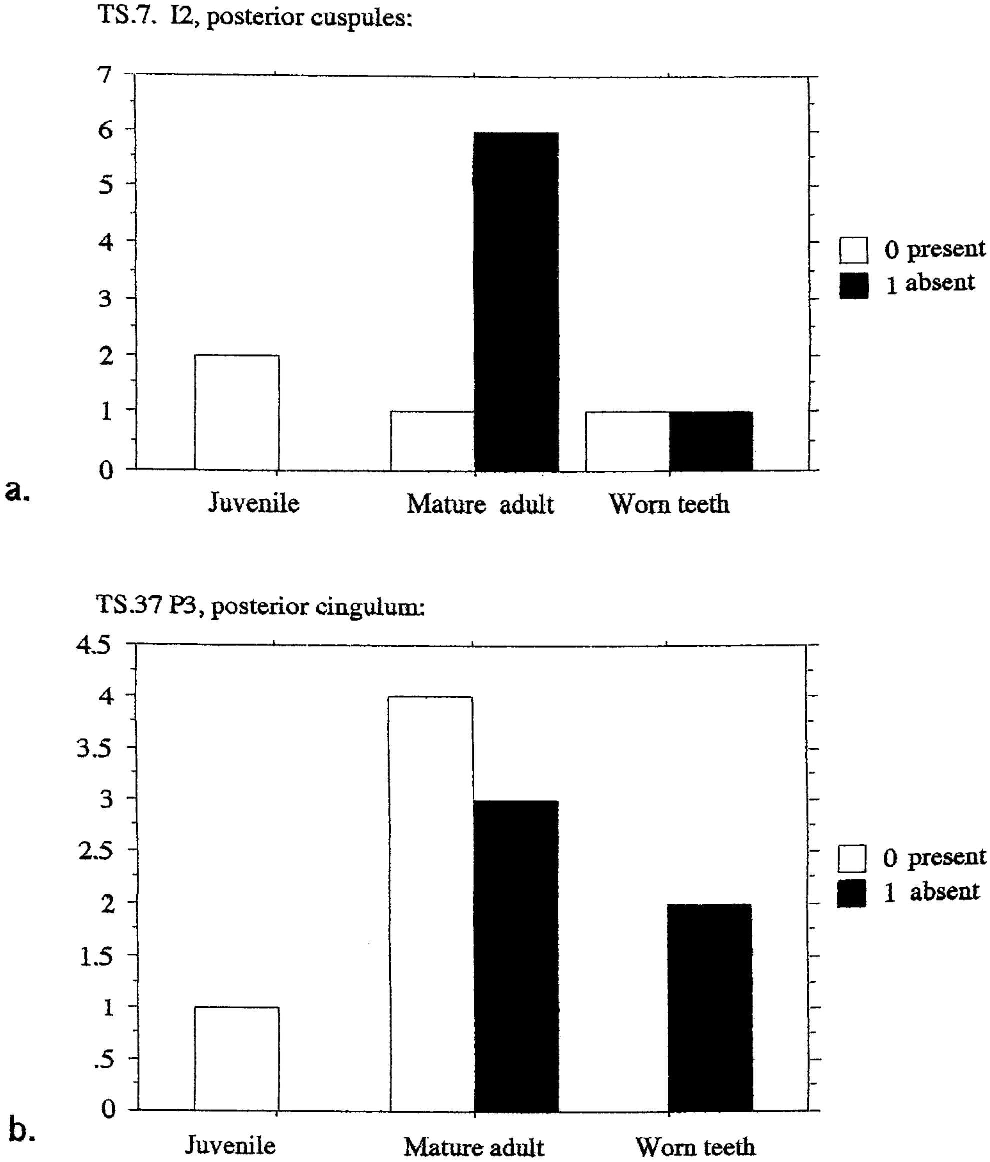

Fig. 8. An example of ambiguous distribution of character states; (**a**) I2 cuspules always present in the juveniles and polymorphic for the adults (*Hylomys suillus*); (**b**) expression of the P3 posterior cingulum is a consequence of wear (*Erinaceus amurensis*).

other two age categories, both present and absent conditions are observed. It is unclear from this distribution whether we are looking at: (1) distinct deciduous morphology (presence) and polymorphism in the adults; (2) the effects of wear in only some individuals; or (3) a poor sampling of juveniles resulting in no detection of polymorphism. These distributions become even more problematic when it is unclear whether a juvenile's teeth are deciduous or permanent. Consequently, all the taxon-specific character distributions that were ambiguous (like this one) were considered equivocal.

In figure 8b, the distribution of the P3 posterior cingulum (present [0], absent [1]) strongly indicates that wear accounts for the observed polymorphism. Distributions such as this one were considered evidence of covariation.

DDA 1: POLYMORPHISM AND ASYMMETRY: Polymorphism and asymmetry are prevalent in all of the taxa reviewed (table 1, appendix 3; see also Gould, 1997, appendices 9–18). For all the transformation series considered, overall polymorphism within a given taxon ranges from 25% to 44.5%, asymmetry being slightly more conservative, ranging from 4.1% to 39.8%.

The overall amount of polymorphism (and asymmetry) detected across and within 10 taxa and 246 transformation series does not seem too surprising considering the quantity of characters reviewed. What is surprising, however, are the characters that are consistently polymorphic across all the taxa—the number of upper canine roots, the number of P2 roots, the presence and absence of the P3 lingual lobe, and the shape of the P4 and condition of its lingual roots, to mention a few (appendix 3). These character states have all been cited in the literature as diagnostic for a taxon, either at the species level or higher (see appendix 1). Moreover, the polymorphic presence and absence of an entire tooth (I2, I3, P1, and P3) within a species is even more disconcerting (appendix 1). Without large series of individuals from a single population by which to detect such variation, these characters could be considered evidence of multiple species.

DDA 2: COVARIATION OF POLYMORPHISM AND SEXUAL DIMORPHISM: The results of this analysis suggest that there is no expression of sexual dimorphism in the discrete dental characters among the reviewed taxa, and most probably throughout the living erinaceids as well.

DDA 3: COVARIATION OF POLYMORPHISM WITH RELATIVE AGE: All positively correlated results of polymorphism with the relative age of an individual (wear stage and deciduous vs. permanent teeth) are illustrated in table 2 (see also Gould, 1997, appendix 4).

In some taxa, the deciduous dentition can be quite different from the permanent teeth. Results of this analysis, however, indicate that among hedgehogs, the morphology of deciduous and permanent teeth is not easily distinguishable. Of the 10 taxa reviewed, only 3 distinctly demonstrate polymorphism in deciduous and adult teeth (see table 2): *Hylomys suillus* (upper canine size relative to postcanines); *Atelerix algirus* (presence of I3 posterior cingulum); and *Hemiechinus auritus* (P3 is reduced, dP3 protocone is present). (see also Gould, 1997, appendix 4, figs. 5, 18, and 34, respectively.)

Thirty-nine characters were found to be positively correlated with wear (table 2; see also Gould, 1997, appendix 4, figs. 2–4, 6–17, 19–33, 36–51); those that are consistently affected are: premolar cuspules, cingula, parastyle, and cristae. These wear-dependant characters are not tooth specific, they tend to be unfailingly distributed across almost all the teeth that exhibit that particular character state. For example, the parastyle is subject to wear on the P3, P4, M1 and M3; cingula are subject to wear on the upper canine through the M3, and the m2 (table 2). These wear patterns are directly correlated with occlusal surfaces of the parastyle: the P4 parastyle occludes with the posterior crest on the lower canine; the M1 parastyle occludes with m1 protoconule; the M2 parastyle occludes with m2 protoconule; and the M3 parastyle occludes with the m3.

The wear of the cingula is not as clear cut. Only two of the four cingula (on a premolar, upper molar, or lower molar) are occlusal surfaces: the anterior and posterior cingula, which occlude with the protocones and protoconids, respectively. Wear of the labial and lingual cingula among erinaceids must be a result of diet (or ‘‘bug wear,’’ sensu D. R. Frost). Hedgehogs have a varied diet, including: insects, snakes, eggs, small mammals, and small lizards (Lui, 1937; Krishna, 1956; Brockie, 1959; Burton, 1969; Herter, 1969; Campbell, 1973; Roberts, 1977; Merrit, 1981; Maheshwari, 1984; Corbet, 1988; also see Reeve, 1994 for a complete review), all of which can be abrasive to teeth. Hedgehogs are also known to dispatch relatively large invertebrates using their molars (Reeve, 1994; pers. obs.), instead of tearing with their incisors, or even canines. This observation would explain the wear of the labial cingulum recorded in this analysis.

DDA 4: COVARIATION OF POLYMORPHISM WITH GEOGRAPHIC LOCATION: Only one taxon, *Echinosorex* (fig. 3), exhibited dental variation (presence/absence of I1) that conclusive-

TABLE 2

Transformation Series Found to Covary with Deciduous (=d) versus Permanent Dentition, Wear Stage (= w), and Geographic Variation (=g)

Abbreviations follow those of Frost et al. (1991); ECHG = *Echinosorex gymnura;* HYLU = *Hylomys suillus;* ATXA = *Atelerix albiventris;* ATXG = *A. algirus;* ERIA = *Erinaceus amurensis;* ERIAE = *E. europaeus;* HEME = *Hemiechinus aethiopicus;* HEMA = *H. auritus;* HEMH = *H. hypomelas.*

	Taxon								
Transformation series	ECHG	HYLU	ATXA	ATXG	ERIA	ERIAE	HEME	HEMA	HEMH
Polymorphism: Deciduous vs. Permanent Dentition (total = 4)									
16. I3, posterior cingulum				d					
18. UC, size relative to postcanines		d							
39. P3, morphology								d	
52. P3, roots								d	
Polymorphism: Wear Stage (total = 39)									
21. Upper canine, anterior cingulum								w	
23. Upper canine, posterior cuspule					w				
30. P2, posterior cuspule		w							
37. P3, posterior cingulum					w				
41. P3, protocone position relative to paracone									w
48. P3, parastyle	w								
54. P4, hypocone									w
61. P4, protocone-hypocone crest	w								w
62. P4, metastyle					w				
63. P4, parastyle	w								
64. P4, anterior cingulum								w	
73. M1, metaconule		w							
74. M1, metaconule shape			w						
75. M1, postmetaconule crista			w						
76. M1, protocone height		w							
85. M1, centrocrista		w	w						
89. M1, paraconule		w		w				w	
90. M1, paraconule crista				w					
98. M1, parastyle					w				
100. M1, cingulum							w		
101. M1, lingual cingulum					w				w
104. M1, labial cingulum		w							
114. M1, paraconule								w	
125. M2, anterior cingulum				w					w
126. M2, labial cingulum				w					w
127. M2, posterior cingulum									w
136. M3, parastyle						w			
137. M3, anterior cingulum									w
139. M3, posterolabial cingulum									
154. LC, position relative to preceding incisor									w
155. LC, anterior midline crest									w
157. LC, posterior ridge			w						
166. p2, cingulum			w						
169. p2, anterior midline crest							w		
214. m1, hypocristid							w	w	
217. m1, entoconulid			w						
227. m2, paraconid swelling								w	
231. m2, posterior lingual extension									w
242. m2, labial cingulum					w				
Polymorphism: Geographic Variation (total = 1)									
4. I1, presence/absence	g								

ly covaried with geographic locality (table 2; see also Gould, 1997, appendix 4, fig. 1).

Echinosorex is the largest member of the Erinaceidae, and as well, the largest of the living lipotyphlans (Frost et al., 1991). Its known distribution extends throughout the Indonesian Peninsula and the Malayan Archipelago (Lim, 1967), to include the islands of Burma, Sumatra, Malaya, Thailand, and Borneo. The genus *Echinosorex* has been previously thought to contain at least three [sub]species: *E. dealabatus*, *E. alba*, and *E. gymnura* (Corbet, 1988). I bracket the [sub] as these taxonomic designations have not been consistent. Recent revisions of the taxonomy of Erinaceidae considered *Echinosorex* to be a monospecific taxon (Corbet, 1988; Frost et al., 1991). In this analysis, the absence of the I1 seems to be apomorphic for the population in Borneo, although this is based on a review of only five specimens.

BRIEF SYNOPSIS: Polymorphism and asymmetry were discovered to be quite common across all of the taxa reviewed in this analysis. Of the 246 transformation series considered, 204 (83%) were found to exhibit intraspecific variation. Of all the polymorphism exhibited, very little could be attributed unequivocally to any of the variables (age, sex, geography) considered in this analysis. This does not suggest that the discrete dental characters do not covary with these variables (except perhaps for sexual dimorphism); it simply suggests that it is very difficult to discern covariation from random individual variation.

Hylomys suillus (fig. 4) and *Erinaceus amurensis* (fig. 6) have the least amount of polymorphism (and asymmetry) relative to all of the taxa reviewed, with *Atelerix albiventris* (fig. 5) exhibiting the most. The relatively low frequencies of polymorphism in the two above mentioned taxa may be attributable to small sample sizes: 16 and 11 individuals, respectively.

PHYLOGENETIC ANALYSIS

METHODS AND JUSTIFICATION

The results of the discrete dental analyses of the 246 transformation series reviewed, indicated that this character suite exhibits considerable amounts of variation across all taxonomic levels within the Family Erinaceidae. Currently, there is no consensus on the treatment of variable or polymorphic characters in a phylogenetic analysis (see Weins 1998, and Kornet and Turner, 1999 for a comprehensive review of methods). Nor is there a consensus on whether or not they should even be included in a phylogenetic analysis (Nixon and Wheeler, 1990; Nixon and Davis, 1991; Kornet and Turner, 1999) despite empirical data to the contrary (Campbell and Frost, 1993; Nixon and Carpenter 1993; Nixon et al, 1994; Weins, 1995, 1998).

It is not my intention that this analysis test methods of phylogenetic reconstruction, or even reconstruct a phylogeny of the Erinaceidae. My intention is to inquire only into the phylogenetic resolving power of discrete dental characters in the absence of all other data. Therefore, given that 83% of the discrete dental characters exhibited intra- and/or interspecific variation, I constrained the phylogenetic analysis to best maximize the resolving power of the ‘‘fixed’’ characters. The question of the phylogenetic resoloving power of polymorphic characters within the Erinaceidae will have to wait for future study.

Interspecific variation was set to a maximum number of three species for a given transformation series. That is, if three or more species demonstrated considerable interspecific variation for a given transformation series, I omitted it from the analysis. In sum, 100 transformation series were retained (appendix 4).

Recorded variation in three of the transformation series included in this analysis—I1 presence/absence, P3 morphology, and P4 hypocone—exhibit positive covariation with geographic locality, deciduous dentition, and/or wear stage, respectively (table 2). It should be noted that I included a transformation series that is known to be affected by wear for two reasons: (1) it was found to covary with wear in only one taxon, *Hemiechinus hypomelas*, which can easily be accounted for a posteriori to any analysis; and (2) the presence/absence of the P4 hypocone has historically been considered apomorphic at some taxonomic level within the Erinaceidae (Butler, 1948, 1988; Novacek, 1985, 1986; Frost et al., 1991).

The data were analyzed following the criteria set by Gould (1995) and Frost et al., (1991) for outgroups (see below) and analysis parameters (e.g., PAUP, branch swapping methods). These criteria were rigorously adhered to in order to maximize the comparability of the discovered trees. Outgroups employed are the tenrecoids and soricoids. The fossil taxon, leptictids, was omitted from this analysis. Omission of this taxon does not affect the topology of the trees of either Frost et al. (1991) or Gould (1995), thus its inclusion did not seem pertinent.

I have coded the outgroups for as many of the transformation series for which I felt comfortable in making statements of ‘‘primary’’ homology (di Pinna, 1991). The sometimes extreme differences in dental morphology (i.e., tribospheny vs dilamdodonty and zalamdodonty) among the ingroup (erinaceids) and outgroups (soricoids and tenrecoids) prohibits statements of homology.

All characters were polarized according to the outgroup criterion (see Nixon and Carpenter, 1993), and all multistate transformation series were left unordered. Although I am not comfortable leaving the multistates unordered, many of the position or size-related characters lack evidence to justify additivity (e.g., entoconid size: (0) > hypoconid; (1) > paraconid; (2) = to both cusps; (3) > both cusps).

In order to test the phylogenetic resolving power of any data set, in this case discrete dental characters, a standard must be used against which to test it. As mentioned in the Introduction, Frost et al. (1991) and Gould (1995) posited hypotheses of the erinaceid phylogenetic relationships based on general morphology. These hypotheses are congruent, despite the somewhat different data sets analyzed (both in terms of taxonomic and character composition, see fig. 1) and are thus employed as the standard with which to compare the results of Data Set 1.

As a secondary internal test, Gould’s dental data (1995; Data Set 2 = 29 characters) were isolated and reanalyzed. Phylogenetic analysis 2a includes only those 10 taxa reviewed in this analysis. PA 2b considers the 19 living taxa included in Gould’s original analysis, as well as that of Frost et al. (1991). As with Data Set 1, the same outgroup criteria were employed.

Given that this analysis does not set out to reconstruct phylogenetic relationships, but rather to look at the topological effects of using a single suite of characters for phylogenetic inference within hedgehogs, incongruence length difference and significance tests (Mickevitch and Farris, 1981) were not considered here.

The computer-assisted parsimony program PAUP (Swofford, 1993) was used to analyze the data. A heuristic search was conducted, using random tree stepwise addition, and tree bisection branch-swapping algorithms. The outgroup option was employed, and both ACCTRAN and DELTRAN optimizations were considered.

Abbreviations: CI = consistency index; RI = retention index; RC = rescale consistency index.

RESULTS OF PHYLOGENETIC ANALYSIS

PHYLOGENETIC ANALYSIS 1: DATA SET 1: Analysis of the 100 transformation series from the discrete dental analysis and 10 taxa discovered six trees of 105 steps, with the following statistics (excluding uninformative characters): CI = 0.634; RI = 0.528; and RC = 0.357; the strict consensus and the Adams tree are depicted in figs. 9a and b, respectively. In all the trees discovered, every polytypic genus is rendered paraphyletic (except *Erinaceus*), and the monophyly of both extant subfamilies is challenged (compare with figs. 1a and b).

PHYLOGENETIC ANALYSIS 2: DATA SET 2: Analysis of Frost et al.’s (1991) dental data across the 10 taxa reviewed in this investigation discovered 4 trees: length 38; CI = 0.816, and 0.80 (excluding uninformative characters); RI = 0.897; RC = 0.732. The strict consensus tree and the Adams tree are the same (fig. 9c). The only genus discovered to be monophyletic is *Erinaceus*, both subfamilies are rendered paraphyletic.

Analysis of Frost et al.’s (1991) dental data and the 19 living taxa they considered discovered 9 trees: length: 41; CI = 0.756 and 0.744 (excluding uninformative characters); RI = 0.917; RC = 0.694. The strict consensus and Adams tree are illustrated in figs. 9d

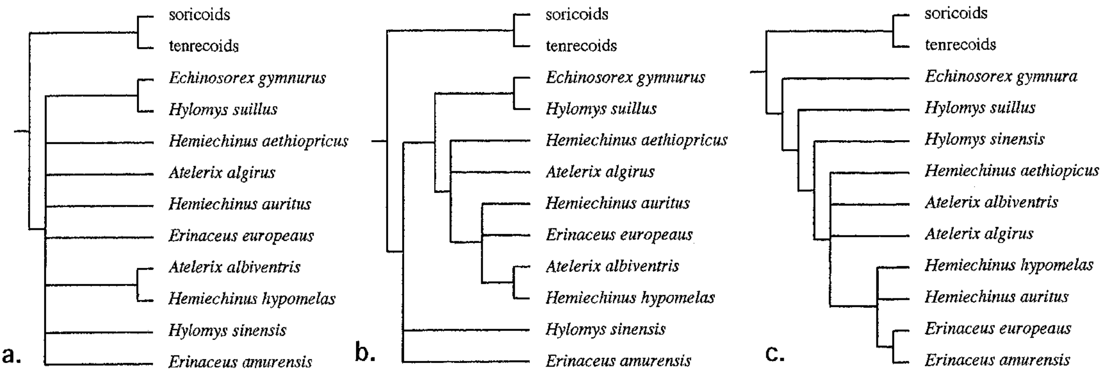

Fig. 9. (**a**) Phylogenetic analysis 1 (data set A); strict consensus tree; (**b**) majority rule tree; (**c**) phylogenetic analysis 2a (Gould, 1995) strict consensus tree. (**d**) Phylogenetic analysis 2b (Gould, 1995) strict consensus tree; (**e**) majority rule tree.

and e, respectively: hylomyine monophyly is challenged; *Hylomys* is never discovered to be a member of that group. Moreover, monophyly of all the living genera is suspect except for *Erinaceus.*

BRIEF SYNOPSIS: The recovered trees for all three analyses differ in overall topology both among themselves and with the hypotheses posited by Frost et al., (1991) and Gould (1995; figs. 1a and b). In each of the discovered topologies, *all* the taxa were rendered paraphyletic. Interestingly, the most parsimonious trees discovered in *all* three analyses were seemingly well supported, as evidenced by the high indices.

The apomorphy lists for two discovered trees are presented in appendices 5 and 6 with their respective data matrices. In all three analyses, Tree #1 was selected as the token topology from which to generate an apomorphy list (the strict consensus trees for the analyses are depicted in figs. 9a, c, and d). This arbitrary decision was based on the fact that not one of the discovered trees remotely approximates any of the previously posited phylogenetic hypotheses that are based on all available morphological data (see Corbet, 1988; Frost et al., 1991; Gould, 1995).

The purpose of this analysis is not to propose a phylogenetic hypothesis, but to explore the phylogenetic resolving power of the discrete dental characters. Given the incongruous results with the most recent hypotheses of extant erinaceid relationships (Corbet, 1988; Frost et al., 1991; Gould, 1995), detailed discussion of character support is foregone.

DISCUSSION

Briefly, the results of this investigation are: (1) variation is discovered to be rampant both inter- and intraspecifically, as well as within an individual; (2) correlation of some polymorphic characters with wear stage is demonstrated, although it is not consistent across the taxa reviewed; (3) polymorphism as a result of morphological difference between deciduous and permanent dentition is discovered to be minimal and very difficult to detect without large sample sizes; (4) clinal variation and sexual dimorphism of discrete dental characters are rare or nonexistent (respectively) among the taxa reviewed; and (5) dental characters, as a partitioned data set, recovered estimates of phylogeny that are globally incongruent with those based on comprehensive morphological data sets.

These results are not surprising. Variation of discrete dental characters across many mammalian taxa is already well documented (see Introduction). Within the Erinaceidae, it seems that the magnitude of discrete dental characters cited in the literature is a result of oversplitting of character transformations.

Wear is the primary cause of the altering of appearance of specific dental characters. It is not exclusively a function of age, but may also be a consequence of geographically (or individually) varying diets and/or individual pathology. For example, some individuals of

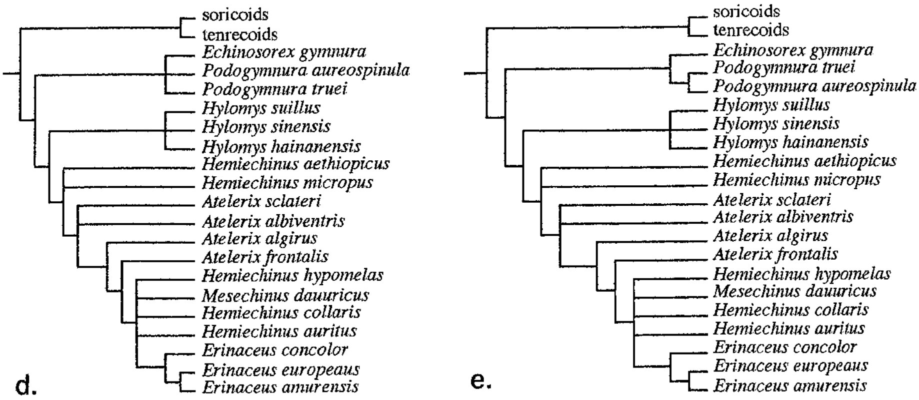

Fig. 9. Continued.

Hemiechinus auritus were observed to have filled open cavities with sand grains (personal obs.), a condition most likely due to serendipity. Nevertheless, a desert-dwelling hedgehog inadvertently ingesting sand particles during a meal may not only fill a cavity, it is most likely going to wear down its teeth at a much more rapid rate (and in a different fashion) than a hedgehog living on a British Isle that takes in fine dirt and debris with its diet of earthworms and insect larvae (see Reeve, 1994, for a comprehensive review).

Theoretically these wear patterns could be apomorphic at some taxonomic level: it has been demonstrated that wear patterns can be indicative of behavioral characteristics: e.g., grazer vs. browser, habitat conditions, and even preferred diet (Solounias and Dawson-Saunder, 1988; Hayek et al., 1991; Solounias and Moelleken, 1992a, b, 1993; Solounias and Hayek, 1993). Hedgehogs are opportunistic feeders, the only constraint on their diet being environment; therefore, such wear patterns cannot be used as statements of homology. In this analysis, I attempted to tease out ontogenetic variation (e.g., a function of wear) from ontological variation (e.g., sexual dimorphism, clinal or individual variation) which proved to be very difficult.

Although it is clear that wear occurs and that it alters tooth morphology over time, it is not easy to demonstrate empirically that wear is the principal cause of much of the observed variation. This is evidenced by the fact that 204 of the 246 characters reviewed were discovered to vary *intraspecifically,* and of these, only 46 (see table 2 and appendix 4) could unequivocally be attributed to wear. Clearly, many more of the polymorphisms recorded in this analysis are a direct result of wear early in ontogeny; however, in most cases, little or no evidence of mechanical wear can be observed with a standard microscope. Only a comprehensive review of the various stages of molar eruption could demonstrate that the cingula were being worn off very early in the animal's life. Without adequate sample sizes (and in some cases sophisticated methods of visualization [e.g., SEM scans]), the subtle topological manifestations of wear are not apprehendable using standard multivariate statistics.

To muddy the waters even more, premolars are both deciduous and permanent. In some mammalian taxa, deciduous dentition is different from that of the adult dentition; among erinaceids, however, deciduous and permanent dentition are quite similar (Kindahl, 1959)—only 4 characters across 3 taxa exhibit differing morphology (table 2). Nevertheless, I suspect that the low frequency of polymorphism due to distinct deciduous and permanent dentition is subsumed in the variation of the adult dentition and/or the retention of milk teeth into adult life. With respect to the latter, without either clear signs of tooth eruption or X-rays, the nature of the variation is ambiguous. To compound the problem, deciduous teeth, like adult dentition, most likely vary intraspecifically, as well through wear.

Clinal variation and sexual dimorphism,

expressed in the dental morphology, are even more elusive, if they exist at all. Among the sampled taxa, sexual dimorphism was found to play no role in the polymorphism. I had not anticipated that any teeth, other than possibly the canines, would exhibit secondary sexual characteristics. Sexual dimorphism has never been demonstrated within the extant hedgehogs; however among the fossil taxa, it has been suggested that the giant Italian Miocene hedgehog, *Deinogalerix* expressed sexual dimorphism in its overall size and number of premolars (Freudenthal, 1972; however see Butler 1980). Personal observation of series of *Echinosorex gymnura* indicated (to me) that this taxon may also express sexual dimorphism in the size of the skull.

Although it was demonstrated that there is some geographic variation in discrete dental data (i.e., *Echinosorex*), it should be noted that only one character (#4; presence/absence of I1) of the 246 reviewed, across 10 taxa could be directly correlated with geographic location: *Echinosorex gymnura*, a monotypic taxon distributed both on the mainland of Indochina and the Indonesian and Malayan islands, exhibits geographically delimitable variation (see DDA 4, Results). This variation may be in fact apomorphies indicating more than one phylogenetic species, not clinal variation. This hypothesis has not been rigorously tested, and without larger sample sizes, I decline to re-establish another species of *Echinosorex*.

Results of the phylogenetic analyses of three overlapping discrete dental data sets indefatigably indicate that discrete dental characters, *in the absence of all other morphological data*, are insufficient for addressing questions of historical relationships among the extant taxa reviewed. This is evidenced by the fact that all of the discovered trees (Data set 1 and 2a/b) posit paraphyly and/or polyphyly of all the extant groups, across all taxonomic levels (see Butler, 1948; Rich, 1981; Corbet, 1988; Frost et al., 1991; Gould, 1995).

Given the frequency of polymorphism discovered in the discrete dental analysis, these results are not terribly surprising. What is disturbing is the number of trees discovered in each analysis and their respective indices. The maximum number of trees discovered for all of the data sets was 9, and the lowest CI was 0.63. If there were no other previously postulated hypotheses of relationships that strongly corroborated one another, these hypotheses of phylogenetic relationships, based strictly on the number of discovered trees and their strong stem support, would be considered robust. One must not summarily dismiss these results as coincidental. We know that a mammal tooth is specialized based on its ability to occlude with its counterpart. One would assume, that the variation would be somewhat consistent to ensure that the teeth still remain functional (i.e., occlude), and further, that wear would perhaps enhance occlusion, consequently making many of these discrete dental characters dependent on one another (evocative of concerted evolution and/or concerted ontogeny).

The principal questions being addressed in this investigation relate to how reliable dental data are as the sole source of phylogenetic inference for the fossil record. Given the results of the discrete dental analysis, the causes of dental variation are elusive. I suspect that many of the variables reviewed in this analysis play some role in the exhibited variation. However, current methodology may be inadequate for teasing out which morphologic variation is real and which is an artifact of wear. Adding to these doubts are the well-supported results of the phylogenetic analyses that hypothesize nonindependence of characters and global paraphyly among the extant taxa of hedgehogs. In light of these results, I would be reluctant to place much weight on the phylogenetic resolving power of this particular suite of characters in the absence of other data. More specifically, I would hesitate to propose a taxonomy of fossil erinaceids based on fragmentary jaws and isolated teeth.

Within the field of paleomammalogy, the reliance on dental morphology as the sole indicator of phylogenetic affinities is fairly common. Understandably, this reliance is in direct response to what most researchers studying fossil mammals (especially small mammals) have to work with—isolated teeth or fragmentary jaws. Enamel survives otherwise harsh deteriorative and/or erosive environments. Among some groups of mammals (e.g., dryolestids, triconodonts, ptilodonts, and taeniolabids), teeth and jaws are the only record we have indicating that a lineage once existed. As a result, mammalian paleontological literature is replete with developmental odontology, discrete dental morphology, microwear, and odontological morphometrics as standard methods for determining phylogenetic relationships among certain taxa. If the dental data across all mammalian taxa is similar in behavior to that discovered within the extant Erinaceidae, these data may be misleading us. Certainly, it would be faulty reasoning to presume a priori that this dental homoplasy phenomenon is global for the Mammalia; nevertheless, it casts doubt on the reliability of such data, especially when a cursory review of the literature suggests that similar observations are common within other mammalian taxa (see Introduction), to include *Homo sapiens* (Hillson, 1986; Melvin Moss, personal commun.).

Given the results of this analysis and others, it seems wise that, when possible, measures should be taken to test the phylogenetic signals of the dental data on living taxa before applying them to the fossil record. Nor should this type of approach be exclusive to mammalian teeth—all seriously depauperate data sets (those that use only one particular system of the animal to reconstruct evolutionary histories, should be rigorously tested before weighting them a priori (see Naylor and Marcus, 1994, and Sánchez-Villagra and Williams, 1998, for other methods of testing such data for application to the fossil record).

CONCLUSION

The results of the analyses of the discrete dental data conducted in this investigation strongly indicate that the expression of many characters commonly used (i.e., parastyle, cingula, cristae) to diagnose fossil erinaceid taxa are compromised by wear early in ontogeny (and in many cases little or no evidence of mechanical wear can be observed); they are subject to intractable, and global intra- and interspecific variation, and/or they are subject to concerted evolution. These data suggest further that intraspecific variation, not unexpectedly, increases with sample size (discrete dental analysis and phylogenetic analysis). This issue is most pertinent within the discipline of paleontological systematics. Not only is there scant material for review; in more instances than not, the taxon under consideration has no close living representatives (e.g., sauropods, parieasaurs, or nectridians) from which to get a better understanding of the nature of the available fossil material. In such cases, there are no alternatives but to use the available material—a poor estimate of phylogenetic relationships may be preferable to no estimate of relationships at all.

For those taxonomic groups that have both living and extant representatives, a rigorous investigation of the phylogenetic signal of the available data for incomplete fossil taxa should be a prerequisite to any phylogenetic reconstruction (see Naylor and Marcus, 1994). As with any other data considered, such an investigation would minimally satisfy some of the criteria of a more rigorous methodological approach for phylogenetic inference by identifying characters too plastic to be useful (see Nixon and Davis, 1991, for an overview of the problems).

In sum, the factors reviewed herein—wear stage, clinal variation, gratuitous variation, and nonindependence of characters—can greatly alter our interpretation of the fossil record when the only evidence being reviewed consists of teeth. Without consideration of these problems, the fossil species diagnosed on such data must consequently affect all hypotheses of speciation events, migrations patterns, and hypotheses of evolutionary processes.

The results of this analysis presented here pertain only to the taxa that have been reviewed herein. Admittedly it is difficult, if not impossible, to demonstrate empirically that these results also pertain to the erinaceid fossil record. Nevertheless, the usefulness of dental data for reconstructing their phylogenetic histories is now undeniably suspect.

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APPENDIX 1

Transformation Series Considered in Discrete Dental Analyses

Numbering starts at 4 to maintain consistency with the numbering in each of the taxon matrices in Gould's dissertation (1997 [1–3 are specimen number, sex, and age, respectively]).

4. I1: (0) present; (1) absent.
5. I1, size: (0) normal; (1) enlarged (Rich, 1981; Butler, 1948; Frost et al., 1991; Gould, 1995).
6. I2: (0) present; (1) absent.
7. I2, posterior cuspule: (0) distinct; (1) weak; (2) absent.
8. I2, size relative to I3: (0) greater; (1) approximately equal; (2) smaller (Novacek, 1985, 1986; Frost et al., 1991; Gould, 1995).
9. I2, position: (0) displaced medially; (1) not (Rich, 1981; Frost et al., 1991; Gould, 1995).
10. I3: (0) present; (1) absent (Rich, 1981).
11. I3 roots: (0) one; (1) two separate; (2) two fused (Matthew, 1929; Butler, 1948; Rich, 1981; Robbins and Setzer, 1985; Corbet, 1988; Frost et al., 1991; Gould, 1995).
12. I3, paracone position: (0) directly ventral to the anterior root; (1) not (Rich, 1981).
13. I3, shape: (0) nearly rectangle in occlusal view; (1) not (Rich, 1981).
14. I3, paracrista: (0) well developed; (1) not (Matthew, 1929; Rich, 1981).
15. I3, metacrista: (0) well developed; (1) not (Matthew, 1929; Rich, 1981).
16. I3, posterior cingulum: (0) well developed; (1) not (Rich, 1981).
17. I3, posterior cuspule: (0) distinct; (1) weak; (2) absent.
18. Upper canine size relative to postcanines: (0) significantly larger; (1) slightly larger; (2) approximately equal.
19. Upper canine, roots: (0) two; (1) one; (2) two fused (Butler, 1948; Rich, 1981; Robbins and Setzer, 1985; Novacek, 1985; Novacek et al., 1985; Corbet, 1988; Frost et al., 1991; Gould, 1995).
20. Upper canine size relative to I3: (0) greater; (1) approximately equal; (2) smaller (Matthew, 1929; Butler, 1948; Rich, 1981; Corbet, 1988; Frost et al., 1991; Gould, 1995).
21. Upper canine, anterior cingulum: (0) present; (1) absent (Matthew, 1929; Rich, 1981).
22. Upper canine, posterior cingulum: (0) present; (1) absent (Matthew, 1929; Rich, 1981).
23. Upper canine, posterior cuspule: (0) distinct; (1) weak; (2) absent.
24. P1: (0) present; (1) absent (Butler, 1948; Frost et al., 1991; Gould, 1995).
25. P1, anterior cuspule: (0) distinct; (1) weak; (2) absent.
26. P1, posterior cuspule: (0) distinct; (1) weak; (2) absent (Butler, 1948).
27. P1, roots: (0) one; (1) two.
28. P2: (0) present; (1) absent.
29. P2, anterior cuspule: (0) distinct; (1) weak; (2) absent.
30. P2, posterior cuspule: (0) distinct; (1) weak; (2) absent.
31. P2, roots: (0) two separate; (1) one; (2) two fused; (3) three (Butler, 1948; Frost et al., 1991; Gould, 1995).
32. P3: (0) present; (1) absent.
33. P3, posterolingual cingulum: (0) present; (1) absent (Munthe and West, 1980).
34. P3, lingual lobe: (0) present; (1) vestigial or absent (Butler, 1948; Rich, 1981; Corbet, 1988; Frost et al., 1991; Gould, 1995).
35. P3, lingual cingulum: (0) strong; (1) weak; (2) absent (Munthe and West, 1980; Rich, 1981).
36. P3, labial cingulum: (0) present; (1) absent (Munthe and West, 1980; Rich, 1981).
37. P3, posterior cingulum: (0) present; (1) absent (Rich, 1981).
38. P3, posterior cingulum condition: (0) small; (1) large (Rich, 1981).
39. P3: (0) normal; (1) reduced (Butler, 1948; Stevens, 1977; Munthe and West, 1980; Rich, 1981; Robbins and Setzer, 1985; Novacek, 1985; Novacek et al., 1985; Corbet, 1988; Frost et al., 1991; Gould, 1995).
40. P3, protocone: (0) present; (1) absent (Butler, 1948; Stevens, 1977; Munthe and West, 1980; Rich, 1981; Robbins and Setzer, 1985; Novacek, 1985; Novacek et al., 1985; Corbet, 1988; Frost et al., 1991; Gould, 1995).
41. P3, protocone position relative to the paracone: (0) anterior; (1) posterior; (2) adjacent (Butler, 1948).
42. P3, protocone height relative to the paracone: (0) approximately twice as small; (1) much smaller (Rich, 1981).
43. P3, paracone shape: (0) conical; (1) crescentic (Munthe and West, 1980).
44. P3, postparacrista: (0) present; (1) absent (Rich, 1981; Munthe and West, 1980).
45. P3, metacone: (0) present; (1) absent.
46. P3, centrocrista: (0) present; (1) absent (Munthe and West, 1980).
47. P3, hypocone: (0) present; (1) vestigial or absent (Munthe and West, 1980; Butler, 1948; Gould, 1995).
48. P3, parastyle: (0) strong; (1) weak; (2) absent (Stevens, 1977).
49. P3, metastyle: (0) present; (1) absent (Rich, 1981).
50. P3, preparacrista: (0) present; (1) absent (Stevens, 1977; Rich, 1981).
51. P3, preparacrista extension: (0) to parastyle; (1) not (Stevens, 1977; Rich, 1981).
52. P3, roots: (0) three; (1) fewer (Butler, 1948; Rich, 1981; Corbet, 1988; Frost et al., 1991; Gould, 1995).
53. P4, shape: (0) quadrate; (1) rectangular; (2) triangular (Crusafont et al., 1955; Black et al., 1980).
54. P4, hypocone: (0) present; (1) absent (Butler, 1948, 1988; Novacek, 1985; Novacek et al., 1985; Frost et al., 1991).
55. P4, hypocone height relative to the protocone: (0) smaller; (1) approximately equal (Matthew, 1929; Black et al., 1980).
56. P4, hypocone gross size relative to protocone: (0) smaller; (1) approximately equal (Rich, 1981; Storch and Qiu, 1991).

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57. P4, protocone position with respect to that of the paracone: (0) anterior; (1) posterior (Matthew, 1929; Rich, 1981; Butler, 1948).
58. P4, carnassiform notch: (0) present; (1) absent (Rich, 1981).
59. P4, lingual roots: (0) one; (1) two fused; (2) two (Butler, 1948; Frost et al., 1991; Storch and Qiu, 1991).
60. P4, hypocone position relative to the protocone: (0) lingual; (1) labial; (2) aligned (Storch and Qiu, 1991).
61. P4, link between protocone and hypocone: (0) crest; (1) adjoined by base proximity, no crest; (2) hypocone isolated (Matthew, 1929; Rich, 1981).
62. P4, metastyle: (0) high; (1) low; (2) absent (Stevens, 1977; Butler, 1948).
63. P4, parastyle: (0) distinct; (1) weak; (2) absent (Matthew, 1929; Butler, 1948; Stevens, 1977; Black et al., 1980; Rich, 1981).
64. P4, anterior cingulum: (0) present; (1) absent; (2) partial (Matthew, 1929; Rich, 1981).
65. P4, cingulum: (0) extends around hypocone; (1) not; (2) absent (Butler, 1948).
66. P4, labial cingulum: (0) present; (1) absent (Matthew, 1929; Rich, 1981).
67. P4/M1 position: (0) oblique to tooth row; (1) not (Butler, 1948).
68. M1, size: (0) largest tooth of dentary; (1) not (Matthew, 1929; Munthe and West, 1980; Rich, 1981; Storch and Qiu, 1991).
69. M1, shape: (0) transversely rectangle; (1) antero-posteriorly rectangle; (2) quadrate (de Blainville, 1840; Koerner, 1940; Butler, 1948, 1988; Crusafonte et al., 1955; Stevens, 1977; Munthe and West, 1980; Rich, 1981; Storch and Qiu, 1991).
70. M1, anterior border: (0) straight; (1) concave; (2) convex (Rich, 1981).
71. M1, lingual roots: (0) separate; (1) fused (Storch and Qiu, 1991).
72. M1, metaconule: (0) present; (1) absent (Matthew, 1929; Viret, 1938; Butler, 1948, 1988; Black et al., 1980; Munthe and West, 1980; Storch and Qiu, 1991).
73. M1, metaconule: (0) isolated; (1) not (Matthew, 1929; Viret, 1938; Butler, 1948, 1988; Black et al., 1980; Munthe and West, 1980; Storch and Qiu, 1991).
74. M1, metaconule shape: (0) conical; (1) elliptical; (2) crescentic (Munthe and West, 1980).
75. M1, postmetaconule crista extension: (0) to the metacone; (1) not; (2) absent (Matthew, 1929; Rich, 1981).
76. M1, protocone height: (0) tallest cusp; (1) second tallest cusp; (2) third tallest cusp; (3) approximately equal in height to all other cusps (Stevens, 1977; Rich, 1981).
77. M1, protocone shape: (0) crescentic; (1) conical (Munthe and West, 1980).
78. M1, protocone position relative to the paracone: (0) anterior; (1) posterior; (2) equivalent (Matthews, 1929; Stevens, 1977; Rich, 1981).
79. M1 protocone position relative to the hypocone: (0) lingual; (1) labial; (2) aligned (Storch and Qiu, 1991).
80. M1, protocone base: (0) anteromedially expanded toward the P4; (1) not (Stevens, 1977).
81. M1, paracone shape: (0) conical; (1) crescentic (Munthe and West, 1980).
82. M1, paracone size relative to the metacone: (0) approximately equal; (1) smaller; (2) larger (Munthe and West, 1980).
83. M1, paracone height: (0) largest cusp; (1) second largest cusp; (2) third largest cusp; (3) smallest cusp; (4) all cusps approximately equal in size (Matthews, 1929; Stevens, 1977; Rich, 1981).
84. M1, paracone position relative to the metacone: (0) labial; (1) lingual; (2) aligned (Koerner, 1940).
85. M1, centrocrista: (0) present; (1) absent (Rich, 1981).
86. M1, preparacrista: (0) strong; (1) weak; (2) absent (Rich, 1981).
87. M1, metacone shape: (0) crescentic; (1) conical (Munthe and West, 1980).
88. M1, hypocone height relative to all of the other cusps: (0) tallest; (1) shortest; (2) approximately equal (Rich, 1981; Butler, 1948; Storch and Qiu, 1991).
89. M1, paraconule: (0) present; (1) absent (Matthews, 1929; Munthe and West, 1980; Rich, 1981; Butler, 1948).
90. M1, preparaconule crista: (0) well developed; (1) not (Rich, 1981).
91. M1, preprotocrista: (0) well developed; (1) not (Rich, 1981).
92. M1, crest between protocone and metaconule: (0) present; (1) absent (Rich, 1981; Butler, 1948; Storch and Qiu, 1991).
93. M1, hypocone: (0) crest joins it to the protocone-metaconule crest; (1) not (isolated) (Matthews, 1929; Munthe and West, 1980; Rich, 1981; Butler, 1948; Storch and Qiu, 1991).
94. M1, metastyle: (0) present; (1) absent (Viret, 1938; Storch and Qiu, 1991).
95. M1, metastyle apex: (0) high; (1) low (Munthe and West, 1980).
96. M1, metastyle position relative to the metacone: (0) labial; (1) posterior (Butler, 1948).
97. M1, mesostyle: (0) present; (1) absent (Munthe and West, 1980; Rich, 1981).
98. M1, parastyle: (0) present; (1) absent (Black et al., 1980).
99. M1, metacrista: (0) present; (1) absent (Matthews, 1929; Munthe and West, 1980; Rich, 1981).
100. M1, cingulum: (0) surrounds tooth; (1) discontinuous; (2) absent (Matthews, 1929; Rich, 1981).
101. M1, lingual cingulum: (0) present; (1) absent; (2) beading (Stevens, 1977; Munthe and West, 1980; Rich, 1981).
102. M1, anterior cingulum: (0) present; (1) absent (Stevens, 1977; Munthe and West, 1980; Rich, 1981).

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103. M1, postcingulum: (0) present; (1) absent (Stevens, 1977; Munthe and West, 1980; Rich, 1981).
104. M1, labial cingulum: (0) present; (1) absent (Matthew, 1929; Stevens, 1977; Rich, 1981).
105. M2, shape: (0) transversely rectangle; (1) antero-posteriorly rectangle; (2) quadrate (Koerner, 1940; Black et al., 1980; Storch and Qiu, 1991).
106. M2, lingual roots: (0) fused; (1) separate (Butler, 1948; Black et al., 1980; Frost et al., 1991; Gould, 1995).
107. M2, anterior margins: (0) convex; (1) concave; (2) straight (Black et al., 1980).
108. M2, posterior margin: (0) convex; (1) concave; (2) straight (Black et al., 1980).
109. M2, protocone size relative to the paracone: (0) equal; (1) larger; (2) smaller.
110. M2, paracone position relative to the metacone: (0) lingual; (1) labial; (2) aligned (Black et al., 1980).
111. M2, hypocone: (0) isolated; (1) not (Matthews, 1929; Munthe and West, 1980; Rich, 1981; Butler, 1948; Storch and Qiu, 1991).
112. M2, metaconule: (0) present; (1) absent (Black et al., 1980; Munthe and West, 1980).
113. M2, metaconule: (0) isolated; (1) not (Black et al., 1980; Storch and Qiu, 1991).
114. M2, paraconule: (0) present; (1) absent (Black et al., 1980; Munthe and West, 1980).
115. M2, metaconule postion relative to the paraconule: (0) labial; (1) lingual (Black et al., 1980).
116. M2, metaconule size: (0) twice the size of the paraconule; (1) not (Black et al., 1980).
117. M2, metastyle: (0) present; (1) absent (Black et al., 1980; Munthe and West, 1980).
118. M2, parastyle: (0) present; (1) absent (Black et al., 1980; Munthe and West, 1980).
119. M2, mesostyle: (0) present; (1) absent (Black et al., 1980).
120. M2, posthypocrista: (0) present; (1) absent (Black et al., 1980; Storch and Qiu, 1991).
121. M2, posthypocrista extension: (0) to postcingulum; (1) not (Black et al., 1980).
122. M2, preprotocrista extension: (0) to paraconule; (1) not (Black et al., 1980).
123. M2, preprotocrista extension: (0) to paracone; (1) not (Matthews, 1929; Rich, 1981).
124. M2, lingual cingulum: (0) present; (1) absent (Rich, 1981).
125. M2, anterior cingulum: (0) distinct; (1) partial; (2) absent (Rich, 1981).
126. M2, labial cingulum: (0) present; (1) absent; (2) partial (Rich, 1981).
127. M2, posterior cingulum: (0) present; (1) absent; (2) partial (Rich, 1981).
128. M2, cingula condition: (0) weak; (1) strong (Rich, 1981).
129. M3: (0) present; (1) absent (Rich, 1981; Novacek, 1985; Novacek et al., 1985; Gould, 1995).
130. M3, roots: (0) four; (1) three; (2) two separate; (3) two fused (Butler, 1948; Rich, 1981; Frost et al., 1991; Gould, 1995).
131. M3, hypocone: (0) present, sits on cingulum; (1) absent; (2) fused to metacone (= metastylar spur) (Koerner, 1940; Butler, 1948; Munthe and West, 1980; Novacek, 1985; Novacek et al., 1985; Frost et al., 1991; Storch and Qiu, 1991; Gould, 1995).
132. M3, metacone: (0) large; (1) small; (2) absent (Koerner, 1940; Butler, 1948; Munthe and West, 1980; Novacek, 1985; Novacek et al., 1985; Frost et al., 1991; Storch and Qiu, 1991; Gould, 1995).
133. M3, protocone size; (0) large; (1) small.
134. M3, main cusps: (0) equally developed; (1) not (Munthe and West, 1980).
135. M3, metaconule: (0) present; (1) absent (Butler, 1948; Munthe and West, 1980).
136. M3, parastyle: (0) present; (1) absent (Munthe and West, 1980).
137. M3, anterior cingulum: (0) present; (1) absent (Munthe and West, 1980).
138. M3, posterolingual cingulum: (0) present; (1) absent (Munthe and West, 1980).
139. M3, posterolabial cingulum: (0) present; (1) absent; (2) partial (Rich, 1981).
140. M3, posterior cingulum: (0) present; (1) absent.
141. i1: (0) present; (1) absent (Leche, 1902; Butler, 1948, 1988; Stevens, 1977; Rich, 1981; Frost et al., 1991).
142. i1, size relative to i2: (0) approximately equal; (1) larger (Butler, 1948; Novacek, 1986; Rich, 1981; Frost et al., 1991; Storch and Qiu, 1991).
143. i1, shape: (0) spatulate; (1) conical (Rich, 1981).
144. i1, root: (0) short; (1) long (Rich and Rasmussen, 1973).
145. i2: (0) present; (1) absent (Rich, 1981).
146. i2, size: (0) enlarged; (1) reduced (Butler, 1948, 1988; Novacek, 1985; Novacek et al., 1985; Frost et al., 1991; Gould, 1995).
147. i2, shape: (0) spatulate; (1) conical (Stevens, 1977; Munthe and West, 1980).
148. i2, position: (0) overlaps preceding tooth; (1) not (Rich, 1981).
149. i2, anterior midline crest: (0) ends posterior to protoconid; (1) not (Rich, 1981).
150. i3: (0) present; (1) absent (Butler, 1948).
151. i3, size relative to other incisors: (0) smaller; (1) approximately equal; (2) larger (Butler, 1948, 1988; Corbet, 1988; Frost et al., 1991).
152. Lower canine, size relative to p1: (0) approximately equal; (1) greater (Butler, 1948; Rich, 1981; Frost et al., 1991; Storch and Qiu, 1991).
153. Lower canine mophology: (0) like i2/p2; (1) not (Storch and Qiu, 1991).
154. Lower canine: (0) overlaps preceding tooth; (1) not (Rich, 1981).

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155. Lower canine, anterior midline crest: (0) present; (1) absent (Rich, 1981).
156. Lower canine, anterior midline crest: (0) ends posterior to principal cusp; (1) not (Rich, 1981).
157. Lower canine, posterior ridge: (0) present; (1) absent; (2) weak (Rich, 1981).
158. Lower canine, lingual ridge: (0) present; (1) absent (Rich, 1981).
159. Lower canine, basal cuspule: (0) present; (1) absent (Frost et al., 1991; Gould, 1995).
160. p1: (0) present; (1) absent (Butler, 1948, 1988; Rich, 1981; Frost et al., 1991; Storch and Qiu, 1991).
161. p1, roots: (0) single; (1) partly divided (Butler, 1948).
162. p1, cuspules: (0) one; (1) two; (2) three.
163. p2: (0) present; (1) absent (Rich, 1981; Novacek, 1985; Novacek et al., 1985; Gould, 1995).
164. p2, roots: (0) one; (1) two (Koerner, 1940; Butler, 1948, 1988; Black et al., 1980; Munthe and West, 1980; Rich, 1981).
165. p2, cuspules: (0) one; (1) two; (2) three; (3) four; (4) absent.
166. p2, cingulum: (0) present; (1) absent; (2) partial (Munthe and West, 1980).
167. p2, position: (0) overlaps preceding tooth; (1) not (Rich, 1981).
168. p2, anterior midline crest: (0) present; (1) absent (Rich, 1981).
169. p2, anterior midline crest: (0) ends posterior to protoconid; (1) not (Rich, 1981).
170. p2, lingual ridge: (0) present; (1) absent (Rich, 1981).
171. p2, posterior ridge: (0) present; (1) absent (Rich, 1981).
172. p3: (0) present; (1) absent (Butler, 1948; Rich, 1981).
173. p3, roots: (0) two; (1) one; (2) two fused (Butler, 1948; Novacek, 1985; Novacek et al., 1985; Corbet, 1988; Storch and Qiu, 1991).
174. p3, size relative to p2: (0) much larger; (1) approximately equal (Butler, 1948; Munthe and West, 1980).
175. p3, cusps: (0) two; (1) one; (2) three (Munthe and West, 1980).
176. p3, posterior margin; (0) wide; (1) narrow (Munthe and West, 1980).
177. p3, metaconid crest: (0) present; (1) absent (Butler, 1948).
178. p3, posterolingual cusp: (0) prominent; (1) weak or absent (Munthe and West, 1980).
179. p3, cingulum: (0) present; (1) absent; (2) partial (Munthe and West, 1980).
180. p4, talonid: (0) elongated; (1) short (Novacek, 1985; Novacek et al., 1985; Gould, 1995).
181. p4, talonid: (0) greatest breadth of tooth; (1) not (Matthew, 1929; Stevens, 1977; Rich, 1981; Butler, 1948).
182. p4, talonid posterior ridge: (0) present; (1) absent (Matthew, 1929; Rich, 1981; Storch and Qiu, 1991).
183. p4, posterolabial cusp: (0) present; (1) absent (Butler, 1948).
184. p4, paraconid: (0) strong; (1) weak; (2) absent (Matthew, 1929; Rich, 1981; Storch and Qiu, 1991).
185. p4, paraconid height relative to protoconid: (0) approximately equal; (1) shorter (Koerner, 1940; Butler, 1948, 1988; Black et al., 1980; Munthe and West, 1980; Rich, 1981).
186. p4, paraconid position relative to protoconid: (0) anterolingual; (1) directly anterior (Stevens, 1977).
187. p4, paraconid: (0) separated from protoconid by notch; (1) not (Stevens, 1977).
188. p4, protoconid position: (0) cental; (1) labial (Munthe and West, 1980).
189. p4, protoconid size: (0) greater than metaconid; (1) not (Rich, 1981; Butler, 1948).
190. p4, metaconid: (0) present; (1) absent (Matthew, 1929; Rich, 1981).
191. p4, metaconid size: (0) small; (1) large (Butler, 1948, 1988; Stevens, 1977; Munthe and West, 1980; Storch and Qiu, 1991).
192. p4, posterior talonid cuspule(s): (0) present; (1) absent (Stevens, 1977; Rich, 1981; Butler, 1948).
193. p4, number of posterior talonid cuspules: (0) one; (1) two; (2) three (Stevens, 1977; Rich, 1981; Butler, 1948).
194. p4, cingulum: (0) strong; (1) weak; (2) absent (Rich, 1981).
195. p4, size relative to m1: (0) approximately equal; (1) smaller (Storch and Qiu, 1991).
196. Prevallid shear: (0) present; (1) absent (Stevens, 1977; Novacek, 1985, 1986).
197. m1, postcingulum: (0) strong; (1) weak; (2) absent (Black et al., 1980; Rich, 1981; Storch and Qiu, 1991).
198. m1, trigonids: (0) high, short talonid; (1) low, talonid expanded (Matthew, 1929; Stevens, 1977; Rich, 1981; Butler, 1948; Novacek, 1985; Novacek et al., 1985; Frost et al., 1991; Gould, 1995).
199. m1, protoconid: (0) lingually inclined; (1) not (Black et al., 1980).
200. m1, protocristid: (0) contacts metaconid and protoconid; (1) no contact; (2) absent.
201. m1, metaconid position: (0) anterior to protoconid; (1) not (Matthew, 1929; Rich, 1981; Butler, 1948).
202. m1, metaconid height relative to paraconid: (0) greater; (1) approximately equal or smaller (Black et al., 1980).
203. m1, paraconid: (0) large; (1) small; (2) absent (Rich and Rasmussen, 1973; Rich, 1981).
204. m1, labial wall: (0) markedly concave; (1) not (Matthew, 1929; Rich, 1981).
205. m1, lingual wall: (0) markedly concave; (1) not (Matthew, 1929; Rich, 1981).
206. m1, talonid: (0) enclosed lingually by entocristid; (1) not (Rich, 1981; Storch and Qiu, 1991).
207. m1, talonid: (0) opens posteriorly; (1) closed (Stevens, 1977).
208. m1, hypoconid: (0) isolated; (1) not (Black et al., 1980).

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209. m1, entoconid size: (0) larger than the hypoconid; (1) larger than the paraconid; (2) approximately equal to all other cusps; (3) larger than the hypoconid and paraconid (Matthew, 1929; Butler, 1948; Stevens, 1977; Rich, 1981).
210. m1, entostylid: (0) present; (1) absent (Black et al., 1980).
211. m1, entocristid: (0) high; (1) low; (2) absent (Rich, 1981; Butler, 1948; Storch and Qiu, 1991).
212. m1, hypoconulid: (0) present; (1) absent (Butler, 1948).
213. m1, cristid obliqua orientation: (0) antero-posteriorly directed; (1) inclined; (2) absent (Black et al., 1980).
214. m1, hypocristid: (0) extends to posterior cingulum; (1) not; (2) absent (Engesser, 1972; Black et al., 1980).
215. m1, labial cingulum: (0) continuous around hypoconid; (1) not (Stevens, 1977; Rich, 1981; Butler, 1948).
216. m1, labial cingulum: (0) strong; (1) weak; (2) absent (Matthew, 1929; Rich, 1981; Novacek, 1985; Novacek et al., 1985; Gould, 1995).
217. m1, entoconulid: (0) present; (1) absent (Black et al., 1980).
218. m1, paraconid position relative to the metaconid: (0) lingual; (1) labial; (2) aligned.
219. m1, paraconid position relative to the protoconid: (0) lingual; (1) labial; (2) aligned.
220. m1, paracristid: (0) horizontal; (1) attenuated.
221. m1, paracristid lingual extension: (0) terminates at mid-anterior of tooth; (1) extends to lingual border (Rich, 1981; Butler, 1948).
222. m2, size relative to m1: (0) smaller; (1) larger (Matthew, 1929; Stevens, 1977; Rich, 1981; Butler, 1948).
223. m2, trigonids: (0) high, short talonid; (1) low, expanded talonid (Stevens, 1977; Rich, 1981).
224. m2, protoconid height relative to the metaconid: (0) smaller; (1) approximately equal; (2) larger (Matthew, 1929; Rich, 1981).
225. m2, paraconid: (0) present; (1) absent (Rich, 1981; Storch and Qiu, 1991).
226. m2, paraconid shelf: (0) present; (1) absent.
227. m2, paraconid swelling: (0) present; (1) absent (Rich, 1981).
228. m2, paracristid lingual extension: (0) approximately equal to m1; (1) not; (2) more lingual than m1 (Butler, 1948).
229. m2, entostylid: (0) absent; (1) weak; (2) strong (Black et al., 1980).
230. m2, posterior cingulum: (0) present; (1) absent (Rich, 1981).
231. m2, posterior cingulum: (0) connects to entoconid; (1) not (Rich, 1981; Storch and Qiu, 1991).
232. m2, entoconulid: (0) present; (1) absent.
233. m2, paraconid position relative to the metaconid: (0) lingual; (1) labial; (2) aligned.
234. m2, paraconid position relative to the protoconid: (0) lingual; (1) labial; (2) aligned.
235. m2, hypoconid position relative to the protoconid: (0) lingual; (1) labial; (2) aligned (Rich, 1981).
236. m2, entoconid size: (0) approximately equal to the protoconid; (1) tallest cusp; (2) approximately equal to the hypoconid; (3) approximately equal to the metaconid (Matthew, 1929; Rich, 1981).
237. m2, talonid: (0) posteriorly narrow; (1) not (Matthew, 1929; Rich, 1981).
238. m2, talonid basin: (0) lingually enclosed; (1) not.
239. m2, hypoconulid: (0) present; (1) absent (Rich, 1981; Black et al., 1980).
240. m2, cristid obliqua contact point: (0) at the base of the protoconid; (1) midheight of protoconid (Matthew, 1929; Rich, 1981).
241. m2, entocristid: (0) high; (1) low; (2) absent (Rich, 1981; Storch and Qiu, 1991).
242. m2, labial cingulum: (0) continuous; (1) discontinuous; (2) absent (Matthew, 1929; Rich, 1981).
243. m3: (0) present; (1) absent (Rich and Rasmussen, 1973; Stevens, 1977; Rich, 1981; Novacek, 1985; Novacek et al., 1985; Gould, 1995).
244. m3, paraconid: (0) swollen; (1) normal; (2) absent (Rich, 1981; Storch and Qiu, 1991).
245. m3, paraconid shelf: (0) present; (1) absent.
246. m3, postcingulum: (0) present; (1) absent (Koerner, 1940; Rich and Rasmussen, 1973; Rich, 1981; Storch and Qiu, 1991).
247. m3, talonid: (0) present; (1) absent (Koerner, 1940; Rich and Rasmussen, 1973; Munthe and West, 1980; Rich, 1981; Butler, 1948; Frost et al., 1991; Gould, 1995).
248. m3, trigonids: (0) high; (1) short.
249. m3, lingual cingulum: (0) present; (1) absent (Munthe and West, 1980).

APPENDIX 2

Specimens Reviewed in Discrete Dental Analyses

Abbreviations: AMNH = American Museum of Natural History; USNM = United States National Museum (Smithsonian); F = female; M = male; (#) = number of specimens reviewed.

Atelerix

Atelerix albiventris (25)

USNM	378723	M	Nigeria, Kano Prov.
USNM	378725	F	Nigeria, Kano Prov.
USNM	378726	F	Nigeria, NW Zaria
USNM	378728	F	Nigeria, NW Zaria
USNM	378729	F	Nigeria, NW Zaria
USNM	378730	F	Nigeria, NW Zaria
USNM	378731	F	Nigeria, N Sokoto
USNM	378732	F	Nigeria, N Sokoto
USNM	378740	F	Nigeria, N Sokoto
USNM	378741	M	Nigeria, N Sokoto
USNM	378742	M	Nigeria, N Sokoto
USNM	378746	M	Nigeria, N Sokoto
USNM	378747	M	Nigeria, N Sokoto
USNM	378748	M	Nigeria, N Sokoto
USNM	378750	F	Nigeria, not labeled
USNM	378751	F	Nigeria, N Sokoto
USNM	378752	M	Nigeria, N Sokoto
USNM	402179	F	Nigeria, N Sokoto
USNM	402180	F	Nigeria, N Sokoto
USNM	402181	M	Nigeria, N Sokoto
USNM	402182	M	Nigeria, N Sokoto
USNM	402183	M	Nigeria, N Sokoto
USNM	402184	M	Nigeria, N Sokoto
USNM	375927	F	Nigeria, Plateau Prov.
USNM	375928	F	Nigeria, S Kabwir

Atelerix algirus (21)

USNM	476050	F	Morocco, Fes Prov.
USNM	476051	F	Morocco, Oujda Prov.
USNM	476052	F	Morocco, Ksar Es Souk Prov.
USNM	476053	F	Morocco, Ksar Es Souk Prov.
USNM	476054	F	Morocco, Fes Prov.
USNM	476055	M	Morocco, Fes Prov.
USNM	476056	F	Morocco, Al Hoceima Prov.
USNM	476057	F	Morocco, Oujda Prov.
USNM	476058	F	Morocco, Agadir Prov.
USNM	476059	M	Morocco, Adadir Prov.
USNM	476060	M	Morocco, Adadir Prov.
USNM	476061	F	Morocco, Adadir Prov.
USNM	476062	F	Morocco, Tetouan Prov.
USNM	476063	M	Morocco, Oujda Prov.
USNM	476064	M	Morocco, Ksar Es Souk Prov.
USNM	476065	F	Morocco, Ksar Es Souk Prov.
USNM	476066	M	Morocco, Beni-Mellal Prov.
USNM	470578	M	Morocco, Agadir Prov.
USNM	470579	F	Morocco, Agadir Prov.
USNM	482681	M	Morocco, Agadir Prov.
USNM	140766	?	Sud Tunis, Djerba

Echinosorex (32)

Echinosorex gymnurus

USNM	487885	F	west Malaysia
USNM	487887	?	west Malaysia
USNM	487888	M	west Malaysia
USNM	487889	F	west Malaysia
USNM	487890	F	west Malaysia
USNM	487901	M	west Malaysia
USNM	487892	F	west Malaysia
USNM	487893	M	west Malaysia
USNM	487894	M	west Malaysia
USNM	487895	M	west Malaysia
USNM	487896	M	west Malaysia
USNM	487897	M	west Malaysia
USNM	487898	F	west Malaysia
USNM	487899	M	west Malaysia
USNM	487900	F	west Malaysia
USNM	487902	F	west Malaysia
USNM	487903	F	west Malaysia
USNM	283474	F	Malaya
USNM	283475	F	Malaya
USNM	115489	M	Pahang: Rumpin River
USNM	357885	F	Malaysia: Selangor
USNM	3787	?	Singapore
USNM	357886	M	Malaysia
USNM	367888	M	Malaysia
USNM	487886	F	Malaysia
USNM	357887	M	Malaysia

Echinosorex g. "dealbatus"

USNM	83704	MJ	"Butaw" or Tikus Island, Sumatra

Echinosorex g. "alba"

USNM	145581	F	West Borneo, Sempang River
USNM	145582	F	West Borneo, Sempang River
USNM	145584	F	West Borneo, Sempang River
USNM	145585	M	West Borneo, Sempang River
USNM	145586	F	West Borneo, Sempang River

Erinaceus

Erinaceus amurensis (11)

USNM	176251	M	N. China, Tiensin
USNM	199681	M	N. China, Tiensin
USNM	239770	?	China, Ningpo
USNM	239590	?	China, Hunan, Yochow
USNM	239591	F	China, Hunan, Yochow
USNM	239592	F	China, Hunan, Yochow
USNM	197779	F	China, Kirin Prov.
USNM	270541	M	Inner Mongolia, Grter. Khingan
USNM	270542	F	Inner Mongolia, Grter. Khingan
USNM	240325	F	China, Shanghai
USNM	252158	F	China, Shanghai

APPENDIX 2
Continued

Erinaceus europaeus (24)

USNM	153409	M	Wales, Cardiff
USNM	153410	M	England, Wandsworths Comn.
USNM	153411	F	Bavaria, Strass
USNM	153412	M	Germany, Ingelheim
USNM	1856	?	Bavaria
USNM	186556	?	W. Germany, Braunschweig (Saxony)
USNM	251763	?	Germany
USNM	251764	F	Germany
USNM	251765	F	Germany
USNM	251766	F	Germany
USNM	251767	M	Germany
USNM	251768	M	Germany
USNM	271142	M	Germany
USNM	151668	M	W. Germany, Baden Wurtemburg
USNM	37465 (12244)	?	Germany, Heidelburg
USNM	85619	M	Germany, Braunschweig
USNM	86923	F	Ireland, Glenmore County
USNM	36034 (20807)	F	England
USNM	174660	M	Channel Islands, Guernsey
USNM	794	?	England
USNM	795	?	England
USNM	34959 (19246)	M	England (Nat. Zool. Park)
USNM	34960 (19247)	F	England (Nat. Zool. Park)
USNM	84739	F	Switzerland, St. Gallen

Hemiechinus

Hemiechinus aethiopicus (= *Paraechinus*, 25)

USNM	311732	M	Egypt, Sudan Admin. Area
USNM	311737	F	Egypt, Western Desert, Gov.
USNM	311738	M	Egypt, Western Desert, Gov.
USNM	311739	F	Egypt, Sinai, St. Catherine's
USNM	311740	M	Egypt, Sinai, St. Catherine's
USNM	321572	F	SW Saudi Arabia, E. Aden Protectorate, Taribin
USNM	325906	F	Egypt, Sinai
USNM	325907	M	Egypt, St. Catherine's
USNM	325908	F	Egypt, St. Catherine's
USNM	384832	M	Mauritania, Atar
USNM	410872	M	Mauritania, Kiffa
USNM	410873	F	Mauritania, Kiffa
USNM	482512	M	Niger, 5 km NE Agadez
USNM	470563	F	Morocco, Agadir Prov.
USNM	470564	?	Morocco, Agadir Prov.
USNM	470565	F	Morocco, Tarfaya Prov.
USNM	470566	M	Morocco, Ouarzazate Prov.
USNM	470567	M	Morocco, Ouarzazate Prov.
USNM	470568	M	Morocco, Ouarzazate Prov.
USNM	470569	F	Morocco, Ouarzazate Prov.

Hemiechinus aethiopicus (= *Paraechinus*, 25) (*continued*)

USNM	476067	F	Morocco, Ksar Es Souk Prov.
USNM	476068	F	Morocco, Ksar Es Souk Prov.
USNM	476069	M	Morocco, Ksar Es Souk Prov.
USNM	482862	M	Morocco, Agadir Prov.
USNM	482863	M	Morocco, Agadir Prov.

Hemiechinus auritus (25)

AMNH	203197	M	Egypt, Giza, Imbaba, Kafr Hakem
AMNH	203198	M	Egypt, Giza, Imbaba, Manshiyet
AMNH	203199	F	Egypt, Giza, Imbaba, Manshiyet
AMNH	203200	F	Egypt, Giza, Imbaba, Tanash
AMNH	170226	M	Pakistan, Baluchistan, Quetta
AMNH	170227	F	Pakistan, Baluchistan, Quetta
AMNH	170228	M	Pakistan, Baluchistan, Quetta
AMNH	170229	M	Pakistan, Baluchistan, Quetta
AMNH	244379	?	Pakistan, Baluchistan, Kalat
AMNH	244380	?	Pakistan, Baluchistan, Kalat
AMNH	244384	M	Pakistan, Baluchistan, Quetta
AMNH	176282	F	USSR Turkmenskaya SSR
AMNH	87085		USSR, Uzbekskaya SSR Fergana
AMNH	85309	M	USSR, Kazakhsakay SSR
AMNH	85308	M	USSR, Kazakhsakay SSR
AMNH	31248	?	USSR, RS FSR Sarepta, NYZS
AMNH	57216	M	Mongolia, Oyor-Hangay Prov.
AMNH	57217	M	Mongolia, Oyor-Hangay Prov.
AMNH	57222	M	Mongolia, Oyor-Hangay Prov.
AMNH	84001	M	Mongolia, Oyor-Hangay Prov.
AMNH	31246	?	China, Xinjiang Uygur Zizhiqu Kashi
AMNH	184065	?	Israel, Kvutzat-urim Zoo
AMNH	22876	?	NYSZS
AMNH	22889	?	NYSZS
AMNH	80021	?	NYSZS

Hemiechinus hypomelas (19)

USNM	326695	F	Iran, Khursan, Turbat-I-Haibari
USNM	326696	M	Iran, Khursan, Turbat-I-Haibari
USNM	326697	F	Iran, Khursan, Turbat-I-Haibari
USNM	326698	M	Iran, Khursan, Turbat-I-Haibari
USNM	326699	F	Iran, Khursan, Turbat-I-Haibari
USNM	327914	F	Iran, Dasnt-I-Lut Majak
USNM	326700	M	Iran, 6 km N of Kashmar
USNM	326701	F	Iran, Turbat-I-Haibari
USNM	327913	M	Iran, Dasnt-I-Lut Majak
USNM	327915	F	Iran, Majan
USNM	352951	M	Pakistan, Gulistan Quetta Dist.
USNM	368931	M	Pakistan, Muzaffargarh Alipur
USNM	368932	F	Pakistan, Deragazikahn
USNM	368933	F	Pakistan, Deragazikahn
USNM	368934	M	Pakistan, Muzaffargarh Alipur
USNM	368935	M	Pakistan, Muzaffargarh Alipur
USNM	368936	M	Pakistan, Muzaffargarh Alipur
USNM	368937	F	Pakistan, Muzaffargarh Alipur
USNM	410929	M	Pakistan, Deragazikahn

APPENDIX 2
Continued

Hylomys

Hylomys sinenesis (25)

AMNH	115505	F	N. Burma, Kachin Prov.
AMNH	115506	M	N. Burma, Kachin Prov.
AMNH	115508	F	N. Burma, Kachin Prov.
AMNH	115509	F	N. Burma, Kachin Prov.
AMNH	115510	M	N. Burma, Kachin Prov.
AMNH	115511	F	N. Burma, Kachin Prov.
AMNH	115512	M	N. Burma, Kachin Prov.
AMNH	115514	M	N. Burma, Kachin Prov.
AMNH	115515	F	N. Burma, Kachin Prov.
AMNH	115516	F	N. Burma, Kachin Prov.
AMNH	115517	M	N. Burma, Kachin Prov.
AMNH	115518	M	N. Burma, Kachin Prov.
AMNH	115519	M	N. Burma, Kachin Prov.
AMNH	115520	M	N. Burma, Kachin Prov.
AMNH	115522	F	N. Burma, Kachin Prov.
AMNH	115523	M	N. Burma, Kachin Prov.
AMNH	115524	M	N. Burma, Kachin Prov.
AMNH	115525	M	N. Burma, Kachin Prov.
AMNH	44248	F	China, Mu-cheng, Yun-nan Prov.
AMNH	44249	M	China, Mu-cheng, Yun-nan Prov.
AMNH	44267	M	China, Taiping-pu, Yun-nan Prov.

Hylomys sinenesis (25) (*continued*)

AMNH	44268	M	China, Taiping-pu, Yun-nan Prov.
AMNH	44270	F	China, Taiping-pu, Yun-nan Prov.
AMNH	44271	M	China, Taiping-pu, Yun-nan Prov.
AMNH	57199	?	China, Yun-nan Prov.

Hylomys suillus (16)

USNM	481278	F	Java
USNM	481279	F	Java
USNM	481280	F	Java
USNM	481281	F	Java
USNM	481283	F	Java
USNM	481284	F	Java
USNM	481285	F	Java
USNM	481286	F	Java
USNM	481287	M	Java
USNM	481288	M	Java
USNM	481289	F	Java
USNM	481290	F	Java
USNM	521659	M	Java
USNM	521660	M	Java
USNM	521661	M	Java
USNM	155660	F	Java

APPENDIX 3

Frequency Distribution of 246 Transformation Series across 10 Taxa

Abbreviations: N = sample size; M = male; F = female; ? = sex undetermined; J = juvenile; MA = mature adult; W = worn; TS# = transformation series number (see appendix 1); column headings 0, 1, 2, 3, 4 = character state numbers (see appendix 1); A = assymetrical character expression; T = total number of specimens scored.

	Echinosorex gymnura (N = 32; M-14, F-16, ?-2; J-7, MA-18, W-7)							*Hylomys sinensis* (N = 25; M-15, F-9, ?-1; J-0, MA-24, W-1)							*Hylomys suillus* (N = 16; M-5, F-11; J-3, MA-11, W-2)							*Atelerix albiventris* (N = 25; M-11, F-14; J-4, MA-13, W-8)							*Atelerix algirus* (N = 21; M-7, F-13, ?-1; J-5, MA-7, W-9)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
4	27	5					32	25						25	16						16	25						25	21						21
5	32						32	25						25	6	10					16		25					25		21					21
6	32						32	25						25	16						16	25						25	21						21
7	2	5	10				17			23				23	2	2	10			2	16			25				25			20			1	21
8	27						27	25						25	12	4					16			25				25			21				21
9	25						25		25					25		16					16	25						25	21						21
10	30	1					31	25						25	16						16	25						25	21						21
11	29						29	25						25	16						16	25						25	1	14	1			2	18
12							NA		25					25							NA		24					24	20						20
13	26						26		24					24		16					16		25					25		21					21
14	8	12				1	21		23					23		16					16	12		6				18		15					15
15	6	12	1	1			20	12	8					20	3	13					16	6	12					18	6	9					15
16	19					1	20		22	1				23		16					16		25					25	2	19					21
17	27						27			23				23		12	2			2	16	19						19		5	8				13
18	31						31		18	4				22		14	2				16		25					25		19					19
19	24	2	5				31		3	19				22	16						16	24						24	16		1				17
20	32						32	16	5					21	16						16	5	16	1				22		19					19
21	29						29		24					24		16					16	3	20					23	4	15					19
22	29						29		24					24		16					16	2	22					24		19					19
23		7	14			3	24		4	20				24	10	2	4				16	7	6	9			2	24	1	11	7				19
24	29					2	31		25					25	14	1				1	16		25					25		21					21
25	2	14	2			2	20							NA			13			2	15							NA							NA
26	1	17	2				20							NA	6	8				1	15							NA							NA
27	30					1	31							NA	14	1					15							NA							NA
28	31						31	24						24	16						16	25						25	21						21
29		2	14				16			24				24		3	10			3	16	1	6	17			1	25			20				20
30	1	12	2			1	16		16	5				21	15	1					16	10	6	6			2	24	2	4	13				19
31		31					31		20	3				23	4		8			3	15	24	1					25	16		1			1	18
32	32						32	25						25	16						16	22	2				1	25	21						21
33	3	29					32		25					25		16					16		23					23	3	18					21
34	27	5					32		25					25		16					16	8	12				3	23	17	4					21
35		24	8				32			25				25		14	2				16		1	22				23	2	4	15				21
36	6	26					32		25					25		16					16	1	22					23	3	17					20
37	12	17				3	32							NA		16					16	2	20					22	6	13					19
38	15	16					31							NA							NA	1	1					2	3	3					6
39	32						32		25					25		16					16		23					23		21					21
40	32						32		25					25		16					16	12	9				1	22	11	5					16
41							NA							NA							NA		4	4				8	5	1	1			1	8
42							NA							NA							NA		8					8		11					11
43	32						32	25						25	16						16	12	1	7				20	21						21
44	31						31	25						25	13	2				1	16	15	6				2	23	21						21
45	2	29					31		25					25		16					16		21				2	23		21					21
46		1					1		25					25		14					14							NA							NA
47	4	15	7			5	31		25					25		16					16		25					25		21					21
48		2	30				32			25				25	5	8				3	16		2	21			1	23		5	15				20
49	32						32		25					25	16						16		22	1				23	19	2					21
50	16	12				3	31		25					25		16					16	7	15				1	23	1	20					21
51	2						2							NA							NA							NA							NA
52	32						32		25					25		16					16	10	13				1	24	14	3					17
53	26	4	2				32		25					25	16						16	5	13	3				21		21					21
54	32						32	25						25	16						16	22	2				1	25	21						21
55	32						32	25						25	16						16	22						22	21						21
56	32						32	25						25	1	15					16	10	7				3	20	21						21

APPENDIX 3
Continued

	Echinosorex gymnura (N = 32; M-14, F-16, ?-2; J-7, MA-18, W-7)							*Hylomys sinensis* (N = 25; M-15, F-9, ?-1; J-0, MA-24, W-1)							*Hylomys suillus* (N = 16; M-5, F-11; J-3, MA-11, W-2)							*Atelerix albiventris* (N = 25; M-11, F-14; J-4, MA-13, W-8)							*Atelerix algirus* (N = 21; M-7, F-13, ?-1; J-5, MA-7, W-9)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
57	32						32	25						25	15	1					16	23	1					24	21						21
58		31					31	25						25	15	1					16	24	1					25	21						21
59		32					32		25					25		11					11	7	17					24		21					21
60	12	1	13			2	28	5	4	9			7	25	15	1					16	3	13	5			1	22	21						21
61	2	15					17							NA			16				16	11					1	12							NA
62		32					32	25						25		16					16	22	2					24		21					21
63	29	2				1	32			25				25	8	7				1	16	2	1	22				25	2	10	8				20
64	3	26				2	31	9	11	1			4	25	1	15					16		24				1	25	7	13					20
65	14	16				1	31		22	2			1	25		16					16	5	20					25	8	11				2	21
66	19	11				1	31	7	14	3			1	25	1	15					16	1	24					25	6	15					21
67		31					31		25					25		16					16		25					25		21					21
68	32						32	25						25	16						16	25						25	21						21
69			32				32			25				25		4	12				16			25				25			21				21
70	15	14	2			1	32	10	12				3	25	13	3					16	11	3	8			2	24	19	2					21
71	30						30	25						25							NA		2					2		21					21
72	29						29	25						25	15						15	9	2				2	13	20						20
73	9	13				1	23	3	20				1	24	5	4				6	16		6				1	7		19				1	20
74	13	5				2	20	24						24	3	9	2				14	2	4					6	19	1					20
75	23	2				3	28	22		1			1	24			15				15		1	8			2	11			19			1	20
76	6	1	1	5	1		14			25				25		1	14				15			12				12			21				21
77	30						30	25						25	15						15	15						15	21						21
78	23		4				27	25						25	15						15	19		2				21	21						21
79		16	8				24	2	11	10			2	25		16					16		24					24		1	20				21
80	28	2					30		25					25		16					16		25					25		21					21
81	30						30	25						25	16						16	18	1					19	21						21
82	1	26					27		25					25		16					16	11	2	5			4	22	21						21
83			19				19		24					24			14				14	10				3		13	21						21
84			29				29			19			6	25			16				16	10	11				2	23	1		14			2	17
85	13	14				1	28	25						25	4	11					15	2	13				2	17	14	2					16
86	5	15	6				26		8	15			1	24	4	6	3			2	15		6	12			1	19			21				21
87		27					27		24				1	25		15					15	1	18					19		1	20				21
88		16	6				22			25				25		15					15		13					13		21					21
89	11	12				5	25	18	4				2	24	1	14					15	3	8				2	13	2	9					11
90	5	8					13	1	19					20		1					1	2	3					5	1	1					2
91	25						25	24						24	14	1					15	14						14	19						19
92	11	6				5	22	8	10				6	24	3	10				2	15	6	4					10	21						21
93	6	9				2	17	13	1				1	15	3	9				3	15	6	4				1	11	14					1	15
94	30						30	25						25	16						16	25						25	21						21
95		29					29	25						25		15					15		25					25		21					21
96	30						30	25						25	16						16	25						25	21						21
97		29					29		25					25		15					15		23				1	24		21					21
98	8	20				2	30	6	17				2	25	16						16	15	6				2	23	8	9				3	20
99	29						29	25						25	15						15	24						24	21						21
100	4	27					31		25					25		16					16		20	5				25		21					21
101	8	9	12			2	31		25					25		16					16		22				1	23	6	5	9			1	21
102	31						31	18	6				1	25	2	12				2	16	9	13				1	23	20						20
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104	30						30	25						25	15	1					16	9	13				1	23	21						21
105			32				32			25				25			16				16			25				25			21				21
106		32					32		25					25							NA							NA	21						21
107	7		25				32	13	3	4			4	24	16						16	25						25	21						21
108	1	10	21				32	8	2	15				25		16					16		25					25		21					21
109		30					30		24	1				25		15					15		22					22		21					21
110		6	24				30		5	8			12	25		14	2				16		25					25		21					21
111	16	11				2	29		24					24		16					16		25					25		21					21
112	30						30	25						25	12					1	13	5	2					7	15	1					16

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	Echinosorex gymnura (N = 32; M-14, F-16, ?-2; J-7, MA-18, W-7)							*Hylomys sinensis* (N = 25; M-15, F-9, ?-1; J-0, MA-24, W-1)							*Hylomys suillus* (N = 16; M-5, F-11; J-3, MA-11, W-2)							*Atelerix albiventris* (N = 25; M-11, F-14; J-4, MA-13, W-8)							*Atelerix algirus* (N = 21; M-7, F-13, ?-1; J-5, MA-7, W-9)						
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114	9	19				1	29	14	6				4	24		13					13		20					20		12					12
115		10					10	1	11	2			4	18							NA							NA							NA
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118	16	14				1	31	7	14				4	25	11	4					15	23	1					24	9	11					20
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120	1	28					29	24						24	5	11					16		22					22		21					21
121							NA	24						24							NA							NA							NA
122	11						11	24						24							NA							NA	21						21
123	27	2					29		23				1	24	16						16	21						21	21						21
124	4	28					32	1	22	1			1	25		16					16		22					22	3	18					21
125	28		2				30	2	9	11			3	25	4	9	2				15		17	1			1	19	20	1					21
126	31						31	21		3			1	25	14	2					16		7	15				22	20		1				21
127	30						30	2		23				25		16					16			19				19			21				21
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129	32						32	25						25	16						16	25						25	21						21
130	1	31					32		24		1			25		16					16		1		24			25			16			1	17
131	27		3				30		24	1				25			16				16	0	25					25		20	1				21
132		29					29	25						25	14	2					16			25				25			21				21
133	29						29	25						25		16					16	25						25	21						21
134		28					28	25						25	16						16	14	5					19	21						21
135	22	6					28		25					25		15					15		25					25		21					21
136	24	4					28	4	20				1	25	7	8					15	11	9				1	21	6	8					14
137	30						30	20	4					24	7	7				2	16	10	10				1	21	21						21
138	23	5					28	7	18					25	5	11					16	1	21					22	1	19				1	21
139	6	16	7				29		25					25	2	14					16	1	21					22	11		3				14
140	2	27					29		25					25	2	14					16		22					22	9	10					19
141	32						32	2	23					25	16						16		24					24		21					21
142	31						31		2					2		16					16							NA							NA
143	32						32	2						2	16						16							NA							NA
144		31					31		2					2		16					16							NA							NA
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146	32						32	23	2					25	15						15	24						24	21						21
147	32						32	25						25	15						15	24						24	21						21
148		20				1	21	8	10					18	14	1				1	16							NA							NA
149			25				25	1	24					25							NA							NA		21					21
150	32						32	25						25	16						16	25						25	21						21
151	31	1					32	24		1				25	16						16	25						25	21						21
152		31					31							NA		16					16							NA							NA
153		30					30	1	24					25		16					16	25						25		21					21
154		32					32	3	21					24	3	13					16	25						25	19	1					20
155	4	27					31	13	9				1	23	2	14					16	13	11					24	21						21
156		5					5	13	1					14	2						2		13					13	21						21
157	4	22	4				30	9	10	4				23	2	12	1			1	16	1	21					22	2	11	7			1	21
158		30					30	1	22					23		16					16		23					23		21					21
159	10	19				1	30	1	24					24	11	4				1	16	20	1				1	22	12	7				1	20
160	29	2				1	32		25					25	16						16		25					25		21					21
161	30	1					31							NA	16						16							NA							NA
162	11	5	1	1		1	19							NA		9	5			1	15							NA							NA
163	30	2					32	25						25	16						16	25						25	21						21
164	29						29	25						25	16						16	25						25	21						21
165	19	3	2			1	25	2	4			17		23	1	1	13				15	19	1		1	1	3	25	12			7		1	20
166	4	4	15			1	24		23					23		16					16	2	15	7				24	8	5	7				20
167		26					26		22					22		16					16	18	4				3	25	17	4					21
168	23	2					25	2	19					21		15					15		25					25	1	18					19

APPENDIX 3

Continued

	Echinosorex gymnura (N = 32; M-14, F-16, ?-2; J-7, MA-18, W-7)							*Hylomys sinensis* (N = 25; M-15, F-9, ?-1; J-0, MA-24, W-1)							*Hylomys suillus* (N = 16; M-5, F-11; J-3, MA-11, W-2)							*Atelerix albiventris* (N = 25; M-11, F-14; J-4, MA-13, W-8)							*Atelerix algirus* (N = 21; M-7, F-13, ?-1; J-5, MA-7, W-9)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
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170	3	19				1	23		21					21		15					15		25					25	5	15					20
171	17	5				1	23	5	16				1	22		15					15	1	24					25	12	9					21
172	32						32	25						25	16						16		24					24		21					21
173	32						32		25					25	1	6	7			2	16							NA							NA
174	31						31		24					24	1	15					16							NA							NA
175		28	3				31		24					24	3	2	10				15							NA							NA
176	32						32		23					24		16					16							NA							NA
177		32					32	1	23					24		15					15							NA							NA
178		31					31		24					24	8	6				1	15							NA							NA
179	5	15	10				30		24					24		16					16							NA							NA
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182	5	20				2	27	21	4					25	3	11				2	16	19	3					22	19	2					21
183	13	16				1	30		25					25		14					14		25					25		21					21
184	22	5	3			1	31	25						25	6	9				1	16	25						25	19	2					21
185		29					29							NA		16					16		25					25		20					20
186	6	24					30							NA	8	7				1	16	25						25	19	1					20
187	2	26				1	29							NA	9	6				1	16	22						25	17	3					20
188	31						31							NA	16						16		25					25	2	19					21
189	30						30							NA	9						9	11						11							NA
190	25	3					28		25					25	7	6				2	15	9	13				2	24		19					19
191	29	1					30							NA	9						9	11						11							NA
192	3	24				1	28	2	23					25	8	6				2	16	8	13				1	22	1	20					21
193		4					4	2						2	10					1	11	8	1					9	1						1
194	12	15	3			1	31		23	2				25			15			1	16			25				25	3	1	17				21
195		31					31		25					25		16					16		25					25		21					21
196	31						31	25						25	16						16	25						25	19	2					21
197		32					32	16	5					21			15				15		24					24	5	7	3				15
198							NA	25						25		15					15	24						24	21						21
199	4	12				2	18	24	1					25		15					15	13					5	18	21						21
200			32				32		25					25	6	8	1				15	3	2	15			1	21							NA
201	11	10				4	25	19	3				2	24	5	6				5	16	19					1	20	21						21
202	30	1					31	10	10				3	23	13	2					15	20						20	21						21
203	30	1					31	25						25	15						15	23						23	21						21
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206		32					32		25					25		15					15							NA		21					21
207	32						32	25						25	15						15	21						21	21						21
208	32						32		25					25	15						15	23						23		21					21
209			32				32	25						25	15						15	1			8			9			21				21
210		31					31		25					25		15					15		23					23		21					21
211		15	10			1	26			25				25		15					15			23				23		21					21
212		6	26				32		25					25		15					15		24					24	2	18				1	21
213	15	10				3	28	18	6	1				25	7	9					16	2	12	5			1	20	3	3	9			2	17
214		31					31		23					23							NA		17	2				19							NA
215	31						31	6	15				4	25		16					16		22					22		21					21
216	21	9					30	20	3				2	25		16					16	1	21	3				25		20	1				21
217		31					31		25					25		15					15	4	13				4	21	12	8				1	21
218	1		22			4	27			25				25			16				16			21				21	1	1	12			3	17
219	32						32	25						25	16						16	22	1					23	21						21
220		32					32	24						24	15						15	21						21	4	8					12
221		32					32		24					24		16					16		20					20	19	1					20
222	32						32	25						25	16						16	25						25	21						21
223		31					31		25					25		16					16		25					25		21					21
224		31					31	10	4	8				22		16					16		8				1	9	20						20

APPENDIX 3
Continued

	Echinosorex gymnura (N = 32; M-14, F-16, ?-2; J-7, MA-18, W-7)							*Hylomys sinensis* (N = 25; M-15, F-9, ?-1; J-0, MA-24, W-1)							*Hylomys suillus* (N = 16; M-5, F-11; J-3, MA-11, W-2)							*Atelerix albiventris* (N = 25; M-11, F-14; J-4, MA-13, W-8)							*Atelerix algirus* (N = 21; M-7, F-13, ?-1; J-5, MA-7, W-9)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
225	1	30					31		25					25		16					16		25					25		21					21
226	30						30	25						25	16						16	25						25	21						21
227	3	26				1	30	22	1					23		1					1		25					25	6	10					16
228		31					31		25					25		16					16	10	2	9			1	22	21						21
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230	31						31	22	1					23		16					16	14	1				1	16	10	5				1	16
231	31						31	23						23							NA	5	7				2	14	6	5					11
232		31					31		25					25		16					16	9	9				2	20	6	14				1	21
233		29	2				31							NA							NA							NA							NA
234	31						31							NA							NA							NA							NA
235			31				31	25						25		14					14	25						25			21				21
236			30				30	25						25	14						14			1	2		1	4	21						21
237		31					31		25					25		16					16		25					25		21					21
238		31					31		25					25		15					15		25					25		21					21
239		31					31		25					25		16					16		25					25	1	19				1	21
240	31						31	25						25	15						15	22						22	21						21
241		5	24			1	30			25				25		16					16		25					25		21					21
242	31						31		25					25		16					16		25					25		21					21
243	31						31	25						25	16						16	25						25	21						21
244			30				30			25				25			16				16			25				25			21				21
245	30						30	25						25	16						16		25					25	21						21
246	4	25					29	16	8					24		16					16		25					25		16				1	17
247	30						30	25						25	16						16		25					25		21					21
248		30					30	25						25		15					15							NA		21					21
249		31					31	24						24		16					16		25					25		20					20

	Erinaceus amurensis (N = 11; M-3, F-6, ?-2; J-2, MA-7, W-2)							*Erinaceus europaeus* (N = 24; M-10, F-8, ?-6; J-2, MA-15, W-7)							*Hemiechinus aethiopicus* (N = 25; M-13, F-11, ?-1; J-3, MA-15, W-7)							*Hemiechinus auritus* (N = 25; M-12, F-4, ?-9; J-8, MA-11, W-6)							*Hemiechinus hypomelas* (N = 19; M-10, F-9; J-4, MA-11, W-4)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
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5		11					11		24					24		25					25		25					25		19					19
6	4	7					11	24						24	24					1	25	25						25	18					1	19
7	1	5	1				7			23				23			22				22			25				25	1	4	10			1	16
8			10				10			24				24			25				25			25				25			19				19
9	10						10	13	7				2	22	14	10				1	25	4	17					21	2	17					19
10	11						11	23					1	24	25						25	25						25	19						19
11	8		2			1	11	17		4			2	23		17	6			2	25		20	3			1	24		2	17				19
12	3	3					6		24					24	25						25	15	5					20	18						18
13		11					11		24					24	11	14					25	3	19					22	17	2					19
14		8					8		24					24	1	23					24	1	17					18		18					18
15	4	2					6		22					22	17	6					23	19	1					20	13						13
16		6					6		24					24		23					23		22	1				23		18					18
17		1	4				5			22				22	8	6	3			3	20	1	8	6			2	17	2	4	9			2	17
18			10				10		24					24		23	2				25		24					24			19				19
19	7	2	1				10	9	4	6			5	24	22	1	1				24	16		1				17	19						19
20		7	3				10		24					24	19	6					25		24					24		19					19
21	9	1					10	18	4				1	23	2	23					25	5	11					16		19					19
22	9						9	13	10					23		25					25		16					16		18					18
23		2	6			1	9			24				24	1	11	13				25			15				15	1	2	14			1	18
24	1	10					11		24					24		25					25		24					24		19					19
25			1				1							NA							NA							NA							NA
26			1				1							NA							NA							NA							NA
27	1						1							NA							NA							NA							NA

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Continued

	Erinaceus amurensis (N = 11; M-3, F-6, ?-2; J-2, MA-7, W-2)							*Erinaceus europaeus* (N = 24; M-10, F-8, ?-6; J-2, MA-15, W-7)							*Hemiechinus aethiopicus* (N = 25; M-13, F-11, ?-1; J-3, MA-15, W-7)							*Hemiechinus auritus* (N = 25; M-12, F-4, ?-9; J-8, MA-11, W-6)							*Hemiechinus hypomelas* (N = 19; M-10, F-9; J-4, MA-11, W-4)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
28	11						11	22					2	24	25						25	25						25	19						19
29		1	9				10			24				24			25				25	1	4	18				23		4	14			1	19
30			9				9		1	22			1	24	4	3	18				25	3	4	16				23		7	8			4	19
31		8	2				10		14	6			2	22	4	4	14			2	24	9	2	9	1		2	23	2		17				19
32	11						11	23	1					24	13	2				4	19	25						25	19						19
33		10					10	3	5					8			21			1	22	1	22					23	1	8				1	10
34	10						10	19					2	21	1	19	1				21	16	7				1	24	17					1	18
35			10				10			21			1	22		1	20				21		2	21				23			16				16
36	5	4				1	10	14	7	1				22		21					21		24					24	1	14					15
37	5	5					10	12	5				1	18		21					21		23					23	3	7					10
38	4	1					5	11	2					13							NA							NA	2	1					3
39	10						10		22					22		21					21	23	2					25	17	2					19
40	9						9	16					1	17		21					21	9	13				1	23	12	2				1	15
41	3		3			1	7	2		11			3	16							NA	7		3				10	4		1			4	9
42		9					9		16					16							NA	2	7				1	10		16					16
43		10					10	22						22	20						20	25						25	17						17
44	10						10	22						22	9	12					21	20						20	16						16
45		10					10		22					22		21					21		25					25		17					17
46							NA							NA							NA							NA		15					15
47		10					10		22					22		21					21		25					25		17					17
48			9			1	10		2	20				22			21				21		8	14			1	23	2	2	11			2	17
49	10						10	20					1	21							NA	13	10					23	16						16
50		10					10		22					22	8	13					21		18				1	19		15					15
51							NA							NA							NA	1						1							NA
52	11						11	13	6				3	22	1	20					21	15	6				2	23	19						19
53			11				11		24					24		25					25		23	2				25	19						19
54	11						11	24						24	25						25	25						25	17	1					18
55	11						11	24						24	25						25	25						25	18						18
56	11						11		24					24	25						25	25						25		19					19
57	11						11	24						24	25						25	25						25	19						19
58	11						11	24						24		23					23	25						25	7	10					17
59		11					11		24					24	4	21					25	4	16	2				22		17					17
60		11					11	24						24	24						24	25						25	19						19
61	10	1					11			24				24		24					24	15						15	8	2				1	11
62	1	10					11		24					24		25					25	25						25		19					19
63	3		8				11		2	19			1	22	4	10	10				24	4	2	15			2	23	2	6	7	3		1	19
64	10	1					11	18	4				1	23	3	20	1				24	4	20					24	3	16					19
65		9	2				11	1	21	1				23	2	18	5				25			25				25		12	7				19
66	8	3					11	17	6					23		25					25	4	21					25		19					19
67		11					11		24					24		25					25		25					25		18					18
68	11						11	24						24	25						25	25						25	19						19
69			11				11			24				24			25				25			25				25		17	2				19
70	11						11	13	3	5			2	23	8	11	4			2	25	11	6	4				21	9	5	3			1	18
71		11					11		24					24		25					25		25					25							NA
72	11						11	22						22	21	1					22	25						25	18						18
73		11					11		22					22	3	11				3	17		25					25		16					16
74		11					11	1	13				2	16	7	2	2			2	13	23	1					24	16						16
75	4	7					11		20	2				22	5	2	8			5	20		1	23				24	1	4	8			2	15
76			11				11			24				24		1	20				21			25				25			16				16
77	11						11	24						24	24						24	25						25	17						17
78	11						11	21		1			1	23	24						24	25						25	17						17
79	11						11	2	6	9			6	23	24						24		25					25		17					17
80		11					11		24					24		25					25		25					25		17					17
81	11						11		24					24	25						25	25						25	17						17
82	11						11	24						24	25						25	25						25	17						17
83	11						11	24						24	19	1			1		21		25					25					17		17

APPENDIX 3
Continued

	Erinaceus amurensis (N = 11; M-3, F-6, ?-2; J-2, MA-7, W-2)							*Erinaceus europaeus* (N = 24; M-10, F-8, ?-6; J-2, MA-15, W-7)							*Hemiechinus aethiopicus* (N = 25; M-13, F-11, ?-1; J-3, MA-15, W-7)							*Hemiechinus auritus* (N = 25; M-12, F-4, ?-9; J-8, MA-11, W-6)							*Hemiechinus hypomelas* (N = 19; M-10, F-9; J-4, MA-11, W-4)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
84	9		2				11			19			5	24	9		7			8	24	1		14			7	22			17				17
85	11						11		24					24		25					25		25					25	8	5				2	15
86			11				11			24				24			25				25		1	24				25			17				17
87	11						11		24					24		25					25		25					25		17					17
88		11					11		24					24		21					21		25					25		17					17
89		11					11		22					22		18				1	19	1	17					18		15					15
90							NA							NA		1					1	1						1							NA
91	11						11	24						24	17	2				1	20	25						25	16						16
92	11						11	15	1				1	17	11	6				2	19	25						25	15						15
93	11						11	15	1					16	4	12				2	18	25						25	3	7				4	14
94	11						11	24						24	25						25	25						25	17						17
95	11						11	24						24	23						23	25						25		17					17
96	11						11	24						24	25						25	25						25	17						17
97		11					11		22					22	1	22					23		25					25		17					17
98	3	8					11	15	6				3	24	21	2				1	24	25						25	17						17
99	11						11	24						24	24						24	25						25	17						17
100	1	10					11	5	17				2	24		24	1				25		25					25		15					15
101	6	2	3				11	21	1	1			1	24	2	22	1				25		18	4				22	1	14					15
102	11						11	24						24	7	17					24	17	4				1	22	8	7					15
103	11						11	24						24	23						23	18	3					21	15	1					16
104	9	2					11	24						24	8	25				1	24	22						22		15					15
105			11				11			24				24			25				25			25				25			19				19
106	11						11	24						24	24						24	23						23							NA
107	11						11	22		1			1	24	25						25	8	2	12				22	17	1	1				19
108			11				11		24					24		25					25	1	20	1				22	1	18					19
109			11				11			24				24		25					25			25				25	19						19
110			11				11		22	1				23		25					25		25					25		19					19
111		11					11		24					24	6	12				2	20		25					25		16					16
112	11						11	16	5					21	16	4					20	21	2				1	24	15					1	16
113		11					11		16					16		15					15		21					21	1	14					15
114		11					11		16					16		25					25	1	18					19		16					16
115							NA							NA							NA							NA							NA
116							NA							NA							NA							NA							NA
117	11						11	24						24	25						25	25						25	19						19
118	3	8					11	18	6					24	25						25	25						25	19						19
119		11					11		24					24		25					25		25					25		19					19
120		11					11		24					24		25					25		25					25	17					1	18
121							NA							NA							NA							NA		1					1
122							NA							NA							NA							NA							NA
123	11						11	24						24	24	1					25	1	24					25	16						16
124	5	6					11	20	3	1				24	1	23					24	1	21	1				23	5	10	3				18
125	8	2					10	16	7					23		14	10				24	8	13					21	9	5	3				17
126	6	1	4				11	17		7				24	5	5	12			2	24	10		11				21	1	13	4				18
127	8	3					11	17		5				22	3	2	18				23	6		15				21	4	1	13				18
128	9	2					11	12	12					24	19	3					22	14	7					21	19						19
129	11						11	24						24	21	1					22	25						25	19						19
130			7	3			10			8	14		1	23			6	5			11				25			25			2	2			4
131		11					11		24					24		24					24		25					25		19					19
132			11				11			24				24			24				24		25					25		19					19
133	11						11	24						24		24					24	25						25	19						19
134	11						11		24					24		24					24		25					25		19					19
135		11					11		24					24		24					24		25					25		19					19
136	3	8					11	7	12					19	21						21	7	18					25	10	1	6				17
137	11						11	18	1					19	15	4					19	18	2					20	16	1					17
138		11					11		24					24	1	22					23		25					25		19					19
139	5	1	5				11	15	7	2				24	6	14					20		24	1				25		19					19

APPENDIX 3

Continued

	Erinaceus amurensis (N = 11; M-3, F-6, ?-2; J-2, MA-7, W-2)							*Erinaceus europaeus* (N = 24; M-10, F-8, ?-6; J-2, MA-15, W-7)							*Hemiechinus aethiopicus* (N = 25; M-13, F-11, ?-1; J-3, MA-15, W-7)							*Hemiechinus auritus* (N = 25; M-12, F-4, ?-9; J-8, MA-11, W-6)							*Hemiechinus hypomelas* (N = 19; M-10, F-9; J-4, MA-11, W-4)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
140	4	7					11	11	13					24	3	17					20		25					25	4	13				1	18
141		11					11		24					24		25					25		25					25		19					19
142							NA							NA							NA							NA							NA
143							NA							NA							NA							NA							NA
144							NA							NA							NA							NA							NA
145	11						11	24						24	25						25	25						25	19						19
146	11						11	24						24	25						25	25						25	18						18
147	11						11	24						24	25						25	25						25	19						19
148	11						11		24					24							NA							NA							NA
149		11					11		24					24		25					25			25				25		19					19
150	11						11	24						24	25						25	25						25	19						19
151		11					11	24						24	25						25	25						25	19						19
152							NA							NA							NA							NA							NA
153	1						1		24					24							NA		25					25	19						19
154	7	4					11	24						24	19	3				2	24	25						25	14	3				2	19
155	10						10	24						24	12	6					18	1	24					25	4	7					11
156	10						10	23						23	1	11					12	1						1	2	2					4
157	5	3	2				10		23	1				24	1	19				2	22		25					25		13					13
158		10					10		24					24	3	18					21		25					25		13					13
159	5	3					8		24					24	2	18				4	24		25					25		13					13
160		11					11		24					24	1	24					25	25						25		19					19
161							NA							NA							NA							NA							NA
162							NA							NA							NA							NA							NA
163	11						11	24						24	25						25	25						25	17					1	18
164	11						11	24						24	23	2					25	24						24	19						19
165	5				4	2	11	22				1		23	13	2			9		24					24		24	12	2			1	1	16
166	9		1				10		16	8				24		21	2				23			24				24		10	5				15
167	5	6					11	5	19					24	9	13				3	25		24					24	6	13					19
168	10						10	22						22	3	18				1	22		25					25	1	14					15
169	10						10	22						22	1	3					4							NA		1					1
170	2	8				1	11	3	21					24	2	20					22		25					25	5	10					15
171	11						11	3	21					24		23					23		25					25		15					15
172		11					11		24					24		25					25		25					25		19					19
173							NA							NA							NA							NA							NA
174							NA							NA							NA							NA							NA
175							NA							NA							NA							NA							NA
176							NA							NA							NA							NA							NA
177							NA							NA							NA							NA							NA
178							NA							NA							NA							NA							NA
179							NA							NA							NA							NA							NA
180		11					11		24					24		24					24		25					25		19					19
181		11					11		24					24	10	12					22		25					25		19					19
182	11						11	24						24	1	22					23	25						25	18						18
183		11					11		24					24		24					24		25					25		19					19
184	11						11	24						24	23		1				24	25						25	18		1				19
185		11					11		24					24		23					23		25					25		18					18
186	11						11	24						24	23						23	25						25		18					18
187		11					11	24						24	17	4					21	25						25	16						16
188	11						11		24					24	3	20				1	24		25					25	1	18					19
189	11						11	24						24	8						8							NA	9						9
190	11						11	6	16				1	23	7	17					24		25					25	9	9					18
191	11						11	7						7	8						8							NA	7	3					10
192		11					11	1	23					24	2	19				2	23		21					21	5	9				3	17
193							NA	1						1	1	4					5							NA	6		1			1	8
194		5	6				11		1	23				24	3	21					24			25				25			19				19
195		11					11		24					24		24					24		25					25		19					19

APPENDIX 3

Continued

	Erinaceus amurensis (N = 11; M-3, F-6, ?-2; J-2, MA-7, W-2)							*Erinaceus europaeus* (N = 24; M-10, F-8, ?-6; J-2, MA-15, W-7)							*Hemiechinus aethiopicus* (N = 25; M-13, F-11, ?-1; J-3, MA-15, W-7)							*Hemiechinus auritus* (N = 25; M-12, F-4, ?-9; J-8, MA-11, W-6)							*Hemiechinus hypomelas* (N = 19; M-10, F-9; J-4, MA-11, W-4)						
TS#	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T	0	1	2	3	4	A	T
196		11					11	24						24	24						24	25						25	19						19
197	1	6	3				10		2	21				23		12	10			1	23	1	4	8			1	14		14	2				16
198	11						11	24						24		25					25	25						25		18					18
199	11						11	24						24	25						25	25						25	19						19
200	11						11	24						24			25				25		25					25		16					16
201	11						11	8	11				1	20	25						25	13	4					17	13	3				2	18
202		11					11	24						24		25					25	25						25	18						18
203	11						11	24						24	7	13	1			1	22		25					25	13	3					16
204	11						11	24						24		25					25	11	4				4	19		19					19
205		11					11		24					24		25					25		25					25		19					19
206	11						11		24					24		25					25		25					25		19					19
207	11						11	24						24	25						25	25						25	19						19
208		11					11		24					24	21						21		25					25		18					18
209				11			11				24			24				19			19				25			25				17			17
210		11					11		24					24		24					24		25					25		19					19
211		11					11		1	23				24		15	6				21		25					25		19					19
212		11					11		24					24	1	24					25		1	24				25		19					19
213		10					10	1	9	6			4	20	14	1	7			2	24	3	11				4	18	13	3				1	17
214			11				11		24					24		5	7				12		7	1				8		18					18
215		11					11	1	23					24		14					14		9					9		5					5
216	2	9					11		24					24		16	9				25		9	12				21		4	13				17
217		11					11		24					24	1	23	1				25		25					25		17				1	18
218			10			1	11			21				21	2	16	4			2	24	1		16			1	18	1	2	13			2	18
219	11						11	24						24	25						25	25						25	19						19
220	7	4					11	11	6					17	14	5				1	20		25					25	6	6				1	13
221	11						11		24					24		25					25	25						25		15					15
222	11						11	24						24	25						25	25						25	19						19
223		11					11		24					24		25					25		25					25		19					19
224		11					11		24					24		25					25	24	1					25		5					5
225		11					11		24					24		25					25		25					25		19					19
226	11						11	24						24	25						25	25						25	19						19
227	9	1					10	15	4					19		24					24	1	21					22		16					16
228	11						11		24					24		25					25		25					25		19					19
229	11						11	24						24	25						25	25						25	19						19
230	8	2					10	4	20					24	7	14					21	5	10	1				16	7	9					16
231	1	7					8	4						4	1	4					5	1	3					4	5	1					6
232		11					11		24					24	2	19				1	22	1	24					25		18					18
233							NA							NA							NA							NA							NA
234							NA							NA							NA							NA							NA
235			11				11			23				23		24					24	25						25	1	5	10				16
236				11			11	24						24				21			21	25						25			16				16
237		11					11		24					24		24					24		25					25		19					19
238	11						11		24					24		24					24		25					25		19					19
239		11					11		24					24		23				1	24		25					25		19					19
240	11						11	24						24	24						24	25						25	19						19
241		11					11			24				24		19					19		25					25		19					19
242	1	10					11	6	18					24	2	10	11			1	24		8	12				20		5	12				17
243	11						11	24						24	24						24	25						25	19						19
244			11				11			24				24			20				20			25				25			19				19
245	11						11	23	1					24	20						20	25						25	19						19
246	4	7					11	11	9				1	21		20					20		25					25							NA
247		11					11		24					24		20					20		25					25		19					19
248		11					11	23						23							NA	25						25							NA
249		11					11	15	6				1	22		16					16		25					25							NA

APPENDIX 4

Transformation Series Recovered for Phylogenetic Analysis

Abbreviations: PA# = number assigned to the transformation series for the phylogenetic analysis; TS# = transformation series number; ECHG = *Echinosorex gymnura;* HYLU = *Hylomys suillus;* ATXA = *Atelerix albiventris;* ATXG = *A. algirus;* ERIA = *Erinaceus amurensis;* ERIAE = *E. europaeus;* HEME = *Hemiechinus aethiopicus;* HEMA = *H. auritus;* HEMH = *H. hypomelas.*

			Taxon									
PA#	TS#	Transformation series	ECHG	HLYS	HYLU	ATXA	ATXG	ERIA	ERIAE	HEME	HEMA	HEMH
1	4	I1: (0) present; (1) absent	0/1	0	0	0	0	0	0	0	0	0
2	5	I1, size: (0) normal; (1) enlarged (> I2)	1	0	1	1	1	1	1	1	1	1
3	6	I2: (0) present; (1) absent	0	0	0	0	0	0/1	0	0/1	0	0/1
4	8	I2, size: (0) > I3; (1) = I3; (2) < I3	0	0	0/1	2	2	2	2	2	2	2
5	10	I3: (0) present; (1) absent	0	0	0	0	0	0	0/1	0	0	0
6	24	P1: (0) present; (1) absent	0	1	0/1	1	1	0/1	1	1	1	1
7	27	P1, roots: (0) one; (1) two	0	NA	0/1	NA	NA	0	NA	NA	NA	NA
8	28	P2: (0) present; (1) absent	0	0	0	0	0	0	0/1	0	0	0
9	32	P3: (0) present; (1) absent	0	0	0	0/1	0	0	0/1	0/1	0	0
10	39	P3: (0) normal; (1) reduced	0	1	1	1	1	0	1	1	0/1	0/1
11	42	P3, protocone: (0) ½ the height of the paracone; (1) much smaller	NA	NA	NA	1	1	1	1	NA	0/1	1
12	43	P3, paracone shape: (0) conical; (1) crescentic	0	0	0	0/1/2	0	1	0	0	0	0
13	46	P3, centrocrista (paracone-metacone): (0) present; (1) absent	1	1	1	1	NA	NA	NA	NA	NA	1
14	47	P3, hypocone: (0) present; (1) vestigial or absent	0/1/2	1	1	1	1	1	1	1	1	1
15	54	P4, hypocone: (0) present; (1) absent	0	0	0	0/1	0	0	0	0	0	0/1
16	55	P4, hypocone height: (0) < protocone; (1) ≈ protocone	0	0	0	0	0	0	0	0	0	0
17	56	P4, hypocone gross size: (0) < protocone; (1) ≈ protocone	0	0	1	0/1	0	0	1	0	0	1
18	57	P4, protocone position (to paracone): (0) anterior; (1) posterior	0	0	0	0/1	0	0	0	0	0	0
19	67	P4/M1 position: (0) oblique to tooth row; (1) not	1	1	1	1	1	1	1	1	1	1
20	68	M1, size: (0) largest tooth; (1) not	0	0	0	0	0	0	0	0	0	0
21	69	M1, shape: (0) T-rectangle; (1) A/P-rectangle; (2) quadrate	2	2	1/2	2	2	2	2	2	2	1/2
22	71	M1, lingual roots: (0) separate; (1) fused	0	0	NA	1	1	1	1	1	1	NA
23	72	M1, metaconule: (0) present; (1) absent	0	0	0	0/1	0	0	0	0/1	0	0
24	77	M1, protocone shape: (0) crescentic; (1) conical	0	0	0	0	0	0	0	0	0	0
25	78	M1, protocone position (paracone): (0) anterior; (1) posterior; (2) equivalent	0/1	0	0	0/2	0	0	0	0	0	0
26	88	M1, hypocone height: (0) tall; (1) short; (2) approximately equal	0/1	2	1	1	1	1	1	1	1	1
27	93	M1, hypocone: (0) isolated; (1) attached to other crests/cusps	0/1	1	1	1	1	1	1	0/1	1	1
28	94	M1, metastyle: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0
29	95	M1, metastyle apex (cone itself): (0) high; (1) low	1	0	1	1	1	0	0	0	0	1
30	96	M1, metastyle position (relative to metacone): (0) labial; (1) posterior	0	0	0	0	0	0	0	0	0	0
31	99	M1, metacrista: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0
32	105	M2, shape: (0) T-rectangle; (1) A/P-rectangle; (2) quadrate	2	2	2	2	2	2	2	2	2	2
33	106	M2, lingual roots: (0) fused; (1) separate	1	1	NA	NA	0	0	0	0	0	NA
34	109	M2, protocone size: (0) = paracone; (1) larger; (2) smaller	1	1/2	1	NA	1	2	2	1	2	0
35	111	M2, hypocone: (0) isolated; (1) not	0/1	1	1	1	1	1	1	0/1	1	1
36	117	M2, metastyle: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0

APPENDIX 4

Continued

			Taxon									
PA#	TS#	Transformation series	ECHG	HLYS	HYLU	ATXA	ATXG	ERIA	ERIAE	HEME	HEMA	HEMH
37	121	M2, posthypocrista: (0) to postcingulum; (1) not	NA	0	NA	NA	NA	NA	NA	NA	NA	NA
38	129	M3: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0
39	133	M3, protocone size: (0) large; (1) small	0	0	1	0	0	0	0	1	0	0
40	134	M3, main cusps: (0) equally developed; (1) not	1	0	0	0/1	0	0	1	1	1	1
41	135	M3, metaconule: (0) present; (1) absent	0/1	1	1	1	1	1	1	1	1	1
42	141	i1: (0) present; (1) absent	0	0/1	0	1	1	1	1	1	1	1
43	142	i1, size: (0) = i2; (1) > i2	0	1	1	NA	NA	NA	NA	NA	NA	NA
44	143	i1, shape: (0) spatulate; (1) conical	0	0	0	NA	NA	NA	NA	NA	NA	NA
45	144	i1, root: (0) short; (1) long	1	1	1	NA	NA	NA	NA	NA	NA	NA
46	145	i2: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0
47	146	i2: (0) enlarged; (1) reduced	0	1	0	0	0	0	0	0	0	0
48	147	i2, shape: (0) spatulate; (1) conical	0	0	0	0	0	0	0	0	0	0
49	149	i2, anterior midline crest: (0) ends posterior to protoconid; (1) not	2	0/1	NA	NA	1	1	1	1	2	1
50	150	i3: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0
51	151	i3, size (relative to i1/i2): (0) smaller; (1) equal; (2) larger	0	0/2	0	0	0	1	0	0	0	0
52	152	lower canine, size: (0) = p1; (1) > p1	1	NA	1	NA	NA	NA	NA	NA	NA	NA
53	153	lower canine, morphology: (0) like i2/p2; (1) not	1	0/1	1	0	1	1	1	1	1	0
54	160	p1: (0) present; (1) absent	0/1	1	0	1	1	1	1	0/1	0	1
55	161	p1, roots: (0) single; (1) partially divided	0	NA	0	NA	NA	NA	NA	NA	NA	NA
56	163	p2: (0) present; (1) absent	0/1	0	0	0	0	0	0	0	0	0/1
57	164	p2, roots: (0) one; (1) two	0	0	0	0	0	0	0	0/1	0	0
58	172	p3: (0) present; (1) absent	0	0	0	1	1	1	1	1	1	1
59	173	p3, roots: (0) two; (1) one; (2) two fused	0	1	0/1/2	NA	NA	NA	NA	NA	NA	NA
60	175	p3, cusps: (0) two; (1) one; (2) three	1	1	0/1/2	NA	NA	NA	NA	NA	NA	NA
61	176	p3, posterior margin: (0) wide; (1) narrow	0	1	1	NA	NA	NA	NA	NA	NA	NA
62	177	p3, metaconid crest: (0) present; (1) absent	NA	0/1	1	NA	NA	NA	NA	NA	NA	NA
63	178	p3, posterolingual cusp: (0) prominent; (1) weak/absent	1	1	0/1	NA	NA	NA	NA	NA	NA	NA
64	179	p3, cingulum: (0) present; (1) absent; (2) partial	0/1/2	1	1	NA	NA	NA	NA	NA	NA	NA
65	180	p4, talonid: (0) elongated; (1) short	1	1	1	1	1	1	1	1	1	1
66	181	p4, talonid: (0) greatest breadth of tooth; (1) not	0	1	0	1	1	1	1	0/1	1	1
67	183	p4, posterolabial cuspule to protoconid: (0) present; (1) absent	0/1	1	1	1	1	1	1	1	1	1
68	185	p4, paraconid height: (0) = protoconid; (1) < protoconid	1	NA	1	1	1	1	1	1	1	1
69	189	p4, protoconid size: (0) > metaconid; (1) not	0	NA	0	0	NA	0	0	0	NA	0
70	191	p4, metaconid size: (0) small; (1) large	0/1	NA	0	0	NA	0	0	0	NA	0/1
71	195	p4, size: (0) = m1; (1) smaller	1	1	1	1	1	1	1	1	1	1
72	196	prevallid shear: (0) present; (1) absent	0	0	0	0	0/1	1	0	0	0	0
73	198	m1, trigonids: (0) high; (1) low	NA	0	1	0	0	0	0	1	0	1
74	205	m1, lingual wall: (0) markedly concave; (1) not	1	1	1	1	1	1	1	1	1	1
75	206	m1, talonid: (0) enclosed lingually by entocristid; (1) not	1	1	1	NA	1	0	1	1	1	1
76	207	m1, talonid: (0) opens posteriorly; (1) closed	0	0	0	0	0	0	0	0	0	0
77	208	m1, hypoconid: (0) isolated; (1) not	0	1	0	0	1	1	1	0	1	1
78	209	m1, entoconid size: (0) > hypoconid; (1) > paraconid; (2) = cusps; (3) > than both	2	0	0	0/3	2	3	3	0	3	3

APPENDIX 4
Continued

			Taxon									
PA#	TS#	Transformation series	ECHG	HLYS	HYLU	ATXA	ATXG	ERIA	ERIAE	HEME	HEMA	HEMH
79	210	m1, entostylid: (0) present; (1) absent	1	1	1	1	1	1	1	1	1	1
80	219	m1, paraconid to protoconid: (0) lingual; (1) labial; (2) aligned	0	0	0	0/1	0	0	0	0	0	0
81	220	m1, paracristid: (0) terminates at mid-anterior; (1) not	1	1	1	1	0/1	0	1	1	0	1
82	222	m2, size: (0) shorter than m1; (1) larger than m1	0	0	0	NA	0	0	0	0	0	0
83	223	m2 trigonids: (0) high, short talonid; (1) low, expanded talonid	1	1	1	1	1	1	1	1	1	1
84	225	m2, paraconid: (0) present; (1) absent	1	1	1	1	1	1	1	1	1	1
85	226	m2, paraconid shelf: (0) present; (1) absent	0	0	0	NA	0	0	0	0	0	0
86	228	m2, paracristid lingual extension (to m1): (0) equal; (1) labial; (2) lingual	1	1	1	0/1/2	1	0	1	1	1	1
87	229	m2, entostylid: (0) absent; (1) weak; (2) strong	0	0	0	0	0	0	0	0	0	0
88	233	m2, paraconid to metaconid: (0) lingual; (1) labial; (2) aligned	1/2	NA	NA	NA	NA	NA	NA	NA	NA	NA
89	234	m2, paraconid to protoconid: (0) lingual; (1) labial; (2) aligned	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
90	235	m2, hypoconid to protoconid: (0) lingual; (1) labial; (2) aligned	2	1	1	0	2	2	2	1	0	0/1/2
91	236	m2, entoconid size: (0) = protoconid; (1) tallest cusp; (2) = hypoconid; (3) = metaconid	2	0	0	2/3	0	3	0	3	0	2
92	237	m2, talonid: (0) posteriorly narrow; (1) not	1	1	1	1	1	1	1	1	1	1
93	238	m2, talonid basin: (0) lingually enclosed; (1) not	1	1	1	1	1	0	1	1	1	1
94	240	m2, cristid obliqua contact point: (0) base of protoconid; (1) higher	0	0	0	0	0	0	0	0	0	0
95	241	m2, entocristid: (0) high; (1) low; (2) absent	1/2	2	1	2	1	1	2	1	1	1
96	243	m3: (0) present; (1) absent	0	0	0	0	0	0	0	0	0	0
97	244	m3, paraconid: (0) swollen; (1) normal; (2) absent	2	2	2	2	2	2	2	2	2	2
98	245	m3, paraconid shelf: (0) present; (1) absent	0	0	0	1	0	0	0/1	0	0	0
99	247	m3, talonid: (0) present; (1) absent	0	0	0	1	1	1	1	1	1	1
100	248	m3, trigonids: (0) high; (1) short; (2) low expanded	1	0	1	NA	1	1	0	NA	0	NA

APPENDIX 5

Phylogenetic Analysis of Data Set A

(a) Data matrix and (b) results of analysis 1. For transformation series included in the analysis (PA#), refer to appendix 4.

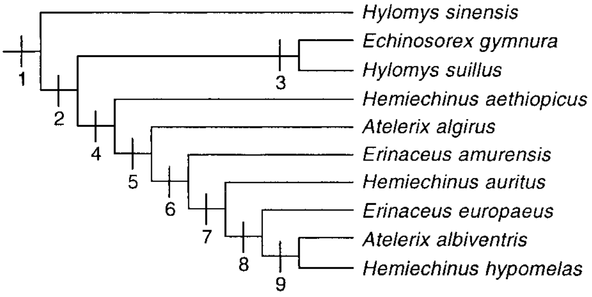
(a) Matrix of 100 transformation series recovered from discrete dental analysis (refer to appendix 4). All characters are polarized according to outgroups (PA# 16, 17, 31, 85, and 98 are unpolarized); all are unordered.

Echinosorex gymnurus	{01}100000000 ?01{012}000010 2000{01}{01}{01}010 0211{01}0?001 {01}000100020 011{01}0{01}0001 0?1{012}10{01}10{01} 10?1100210 1011010{12}02 2110{12}02001
Hylomys sinensis	000001?001 ?011000010 2000021000 021{12}100000 1{01}101010{01}0 {02}?{01}1?00011 1{01}11111??? 1001101010 1011010??1 0110202000
Hylomys suillus	010{01}0{01}{01}001 ?011001010 {12}?00011010 02?110?010 1010100?0 01100000{012}{012} 11{01}1101100 1011100010 1011010??1 0110102001
Atelerix albiventris	010201?0{01}1 1{012}11{01}0{01}{01}10 21{01}0{02}11010 02??10?00{01} 11???000?0 0?01?001?? ????111100 1001?00{03}1{01} 1?11?{012}0??0 {23}11020211?
Atelerix algirus	010201?001 10?1000010 2100011010 020110?000 11???00010 0?11?001?? ????1111?? 1{01}01101210 {01}011010??2 0110102011
Erinaceus amurensis	01{01}20{01}0000 11?1000010 2100011000 020210?000 11???00010 1?11?001?? ????111100 1101001310 0011000??2 3100102011
Erinaceus europaeus	0102{01}1?{01}{01}1 10?1001010 2100011000 020210?001 11???00010 0?11?001?? ????111100 1001101310 1011010??2 0110202{01}10
Hemiechinus aethiopicus	01{01}201?0{01}1 ?0?1000010 21{01}001{01}000 0201{01}0?011 11???00010 0?1{01}?0{01}1?? ????1{01}1100 1011100010 1011010??1 311010201?
Hemiechinus auritus	010201?00{01} {01}0?1000010 2100011000 020210?001 11???00020 0?10?001?? ????1111?? 1001101310 0011010??0 0110102010
Hemiechinus hypomelas	01{01}201?00{01} 1011{01}01010 {12}?00011010 02?010?001 11???00010 0?01?{01}01?? ????11110{01} 1011101310 1011010??{012} 211010201?
Outgroups: Tenrecoids	0{01}0{01}01?0{01}0 10111??111 321??????? ?32????0?? ?{01}{01}000{01}{01}20 {02}?{01}{01}{02}{01}0{01}{01}0 1{01}{01}{12}11{01}10{01} 11{01}02?{02}410 1100?{02}0{12}0{23} 42??201?10
Soricoids	0{01}{01}1{01}01001 20111??21{01} {23}2102{13}100{01} ?20{02}{12}{02}10{01}{01} 10{01}0{01}010?0 {01}1110{01}0001 1?1{01}111??2 1110111210 ?120?{02}020{012} 311{01}201?02

APPENDIX 5

Continued

(b) Phylogenetic Analysis 1, Tree Number 1: Length = 105; consistency index (CI) = 0.676; homoplasy index (HI) = 0.324; CI excluding uninformative characters = 0.634; HI excluding uninformative characters = 0.366; retention index (RI) = 0.528; rescaled consistency index (RC) = 0.357.



Apomorphy list

Branch	PA#	Steps	CI	Change
node 1 → node 2	5	1	1.000	0 → 1
	50	1	1.000	1 ⇒ 0
	98	1	0.333	2 ⇒ 1
	103	1	0.667	0 ⇒ 1
node 2 → node 3	9	1	0.500	1 → 0
	32	1	0.333	0 ⇒ 1
	52	1	0.333	1 → 2
	57	1	0.500	1 → 0
	69	1	1.000	1 ⇒ 0
node 3 → *Echinosorex gymnurus*	13	1	0.333	1 ⇒ 0
	43	1	0.333	0 ⇒ 1
	46	1	1.000	1 ⇒ 0
	64	1	1.000	1 ⇒ 0
	81	1	0.600	0 → 2
	93	1	0.400	1 → 2
	94	1	0.500	0 ⇒ 2
node 3 → *Hylomys suillus*	20	1	0.500	0 ⇒ 1
	42	1	0.500	0 ⇒ 1
node 2 → node 4	7	1	1.000	0 ⇒ 2
	25	1	1.000	0 ⇒ 1
	36	1	0.667	1 → 0
	45	1	1.000	0 ⇒ 1
	61	1	1.000	0 ⇒ 1
	102	1	0.500	0 ⇒ 1
node 4 → node 5	76	1	0.333	1 ⇒ 0
	80	1	0.250	0 → 1
	81	1	0.600	0 → 2
	84	1	0.500	1 → 0
	93	1	0.400	1 → 2
node 5 → node 6	37	1	0.667	1 ⇒ 2
	81	1	0.600	2 → 3
node 6 → node 7	43	1	0.333	0 ⇒ 1
	93	1	0.400	2 → 0
	103	1	0.667	1 ⇒ 0
node 7 → node 8	20	1	0.500	0 ⇒ 1
	84	1	0.500	0 → 1
	98	1	0.333	1 → 2
node 8 → node 9	32	1	0.333	0 ⇒ 1
	37	1	0.667	2 → 0
	56	1	1.000	1 ⇒ 0
	94	1	0.500	0 ⇒ 2
node 9 → *Atelerix albiventris*	80	1	0.250	1 ⇒ 0
	101	1	1.000	0 ⇒ 1
node 9 → *Hemiechinus hypomelas*	76	1	0.333	0 ⇒ 1
	98	1	0.333	2 → 1
node 8 → *Erinaceus europaeus*	93	1	0.400	0 → 2
node 7 → *Hemiechinus auritus*	52	1	0.333	1 ⇒ 2
	57	1	0.500	1 ⇒ 0
node 6 → *Erinaceus amurensis*	13	1	0.333	1 ⇒ 0
	15	1	1.000	0 ⇒ 1
	54	1	1.000	0 ⇒ 1
	75	1	0.500	0 ⇒ 1
	78	1	1.000	1 ⇒ 0
	89	1	0.500	1 ⇒ 0
	94	1	0.500	0 ⇒ 3
	96	1	1.000	1 ⇒ 0
node 5 → *Atelerix algirus*	32	1	0.333	0 ⇒ 1
node 4 → *Hemiechinus aethiopicus*	42	1	0.500	0 ⇒ 1
	43	1	0.333	0 ⇒ 1
	94	1	0.500	0 ⇒ 3
node 1 → *Hylomys sinensis*	29	1	1.000	1 ⇒ 2
	62	1	1.000	0 ⇒ 1
	76	1	0.333	1 ⇒ 0
	80	1	0.250	0 → 1

APPENDIX 6

Phylogentetic Analysis of Data Set B

The 29 discrete dental characters analyzed (a) are listed, along with the accompanying matrix (b) extracted from Gould (1995). The first apomorphy list (c) was generated from tree 1 in analysis 2a (19 extant taxa). The second apomorphy list (d) was generated from tree 1 in analysis 2b (only the 10 taxa considered in analysis 1 [see appendix 5] are treated in this analysis). Numbers in brackets [] refer to original character numbers in Gould (1995); TS# = transformation series number (see appendix 1); * = transformations not exactly as in Gould (1995); for transformation series included in the analysis (PA#), refer to appendix 4.

(a) Dental characters analyzed

1	[60]	TS# 4	i1: (0) present, enlarged; (1) present, small; (2) absent.
2	[61]	TS# *5	i2 relative size: (0) greatly enlarged; (1) nearly equal to other incisors; (2) smaller than other incisors.
3	[62]	TS# 8	I2: (0) greater than I3; (1) less than or equal to I3.
4	[63]	TS# 11	I3, number of roots: (0) one root; (1) two roots, separate; (2) two roots, fused.
5	[64]	TS# 18	C1 size: (0) significantly larger than adjacent post-canine teeth; (1) slightly larger than post-canine teeth; (2) approximately equal in size to adjacent postcanine teeth.
6	[65]	TS# 19	C1, number of roots: (0) two roots; (1) one root or two roots fused.
7	[66]	TS# 20	C1, relative size: (0) equal to, or larger than I3; (1) subequal or slightly smaller than I3.
8	[67]	TS# 152	c1, relative size: (0) approximately equal to, or smaller than P1; (1) significantly larger than p1.
9	[68]	TS# 24	P1: (0) present; (1) absent.
10	[69]	TS# 160	p1: (0) present; (1) absent.
11	[70]	TS# *162	p2: (0) moderate size, two roots; (1) small, peglike, procumbent, one root; (1) absent.
12	[71]	TS# 13	P2 roots: (0) two roots; (1) one root or two roots well fused; (2) absent.
13	[72]	TS# 173	p3: (0) two roots present; larger in size than p2; (1) one root present, nearly equal in size to P; (2) absent.
14	[73]	TS# 34	P3 lingual lobe (= protocone): (0) present, well developed; (1) vestigial or absent.
15	[74]	TS# 39	P3 size: (0) normal; (1) reduced.
16	[75]	TS# 52	P3 roots: (0) three roots; (1) fewer than three roots.
17	[76]	TS# 47	P3 hypocone: (0) absent; (1) present.
18	[77]	TS# 180	p4: (0) with an elongate talonid and talonid basin; (1) with a short, bicuspid or unicuspid heel.
19	[78]	TS# 53	P4 shape, and hypocone: (0) quadrate, hypocone present; (1) triangular, hypocone absent or vestigial.
20	[79]	TS# 59	P4 lingual roots: (0) one lingual root; (1) two unfused roots; (2) two lingual roots, fused.
21	[80]	TS# *198	Trigonids on lower molars: (0) high (significantly taller than talonid), talonid short or vestigial; (1) low trigonid (nearly equal in height with talonid), talonid expanded, large.
22	[81]	TS# *198	m1: (0) trigonid moderate; (1) marked elongation of prevallid shear on m1.
23	[82]	TS# 71	M1 lingual roots: (0) separate; (1) fused for most of the length.
24	[83]	TS# *216/*262	Distinct ectocingulum on labial side of M1 and M2: (0) absent; (1) present.
25	[84]	TS# 129	M3: (0) present; (1) absent.
26	[85]	TS# 130	M3 roots: (0) three roots; (1) two roots.
27	[86]	TS# 131	M3 metastylar spur (referred to as a hypocone): (0) absent or weak; (1) present, well developed on buccal side.
28	[87]	TS# 132	M3 metacone conditions: (0) well developed; (1) small; (2) absent.
29	[88]	TS# 247	m3 talonid: (0) present; (1) absent.

(b) Data matrix extracted from Gould (1995)

Echinosorex gymnurus	1100000100	1100000111	110100110
Podogymnura aureospinula	1110000111	1101000111	110100110
Podogymnura truei	1110000111	1101000111	110100110
Hylomys sinensis	0100201011	1111110111	110100110
Hylomys suillus	1100100000	1111110111	110100110
Hylomys hainanensis	1100100001	1111110111	110100110
Hemiechinus aethiopicus	2211200011	1121110112	111101021
Hemiechinus hypomelas	2211200011	1120100112	111101021

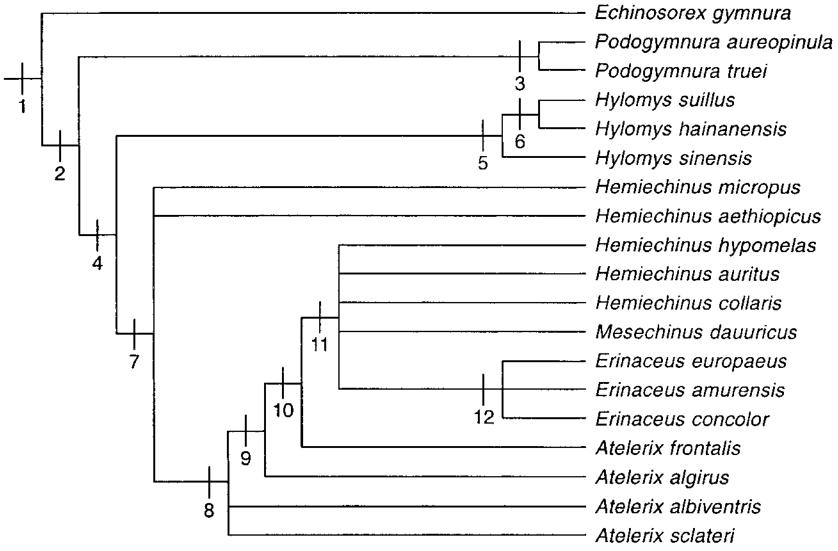
APPENDIX 6

Continued

(b) Data matrix extracted from Gould (1995) (*continued*)

Hemiechinus micropus	2211200011	1121110112	111101021
Hemiechinus auritus	2211200011	1120100112	111101021
Hemiechinus collaris	2211200011	1120100112	111101021
Mesechinus dauuricus	2211200011	1120100112	111101021
Erinaceus amurensis	2212210011	1120100112	111101021
Erinaceus concolor	2212210011	1120100112	111101021
Erinaceus europaeus	2212210011	1120100112	111101021
Atelerix frontalis	2211200011	1020100112	111101021
Atelerix algirus	2211200011	1020110112	111101021
Atelerix albiventris	2211200011	1021110112	111101021
Atelerix sclateri	2211200011	1021110112	111101021
Outgroups: Tenrecoids	11000?0010	0000000100	0?0000000{01}
Soricoids	11000?0010	{12}001000100	0?0000000{01}

(c) Phylogenetic Analysis 2a, Tree Number 1: Length = 41; consistency index (CI) = 0.756; homoplasy index (HI) = 0.244; CI excluding uninformative characters = 0.744; HI excluding uninformative characters = 0.256; retention index (RI) = 0.917; rescaled consistency index (RC) = 0.694.



Apomorphy list

Branch	PA#	Steps	CI	Change
node 1 → *Echinosorex*	9	1	0.500	1 ⇒ 0
node 1 → node 2	3	1	0.500	0 → 1
	10	1	0.500	0 ⇒ 1
	14	1	0.333	0 → 1
node 2 → node 3	8	1	0.750	0 ⇒ 1
node 2 → node 4	5	1	1.000	0 ⇒ 2
	8	1	0.500	1 → 0
	13	1	1.000	0 ⇒ 1
	15	1	1.000	0 ⇒ 1
	16	1	0.500	0 ⇒ 1

Branch	PA#	Steps	CI	Change
node 4 → node 5	3	1	0.500	1 → 0
node 5 → *Hylomys sinensis*	1	1	1.000	1 ⇒ 0
	7	1	1.000	0 ⇒ 1
node 5 → node 6	5	1	1.000	2 ⇒ 1
	9	1	0.500	1 ⇒ 0
node 6 → *Hylomys suillus*	10	1	0.500	1 ⇒ 0
node 4 → node 7	1	1	1.000	1 ⇒ 2
	2	1	1.000	1 ⇒ 2
	4	1	1.000	0 ⇒ 1
	13	1	1.000	1 ⇒ 2

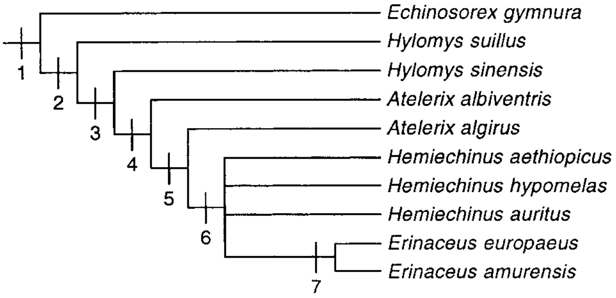
APPENDIX 6
Continued

(c) Phylogenetic Analysis 2a: Apomorphy lists (*continued*)

Branch	PA#	Steps	CI	Change
node 4 → node 7 (*contd.*)	20	1	1.000	1 ⇒ 2
	23	1	1.000	0 ⇒ 1
	26	1	1.000	0 ⇒ 1
	27	1	0.500	1 ⇒ 0
	28	1	1.000	1 ⇒ 2
	29	1	1.000	0 ⇒ 1

Branch	PA#	Steps	CI	Change
node 7 → node 8	12	1	0.333	1 ⇒ 0
node 8 → node 9	14	1	0.333	1 ⇒ 0
node 9 → node 10	16	1	0.500	1 ⇒ 0
node 10 → node 11	12	1	0.333	0 ⇒ 1
node 11 → node 12	4	1	1.000	1 ⇒ 2
	6	1	1.000	0 ⇒ 1

(d) Phylogenetic Analysis 2b, Tree Number 1: Length = 38; consistency index (CI) = 0.816; homoplasy index (HI) = 0.184; CI excluding uninformative characters = 0.800; HI excluding uninformative characters = 0.200; retention index (RI) = 0.897; rescaled consistency index (RC) = 0.732.



Apomorphy list

Branch	PA#	Steps	CI	Change
node 1 → *Echinosorex*	8	1	1.000	0 ⇒ 1
node 1 → node 2	5	1	1.000	0 → 1
	13	1	1.000	0 ⇒ 1
	14	1	0.333	0 → 1
	15	1	1.000	0 ⇒ 1
	16	1	0.500	0 ⇒ 1
node 2 → node 3	5	1	1.000	1 → 2
	9	1	0.500	0 → 1
	10	1	1.000	0 ⇒ 1
node 3 → *Hylomys sinensis*	1	1	1.000	1 ⇒ 0
	7	1	1.000	0 ⇒ 1
node 3 → node 4	1	1	1.000	1 ⇒ 2
	2	1	1.000	1 ⇒ 2
	3	1	1.000	0 ⇒ 1
	4	1	1.000	0 ⇒ 1
	13	1	1.000	1 ⇒ 2
	20	1	1.000	1 ⇒ 2
	23	1	1.000	0 ⇒ 1
	26	1	1.000	0 ⇒ 1
	27	1	0.500	1 ⇒ 0
	28	1	1.000	1 ⇒ 2
	29	1	1.000	0 ⇒ 1

Branch	PA#	Steps	CI	Change
node 4 → node 5	14	1	0.333	1 ⇒ 0
node 5 → node 6	16	1	0.500	1 ⇒ 0
node 6 → node 7	4	1	1.000	1 ⇒ 2
	6	1	1.000	0 ⇒ 1
node 5 → *Atelerix algirus*	12	1	0.333	1 ⇒ 0
node 4 → *Atelerix albiventris*	12	1	0.333	1 ⇒ 0