# american museum <br> Novitates 

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024 Number 3340, 52 pp., 9 figures, 2 tables, 6 appendices June 22, 2001

# 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 recon-
struct 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. $\mathrm{A}=$ Erinaceidae; B $=$ Hylomyinae; $\mathrm{C}=$ Erinaceinae; $\mathrm{D}=$ 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 lit-erature-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; $\mathrm{ms}=$ mesostyle; msd $=$ mesoconid; $\mathrm{mt}=$ metastyle; $\mathrm{mtl}=$ metaconule; $\mathrm{pa}=$ paracone; pac $=$ paracrista (or preparacrista); pacd $=$ postparacrista; pad $=$ paraconid; pag $=$ paracingulum; pcg $=$ precingulum; pmlc $=$ premetaconule crista; pplc $=$ preparaconule crista; pprc $=$ preprotocrista; $\mathrm{pr}=$ protocone; pred $=$ 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; $\mathrm{tb}=$ trigon basin; $\mathrm{tdb}=$ trigonid basin; $\mathrm{tlb}=$ 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 p 4 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 characterstate 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 $0 \rightarrow 4$. 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 de-
scribed 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 spe-
cies. 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.

| Taxon (sample size) | Missing | Polymorphic | Asymmetric | Covariance |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 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 premaxil-lary-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 trans-
formation 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

TS.7. I2, posterior cuspules:


TS. 37 P3, posterior cingulum:


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 8 b , the distribution of the P 3 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 ( P 3 is reduced, dP 3 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, 617, 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 m 2 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 ( $=\mathbf{d}$ ) versus Permanent Dentition, Wear Stage ( $=w$ ), and Geographic Variation ( $=\mathrm{g}$ )
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; $\mathrm{HEMA}=H$. auritus; $\mathrm{HEMH}=H$. hypomelas .

| Transformation series | Taxon |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | ECHG | HYLU | ATXA | ATXG | ERIA | ERIAE | HEME | HEMA | HEMH |
| Polymorphism: Deciduous vs. |  |  |  |  |  |  |  |  |  |
| Permanent Dentition (total $=4$ ) |  |  |  |  |  |  |  |  |  |
| 16. 13, 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. p 2 , cingulum |  |  | w |  |  |  |  |  |  |
| 169. p 2 , anterior midline crest |  |  |  |  |  |  | w |  |  |
| 214. ml, 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
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 tax-
onomic 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 analysisI1 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 2 a includes only those 10 taxa reviewed in this analysis. PA $2 b$ 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: $\mathrm{CI}=$ consistency index; RI $=$ retention index; $\mathrm{RC}=$ 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): $\mathrm{CI}=0.634 ; \mathrm{RI}=0.528$; and RC $=0.357$; the strict consensus and the Adams tree are depicted in figs. 9 a 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; $\mathrm{CI}=$ 0.816 , and 0.80 (excluding uninformative characters); RI $=0.897 ; \mathrm{RC}=0.732$. 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 ; $\mathrm{CI}=0.756$ and 0.744 (excluding uninformative characters); $\mathrm{RI}=0.917 ; \mathrm{RC}=0.694$. 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. $9 \mathrm{a}, \mathrm{c}$, 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), de-
tailed 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 DawsonSaunder, 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,
 dix 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 $2 \mathrm{a} / \mathrm{b}$ ) 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 wellsupported 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 mam-
mals (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 in-tra- 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 materiala 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.

## ACKNOWLEDGMENTS

I thank the following individuals for their invaluable contributions to this investigation: William R. Downs for helping me to collect much of the discrete dental data and for his
willingness to discuss many of the issues presented herein; Leslie F. Marcus for his guidance in the statistical analyses conducted in this investigation; and J. Peter Meyer, for helping me compile some of these data and for his support throughout the duration of this project.

Without the aid and support of the Division of Vertebrate Paleontology at the American Museum of Natural History (AMNH), this work would not have been possible. I thank the following funding agencies for facilitating this study: Smithsonian Collections Study Grant, and the Theodore Roosevelt Memorial Fund, sponsored at the AMNH. I would also like to thank the departments of mammalogy at these institutions for making their collections available for study. I specifically want to thank Linda Gordon at the Smithsonian Institution who was most helpful during the many months of data collection in the Mammal Division.

Much appreciation goes to Marilyn Fox for molding and casting the extant teeth, Lorraine Meeker for photographing and mounting them, and to Tom W. French for contributing to some of the literature reviewed.

Thanks go to Darrel R. Frost, Leslie F. Marcus, Malcolm C. McKenna, Marc A. Carrasco, John Wible, and John Hunter for their comments on early drafts of this manuscript.

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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. II: (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. 13, 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. Pl, 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. P 4 , 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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Continued
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 (Mathew, 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. Ml, 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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Continued
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, 199I; 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. il, 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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Continued
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. pl, 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. p 3 , size relative to p 2 : ( 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 ml : (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. ml, 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. ml, metaconid position: (0) anterior to protoconid; (1) not (Matthew, 1929; Rich, 1981; Butler, 1948).
202. ml , metaconid height relative to paraconid: ( 0 ) greater; (1) approximately equal or smaller (Black et al., 1980).
203. ml, paraconid: (0) large; (1) small; (2) absent (Rich and Rasmussen, 1973; Rich, 1981).
204. ml, 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. ml, 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. ml, hypoconid: (0) isolated; (1) not (Black et al., 1980).

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Continued
209. ml , 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. ml, entostylid: (0) present; (1) absent (Black et al., 1980).
211. ml , entocristid: (0) high; (1) low; (2) absent (Rich, 1981 ; Butler, 1948; Storch and Qiu, 1991).
212. ml, hypoconulid: (0) present; (1) absent (Butler, 1948).
213. ml , cristid obliqua orientation: (0) antero-posteriorly directed; (1) inclined; (2) absent (Black et al., 1980).
214. ml, 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. ml, entoconulid: (0) present; (1) absent (Black et al., 1980).
218. ml , paraconid position relative to the metaconid: (0) lingual; (1) labial; (2) aligned.
219. m 1 , paraconid position relative to the protoconid: $(0)$ lingual; (1) labial; (2) aligned.
220. m1, paracristid: (0) horizontal; (1) attenuated.
221. $m 1$, paracristid lingual extension: (0) terminates at midanterior of tooth; (1) extends to lingual border (Rich, 1981; Butler, 1948).
222. m 2 , size relative to $\mathrm{ml}:(0)$ smaller; (1) larger (Matthew, 1929; Stevens, 1977; Rich, 1981; Butler, 1948).
223. m 2 , trigonids: ( 0 ) high, short talonid; (1) low, expanded talonid (Stevens, 1977; Rich, 1981).
224. m 2 , 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. m 2 , paraconid shelf: (0) present; (1) absent.
227. m 2 , paraconid swelling: (0) present; (1) absent (Rich, 1981).
228. m2, paracristid lingual extension: (0) approximately equal to ml ; (1) not; (2) more lingual than ml (Butler, 1948).
229. m 2 , entostylid: (0) absent; (1) weak; (2) strong (Black et al., 1980).
230. m 2 , 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. m 2 , entoconulid: (0) present; (1) absent.
233. m 2 , paraconid position relative to the metaconid: $(0)$ lingual; (1) labial; (2) aligned.
234. m 2 , paraconid position relative to the protoconid: ( 0 ) lingual; (1) labial; (2) aligned.
235. m 2 , hypoconid position relative to the protoconid: $(0)$ lingual; (1) labial; (2) aligned (Rich, 1981).
236. m 2 , 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. m 2 , talonid: (0) posteriorly narrow; (1) not (Matthew, 1929; Rich, 1981).
238. m2, talonid basin: (0) lingually enclosed; (1) not.
239. m 2 , hypoconulid: (0) present; (1) absent (Rich, 1981; Black et al., 1980).
240. m 2 , 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 (Koemer, 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: $\mathrm{AMNH}=$ 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

## Erinaceas

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 | $?$ | Germany, Heidelburg |
|  | $(12244)$ |  |  |
| USNM | 85619 | M | Germany, Braunschweig |
| USNM | 86923 | F | Ireland, Glenmore County |
| USNM | 36034 | F | England |
|  | $(20807)$ |  |  |
| USNM | 174660 | M | Channel Islands, Guernsey |
| USNM | 794 | $?$ | England |
| USNM | 795 | $?$ | England |
| USNM | 34959 | M | England (Nat. Zool. Park) |
|  | $(19246)$ |  |  |
| USNM | 34960 | F | England (Nat. Zool. Park) |
|  | $(19247)$ |  |  |
| 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. |


| 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. |


| 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) (continued) |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Hylomys sinenesis (25) |  |  |  | AMNH | 44268 | M | China, Taiping-pu, Yun-nan Prov. |
| AMNH | 115505 | F | N. Burma, Kachin Prov. | AMNH | 44270 | F | China, Taiping-pu, Yun-nan Prov. |
| AMNH | 115506 | M | N. Burma, Kachin Prov. | AMNH | 44271 | M | China, Taiping-pu, Yun-nan Prov. |
| AMNH | 115508 | F | N. Burma, Kachin Prov. | AMNH | 57199 | ? | China, Yun-nan Prov. |
| AMNH | 115509 | F | N. Burma, Kachin Prov. |  |  |  |  |
| AMNH | 115510 | M | N. Burma, Kachin Prov. | Hylomys | suillus (1 |  |  |
| AMNH | 115511 | F | N. Burma, Kachin Prov. | USNM | 481278 | F | Java |
| AMNH | 115512 | M | N. Burma, Kachin Prov. | USNM | 481279 | F | Java |
| AMNH | 115514 | M | N. Burma, Kachin Prov. | USNM | 481280 | F | Java |
| AMNH | 115515 | F | N. Burma, Kachin Prov. | USNM | 481281 | F | Java |
| AMNH | 115516 | F | N. Burma, Kachin Prov. | USNM | 481283 | F | Java |
| AMNH | 115517 | M | N. Burma, Kachin Prov. | USNM | 481284 | F | Java |
| AMNH | 115518 | M | N. Burma, Kachin Prov. | USNM | 481285 | F | Java |
| AMNH | 115519 | M | N. Burma, Kachin Prov. | USNM | 481286 | F | Java |
| AMNH | 115520 | M | N. Burma, Kachin Prov. | USNM | 481287 | M | Java |
| AMNH | 115522 | F | N. Burma, Kachin Prov. | USNM | 481288 | M | Java |
| AMNH | 115523 | M | N. Burma, Kachin Prov. | USNM | 481289 | F | Java |
| AMNH | 115524 | M | N. Burma, Kachin Prov. | USNM | 481290 | F | Java |
| AMNH | 115525 | M | N. Burma, Kachin Prov. | USNM | 521659 | M | Java |
| AMNH | 44248 | F | China, Mu-cheng, Yun-nan Prov. | USNM | 521660 | M | Java |
| AMNH | 44249 | M | China, Mu-cheng, Yun-nan Prov. | USNM | 521661 | M | Java |
| AMNH | 44267 | M | China, Taiping-pu, Yun-nan Prov. | USNM | 155660 | F | Java |

## APPENDIX 3

Frequency Distribution of 246 Transformation Series across 10 Taxa
Abbreviations: $\mathrm{N}=$ sample size; $\mathrm{M}=$ male; $\mathrm{F}=$ female; ? = sex undetermined; $\mathrm{J}=$ juvenile; $\mathrm{MA}=$ mature adult; $\mathrm{W}=$ worn; $\mathrm{TS} \#=$ transformation series number (see appendix 1 ); column headings $0,1,2,3,4=$ character state numbers (see appendix 1); $\mathrm{A}=$ assymetrical character expression; $\mathrm{T}=$ total number of specimens scored.

|  | Echinosorex gymnura$\begin{gathered} \mathrm{N}=32 ; \mathrm{M}-14, \mathrm{~F}-16, ?-2 ; \\ \mathrm{J}-7, \mathrm{MA}-18, \mathrm{~W}-7) \end{gathered}$ |  |  |  |  |  |  | Hylomys sinensis$\begin{gathered} (\mathrm{N}=25 ; \mathrm{M}-15, \mathrm{~F}-9, ?-1 \\ \mathrm{J}-0, \mathrm{MA}-24, \mathrm{~W}-1) \end{gathered}$ |  |  |  |  |  | $\begin{aligned} & \text { Hylomys suillus } \\ & (\mathrm{N}=16 ; \mathrm{M}-5, \mathrm{~F}-11 \text {; } \\ & \mathrm{J}-3, \mathrm{MA}-11, \mathrm{~W}-2) \end{aligned}$ |  |  |  |  |  | Atelerix albiventris ( $\mathrm{N}=25$; M-11, F-14; J-4, MA-13, W-8 |  |  |  |  |  | Atelerix algirus$\begin{gathered} \mathrm{N}=21 ; \mathrm{M}-7, \mathrm{~F}-13, ?-1 \\ \mathrm{~J}-5, \mathrm{MA}-7, \mathrm{~W}-9) \end{gathered}$ |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| TS\# |  | 01 | 12 | 3 | 4 | A | T | 0 | 12 | 3 | 4 | A | T | 0 | 1 | 2 | 3 | A | A $T$ | 0 | 1 | 2 | 4 | A | T | 01 | 2 | 3 |  | A T |
| 4 | 27 | 75 | 5 |  |  |  | 32 | 25 |  |  |  |  | 25 | 16 |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  | 21 |
| 5 | 32 |  |  |  |  |  | 32 | 25 |  |  |  |  | 25 |  | 10 |  |  |  | 16 |  | 25 |  |  |  | 25 | 21 |  |  |  | 21 |
| 6 | 32 | 2 |  |  |  |  | 32 | 25 |  |  |  |  | 25 | 16 |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  | 21 |
| 7 |  | 25 | 510 |  |  |  | 17 |  | 23 |  |  |  | 23 | 2 | 21 |  |  |  | 216 |  |  |  |  |  | 25 |  | 20 |  |  | 21 |
| 8 | 27 | 7 |  |  |  |  | 27 | 25 |  |  |  |  | 25 | 12 | 4 |  |  |  | 16 |  |  |  |  |  | 25 |  | 21 |  |  | 21 |
| 9 | 25 | 5 |  |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  | 21 |
| 10 | 30 | 1 |  |  |  |  | 31 | 25 |  |  |  |  | 25 | 16 |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  | 21 |
| 11 | 29 | 9 |  |  |  |  | 29 | 25 |  |  |  |  | 25 | 16 |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 114 | 1 |  |  | 218 |
| 12 |  |  |  |  |  |  | NA |  | 25 |  |  |  | 25 |  |  |  |  |  | NA |  | 24 |  |  |  | 24 | 20 |  |  |  | 20 |
| 13 | 26 | 6 |  |  |  |  | 26 |  | 24 |  |  |  | 24 |  | 16 |  |  |  | 16 |  | 25 |  |  |  | 25 | 21 |  |  |  | 21 |
| 14 |  | 812 |  |  |  |  | 21 |  | 23 |  |  |  | 23 |  | 16 |  |  |  | 16 | 12 |  | 6 |  |  | 18 | 15 |  |  |  | 15 |
| 15 |  | 612 | 21 | 1 |  |  | 20 |  | 8 |  |  |  | 20 |  | 13 |  |  |  | 16 |  | 12 |  |  |  | 18 |  |  |  |  | 15 |
| 16 | 19 | 9 |  |  |  |  | 20 |  | 221 |  |  |  | 23 |  | 16 |  |  |  | 16 |  | 25 |  |  |  | 25 | 219 |  |  |  | 21 |
| 17 | 27 | 7 |  |  |  |  | 27 |  | 23 |  |  |  | 23 |  |  | 2 |  |  | 216 | 19 |  |  |  |  | 19 | 5 | 8 |  |  | 13 |
| 18 | 31 | 1 |  |  |  |  | 31 |  | 18 |  |  |  | 22 |  | 14 | 2 |  |  | 16 |  | 25 |  |  |  | 25 | 19 |  |  |  | 19 |
| 19 | 24 | 4 | 25 |  |  |  | 31 |  | 319 |  |  |  | 22 | 16 |  |  |  |  | 16 | 24 |  |  |  |  | 24 | 16 | 1 |  |  | 17 |
| 20 | 32 | 2 |  |  |  |  | 32 |  | 5 |  |  |  | 21 | 16 |  |  |  |  | 16 |  | 16 | 1 |  |  | 22 | 19 |  |  |  | 19 |
| 21 | 29 | 9 |  |  |  |  | 29 |  | 24 |  |  |  | 24 |  | 16 |  |  |  | 16 |  | 20 |  |  |  | 23 | 415 |  |  |  | 19 |
| 22 | 29 | 9 |  |  |  |  | 29 |  | 24 |  |  |  | 24 |  | 16 |  |  |  | 16 |  | 22 |  |  |  | 24 | 19 |  |  |  | 19 |
| 23 |  |  | 714 |  |  |  | 24 |  | 420 |  |  |  | 24 | 10 | 2 | 4 |  |  | 16 |  | 6 | 9 |  |  | 24 | 111 | 7 |  |  | 19 |
| 24 | 29 | 9 |  |  |  |  | 31 |  | 25 |  |  |  | 25 | 14 | 1 |  |  |  | 116 |  | 25 |  |  |  | 25 | 21 |  |  |  | 21 |
| 25 |  | 214 | 42 |  |  |  | 20 |  |  |  |  |  | NA |  |  | 3 |  |  | 215 |  |  |  |  |  | NA |  |  |  |  | na |
| 26 |  | 117 | 72 |  |  |  | 20 |  |  |  |  |  | NA | 6 | 8 |  |  |  | 115 |  |  |  |  |  | NA |  |  |  |  | NA |
| 27 | 30 | 0 |  |  |  |  | 31 |  |  |  |  |  | na | 14 | 1 |  |  |  | 15 |  |  |  |  |  | NA |  |  |  |  | NA |
| 28 | 31 | 1 |  |  |  |  | 31 | 24 |  |  |  |  | 24 | 16 |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  | 21 |
| 29 |  |  | 214 |  |  |  | 16 |  | 24 |  |  |  | 24 |  | 31 |  |  |  | 316 | 1 | 6 |  |  |  | 25 |  | 20 |  |  | 20 |
| 30 |  | 112 | 22 |  |  |  | 16 |  | 165 |  |  |  | 21 | 15 | 1 |  |  |  | 16 | 10 | 6 | 6 |  | 2 | 24 | 24 |  |  |  | 19 |
| 31 |  | 31 | 1 |  |  |  | 31 |  |  |  |  |  | 23 | 4 |  | 8 |  |  | 315 | 24 | 1 |  |  |  | 25 | 16 | 1 |  |  | 118 |
| 32 | 32 | 2 |  |  |  |  | 32 | 25 |  |  |  |  | 25 | 16 |  |  |  |  | 16 |  | 2 |  |  | 1 | 25 | 21 |  |  |  | 21 |
| 33 |  | 329 |  |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 23 |  |  |  | 23 | 318 |  |  |  | 21 |
| 34 | 27 | 75 | 5 |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 12 |  |  | 3 | 23 | 174 |  |  |  | 21 |
| 35 |  | 24 | 4 |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 14 | 2 |  |  | 16 |  |  | 2 |  |  | 23 | 24 |  |  |  | 21 |
| 36 |  | 626 |  |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 22 |  |  |  | 23 | 317 |  |  |  | 20 |
| 37 | 12 | 1217 |  |  |  |  | 32 |  |  |  |  |  | NA |  | 16 |  |  |  | 16 |  | 20 |  |  |  | 22 | 613 |  |  |  | 19 |
| 38 | 15 | 516 |  |  |  |  | 31 |  |  |  |  |  | NA |  |  |  |  |  | NA | 1 | 1 |  |  |  | 2 |  |  |  |  | 6 |
| 39 | 32 | 2 |  |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 23 |  |  |  | 23 | 21 |  |  |  | 21 |
| 40 | 32 | 2 |  |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 | 12 | 9 |  |  | 1 | 22 | 115 |  |  |  | 16 |
| 41 |  |  |  |  |  |  | nA |  |  |  |  |  | NA |  |  |  |  |  | NA |  | 4 | 4 |  |  | 8 | 51 | 1 |  |  |  |
| 42 |  |  |  |  |  |  | NA |  |  |  |  |  | NA |  |  |  |  |  | Na |  | 8 |  |  |  | 8 | 11 |  |  |  | 11 |
| 43 | 32 | 2 |  |  |  |  | 32 | 25 |  |  |  |  | 25 | 16 |  |  |  |  | 16 | 12 | 1 | 7 |  |  | 20 | 21 |  |  |  | 21 |
| 44 | 31 | 1 |  |  |  |  | 31 | 25 |  |  |  |  | 25 | 13 | 2 |  |  |  | 116 | 15 | 6 |  |  |  | 23 | 21 |  |  |  | 21 |
| 45 |  | 229 |  |  |  |  | 31 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 21 |  |  |  | 23 | 21 |  |  |  | 21 |
| 46 |  |  | 1 |  |  |  | 1 |  | 25 |  |  |  | 25 |  | 14 |  |  |  | 14 |  |  |  |  |  | NA |  |  |  |  | NA |
| 47 |  | 415 | 57 |  |  |  | 31 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 25 |  |  |  | 25 | 21 |  |  |  | 21 |
| 48 |  |  | 230 |  |  |  | 32 |  | 25 |  |  |  | 25 | 5 | 8 |  |  |  |  |  | 2 |  |  | 1 | 23 |  | 15 |  |  | 20 |
| 49 | 32 |  |  |  |  |  | 32 |  | 25 |  |  |  | 25 | 16 |  |  |  |  | 16 |  | 22 | 1 |  |  | 23 | 192 |  |  |  | 21 |
| 50 | 16 | 612 |  |  |  |  | 31 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 15 |  |  | 1 | 23 | 120 |  |  |  | 21 |
| 51 |  | 2 |  |  |  |  | 2 |  |  |  |  |  | NA |  |  |  |  |  | na |  |  |  |  |  | NA |  |  |  |  | na |
| 52 | 32 |  |  |  |  |  | 32 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | 16 |  | 13 |  |  | 1 | 24 | $14 \quad 3$ |  |  |  | 17 |
| 53 | 26 | 264 | 42 |  |  |  | 32 |  | 25 |  |  |  | 25 | 16 |  |  |  |  | 16 |  | 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 |  | 15 |  |  |  | 16 | 10 | 7 |  |  | 3 | 20 | 21 |  |  |  | 21 |

Continued


APPENDIX 3
Continued

| TS\# | Echinosorex gymnura$\begin{gathered} (\mathrm{N}=32 ; \mathrm{M}-14, \mathrm{~F}-16, ?-2 \\ \mathrm{J}-7, \mathrm{MA}-18, \mathrm{~W}-7) \end{gathered}$ |  |  |  |  |  |  | Hylomys sinensis$\begin{gathered} (\mathrm{N}=25 ; \mathrm{M}-15, \mathrm{~F}-9, ?-1 ; \\ \mathrm{J}-0, \mathrm{MA}-24, \mathrm{~W}-1) \end{gathered}$ |  |  |  |  |  |  | Hylomys suillus$\begin{aligned} & (\mathrm{N}=16 ; \mathrm{M}-5, \mathrm{~F}-11 \\ & \mathrm{J}-3, \mathrm{MA}-11, \mathrm{~W}-2) \end{aligned}$ |  |  |  |  |  |  | Atelerix albiventris$\begin{gathered} \mathrm{N}=25 ; \mathrm{M}-11, \mathrm{~F}-14 \\ \mathrm{~J}-4, \mathrm{MA}-13, \mathrm{~W}-8) \end{gathered}$ |  |  |  |  |  | Atelerix algirus$\begin{gathered} (\mathrm{N}=21 ; \mathrm{M}-7, \mathrm{~F}-13, ?-1 ; \\ \mathrm{J}-5, \mathrm{MA}-7, \mathrm{~W}-9) \end{gathered}$ |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 0 | 1 | 2 | 3 | 4 | A | T |  | 01 | 2 | 3 | 4 | A | T | 0 | 1 | 2 | 3 | 4 | A | T | 01 | 2 | 3 | 4 | A |  | 0 | 1 | 2 | 3 | 4 | A | T |
| 113 |  | 622 |  |  |  |  | 29 | 14 | 48 |  |  |  | 2 |  |  | 9 |  |  |  | 3 | 13 | 4 |  |  |  |  | 5 |  | 15 |  |  |  |  | 15 |
| 114 |  | 19 |  |  |  | 1 | 29 |  | 46 |  |  |  |  |  |  | 13 |  |  |  |  | 13 | 20 |  |  |  |  | 20 |  | 12 |  |  |  |  | 12 |
| 115 |  | 10 |  |  |  |  | 10 |  | 111 | 2 |  |  | 4 |  |  |  |  |  |  |  | NA |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 116 | 6 | 64 |  |  |  |  | 10 | 16 | 6 2 |  |  |  |  | 18 |  |  |  |  |  |  | NA |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 117 | 31 |  |  |  |  |  | 31 | 25 |  |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 23 |  |  |  |  | 23 | 21 |  |  |  |  |  | 21 |
| 118 | 16 | 14 |  |  |  |  | 31 |  | 714 |  |  |  | 4 | 25 | 11 | 4 |  |  |  |  | 15 | 231 |  |  |  |  | 24 |  | 11 |  |  |  |  | 20 |
| 119 |  | 31 |  |  |  |  | 31 |  | 123 |  |  |  |  | 24 |  | 16 |  |  |  |  | 16 | 22 |  |  |  |  | 22 |  | 21 |  |  |  |  | 21 |
| 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 |  |  |  |  | 24 | 16 |  |  |  |  |  | 16 | 21 |  |  |  |  | 21 | 21 |  |  |  |  |  | 21 |
| 124 |  | 428 |  |  |  |  | 32 |  | 122 | 1 |  |  | 1 | 25 |  | 16 |  |  |  |  | 16 | 22 |  |  |  |  | 22 | 3 | 18 |  |  |  |  | 21 |
| 125 | 28 |  | 2 |  |  |  | 30 |  | 29 | 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 |  |  | 11 |  |  |  | 21 |
| 128 | 14 | 16 |  |  |  |  | 30 | 25 |  |  |  |  |  | 25 | 12 | 2 |  |  |  |  | 14 | 23 |  |  |  |  | 23 |  | 20 |  |  |  |  | 21 |
| 129 | 32 |  |  |  |  |  | 32 | 25 |  |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  |  |  | 21 |
| 130 | 1 | 31 |  |  |  |  | 32 |  | 24 |  | 1 |  |  | 25 |  | 16 |  |  |  |  | 16 | 1 |  | 24 |  |  | 25 |  |  | 6 |  |  | 1 | 17 |
| 131 | 27 |  | 3 |  |  |  | 30 |  | 24 | 1 |  |  |  | 25 |  |  | 16 |  |  |  | 16 | 025 |  |  |  |  | 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 | $14 \quad 5$ |  |  |  |  | 19 | 21 |  |  |  |  |  | 21 |
| 135 | 22 | 6 |  |  |  |  | 28 |  | 25 |  |  |  |  | 25 |  | 15 |  |  |  |  | 15 | 25 |  |  |  |  | 25 |  | 21 |  |  |  |  | 21 |
| 136 | 24 | 4 |  |  |  |  | 28 |  | 420 |  |  |  | 1 | 25 | 7 | 8 |  |  |  |  | 15 | 119 |  |  |  | 1 | 21 | 6 | 8 |  |  |  |  | 14 |
| 137 | 30 |  |  |  |  |  | 30 | 20 | - 4 |  |  |  |  | 24 | 7 | 7 |  |  |  | 2 | 16 | 1010 |  |  |  | 1 | 21 | 21 |  |  |  |  |  | 21 |
| 138 | 23 | 5 |  |  |  |  | 28 |  | 718 |  |  |  |  | 25 | 5 | 11 |  |  |  |  | 16 | 121 |  |  |  |  | 22 |  | 19 |  |  |  | 1 | 21 |
| 139 | 6 | 616 | 7 |  |  |  | 29 |  | 25 |  |  |  |  | 25 |  | 14 |  |  |  |  | 16 | 121 |  |  |  |  | 22 | 11 |  | 3 |  |  |  | 14 |
| 140 | 2 | 27 |  |  |  |  | 29 |  | 25 |  |  |  |  | 25 |  | 14 |  |  |  |  | 16 | 22 |  |  |  |  | 22 |  | 10 |  |  |  |  | 19 |
| 141 | 32 |  |  |  |  |  | 32 |  | 223 |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 24 |  |  |  |  | 24 |  | 21 |  |  |  |  | 21 |
| 142 | 31 |  |  |  |  |  | 31 |  | 2 |  |  |  |  | 2 |  | 16 |  |  |  |  | 16 |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 143 | 32 |  |  |  |  |  | 32 | 2 | 2 |  |  |  |  | 2 | 16 |  |  |  |  |  | 16 |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 144 |  | 31 |  |  |  |  | 31 |  | 2 |  |  |  |  | 2 |  | 16 |  |  |  |  | 16 |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 145 | 32 |  |  |  |  |  | 32 | 25 |  |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 24 |  |  |  |  | 24 | 21 |  |  |  |  |  | 21 |
| 146 | 32 |  |  |  |  |  | 32 | 23 | 32 |  |  |  |  | 25 | 15 |  |  |  |  |  | 15 | 24 |  |  |  |  | 24 | 21 |  |  |  |  |  | 21 |
| 147 | 32 |  |  |  |  |  | 32 | 25 |  |  |  |  |  | 25 | 15 |  |  |  |  |  | 15 | 24 |  |  |  |  | 24 | 21 |  |  |  |  |  | 21 |
| 148 |  | 20 |  |  |  |  | 21 |  | 810 |  |  |  |  | 18 | 14 |  |  |  |  |  | 16 |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 149 |  |  | 25 |  |  |  | 25 |  | 124 |  |  |  |  | 25 |  |  |  |  |  |  | NA |  |  |  |  |  | NA |  | 21 |  |  |  |  | 21 |
| 150 | 32 |  |  |  |  |  | 32 | 25 | 5 |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  |  |  | 21 |
| 151 | 31 | 1 |  |  |  |  | 32 | 24 | 4 | 1 |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  |  |  | 21 |
| 152 |  | 31 |  |  |  |  | 31 |  |  |  |  |  |  | NA |  | 16 |  |  |  |  | 16 |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 153 |  | 30 |  |  |  |  | 30 |  | 124 |  |  |  |  | 25 |  | 16 |  |  |  |  | 16 | 25 |  |  |  |  | 25 |  | 21 |  |  |  |  | 21 |
| 154 |  | 32 |  |  |  |  | 32 |  | 321 |  |  |  |  | 24 |  | 13 |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 19 | 1 |  |  |  |  | 20 |
| 155 | 4 | 427 |  |  |  |  | 31 | 13 | 3 |  |  |  | 1 | 23 |  | 14 |  |  |  |  | 16 | 1311 |  |  |  |  | 24 | 21 |  |  |  |  |  | 21 |
| 156 |  | 5 |  |  |  |  | 5 | 13 | 31 |  |  |  |  | 14 | 2 |  |  |  |  |  | 2 | 13 |  |  |  |  | 13 | 21 |  |  |  |  |  | 21 |
| 157 | 4 | 422 | 4 |  |  |  | 30 |  | 910 | 4 |  |  |  | 23 |  | 12 | 1 |  |  | 1 | 16 | 121 |  |  |  |  | 22 | 2 | 11 | 7 |  |  |  | 21 |
| 158 |  | 30 |  |  |  |  | 30 |  | 122 |  |  |  |  | 23 |  | 16 |  |  |  |  | 16 | 23 |  |  |  |  | 23 |  | 21 |  |  |  |  | 21 |
| 159 | 10 | 19 |  |  |  |  | 30 |  | 124 |  |  |  |  | 24 | 11 | 4 |  |  |  | 1 | 16 | $20 \quad 1$ |  |  |  | 1 | 22 | 12 | 7 |  |  |  |  | 20 |
| 160 | 29 | 2 |  |  |  |  | 32 |  | 25 |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 25 |  |  |  |  | 25 |  | 21 |  |  |  |  | 21 |
| 161 | 30 |  |  |  |  |  | 31 |  |  |  |  |  |  | NA | 16 |  |  |  |  |  | 16 |  |  |  |  |  | NA |  |  |  |  |  |  | NA |
| 162 | 11 | 5 | 1 | 1 |  |  | 19 |  |  |  |  |  |  | NA |  | 9 | 5 |  |  |  | 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 |  |  |  | 25 |  | 24 |  |  | 17 |  | 23 |  | 1 | 13 |  |  |  | 15 | 191 |  | 1 | 1 | 3 | 25 | 12 |  |  | 7 |  | 1 | 20 |
| 166 | 4 | 4 |  |  |  |  | 24 |  | 23 |  |  |  |  | 23 |  | 16 |  |  |  |  | 16 | 215 | 7 |  |  |  | 24 | 8 | 5 | 7 |  |  |  | 20 |
| 167 |  | 26 |  |  |  |  | 26 |  | 22 |  |  |  |  | 22 |  | 16 |  |  |  |  | 16 | $18 \quad 4$ |  |  |  | 3 | 25 | 17 | 4 |  |  |  |  | 21 |
| 168 | 23 | , 2 |  |  |  |  | 25 |  | 219 |  |  |  |  | 21 |  | 15 |  |  |  |  | 15 | 25 |  |  |  |  | 25 |  | 18 |  |  |  |  | 19 |

APPENDIX 3
Continued


## APPENDIX 3

Continued

|  | Echinosorex gymnura$\begin{gathered} (\mathrm{N}=32 ; \mathrm{M}-14, \mathrm{~F}-16,9-2 \\ \mathrm{J}-7, \mathrm{MA}-18, \mathrm{~W}-7) \end{gathered}$ |  |  |  |  |  |  | Hylomys sinensis$\begin{gathered} (\mathrm{N}=25 ; \mathrm{M}-15, \mathrm{~F}-9, ?-1 ; \\ \mathrm{J}-0, \mathrm{MA}-24, \mathrm{~W}-1) \end{gathered}$ |  |  |  |  |  |  | Hylomys suillus$\begin{gathered} (\mathrm{N}=16 ; \mathrm{M}-5, \mathrm{~F}-11 ; \\ \mathrm{J}-3, \mathrm{MA}-11, \mathrm{~W}-2) \end{gathered}$ |  |  |  |  |  |  | Atelerix albiventris$\begin{gathered} (\mathrm{N}=25 ; \mathrm{M}-11, \mathrm{~F}-14 ; \\ \mathrm{J}-4, \mathrm{MA}-13, \mathrm{~W}-8) \end{gathered}$ |  |  |  |  |  | Atelerix algirus$\begin{gathered} (\mathrm{N}=21 ; \mathrm{M}-7, \mathrm{~F}-13, ?-1 ; \\ \mathrm{J}-5, \mathrm{MA}-7, \mathrm{~W}-9) \end{gathered}$ |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| TS\# | 0 | 1 | 2 | 3 | 4 | A |  |  | 1 | 1 | 2 | 3 | 4 | A T |  | 1 | 2 | 3 | 4 | A | T | 0 | 1 | 2 | 3 | 4 | A T |  | 1 | 2 | 3 | 4 A | A T |
| 225 |  | 30 |  |  |  |  | 31 |  | 25 | 5 |  |  |  | 25 |  | 16 |  |  |  |  | 16 |  | 25 |  |  |  | 25 |  | 21 |  |  |  | 21 |
| 226 | 30 |  |  |  |  |  | 30 | 25 |  |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  |  | 21 |
| 227 |  | 26 |  |  |  | 1 | 30 | 22 | 1 |  |  |  |  | 23 |  | 1 |  |  |  |  | 1 |  | 25 |  |  |  | 25 |  | 610 |  |  |  | 16 |
| 228 |  | 31 |  |  |  |  | 31 |  | 25 | 5 |  |  |  | 25 |  | 16 |  |  |  |  | 16 | 10 | 2 | 9 |  |  | 122 | 21 |  |  |  |  | 21 |
| 229 | 31 |  |  |  |  |  | 31 | 25 |  |  |  |  |  | 25 | 16 |  |  |  |  |  | 16 | 25 |  |  |  |  | 25 | 21 |  |  |  |  | 21 |
| 230 | 31 |  |  |  |  |  | 31 | 22 | 1 |  |  |  |  | 23 |  | 16 |  |  |  |  | 16 | 14 | 1 |  |  |  | 116 |  | 5 |  |  |  | 116 |
| 231 | 31 |  |  |  |  |  | 31 | 23 |  |  |  |  |  | 23 |  |  |  |  |  |  | NA | 5 | 7 |  |  |  | 214 |  | 65 |  |  |  | 11 |
| 232 |  | 31 |  |  |  |  | 31 |  | 25 | 5 |  |  |  | 25 |  | 16 |  |  |  |  | 16 | 9 | 9 |  |  |  | 220 |  | 614 |  |  |  | 121 |
| 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 |  | 14 | 21 |  |  |  |  | 21 |
| 237 |  | 31 |  |  |  |  | 31 |  | 25 | 5 |  |  |  | 25 |  | 16 |  |  |  |  | 16 |  | 25 |  |  |  | 25 |  | 21 |  |  |  | 21 |
| 238 |  | 31 |  |  |  |  | 31 |  | 2.5 | 5 |  |  |  | 25 |  | 15 |  |  |  |  | 15 |  | 25 |  |  |  | 25 |  | 21 |  |  |  | 21 |
| 239 |  | 31 |  |  |  |  | 31 |  | 25 | 5 |  |  |  | 25 |  | 16 |  |  |  |  | 16 |  | 25 |  |  |  | 25 |  | 19 |  |  |  | 121 |
| 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 |  | 2. | 5 |  |  |  | 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 |  | 25 |  |  |  |  | 29 | 16 | 68 | 8 |  |  |  | 24 |  | 16 |  |  |  |  | 16 |  | 25 |  |  |  | 25 |  | 16 |  |  |  | $1 \quad 17$ |
| 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 |



APPENDIX 3
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APPENDIX 3
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APPENDIX 3
Continued

| TS\# | Erinaceus amurensis$\begin{gathered} \mathrm{N}=11 ; \mathrm{M}-3, \mathrm{~F}-6, ?-2 \\ \mathrm{~J}-2, \mathrm{MA}-7, \mathrm{~W}-2) \end{gathered}$ |  |  |  |  |  |  | Erinaceus europaeus$\begin{gathered} \mathrm{N}=24 ; \mathrm{M}-10, \mathrm{~F}-8, ?-6 ; \\ \mathrm{J}-2, \mathrm{MA}-15, \mathrm{~W}-7) \end{gathered}$ |  |  |  |  |  |  | Hemiechinus aethiopicus$\begin{gathered} (\mathrm{N}=25 ; \text { M-13, F-11, ?-1 } \\ \mathrm{J}-3, \mathrm{MA}-15, \mathrm{~W}-7) \end{gathered}$ |  |  |  |  |  |  | Hemiechinus auritus$\begin{gathered} \mathrm{N}=25 ; \mathrm{M}-12, \mathrm{~F}-4, ?-9 \\ \mathrm{~J}-8, \mathrm{MA}-11, \mathrm{~W}-6) \end{gathered}$ |  |  |  |  |  | Hemiechinus hypomelas$\begin{gathered} (\mathrm{N}=19 ; \mathrm{M}-10, \mathrm{~F}-9 \\ \mathrm{J}-4, \mathrm{MA}-11, \mathrm{~W}-4) \end{gathered}$ |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 011 | 2 | 3 | 4 | A | T | 0 | 01 | 2 | 3 | 4 | A |  |  | - 1 | 2 | 3 | 4 | A |  | 0 | 1 | 2 | 3 | 4 | A T | 0 |  | 2 | 3 | 4 | A | T |
| 196 |  | 11 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 197 |  | 16 | 3 |  |  |  | 10 |  | 2 | 21 |  |  |  | 23 |  | 12 |  |  |  | 1 | 23 |  | 4 | 8 |  |  | 114 |  | 14 | 2 |  |  |  | 16 |
| 198 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 | 25 |  |  |  |  | 25 |  | 18 |  |  |  |  | 18 |
| 199 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  |  | 25 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 200 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 |  |  | 25 |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 16 |  |  |  |  | 16 |
| 201 | 11 | 1 |  |  |  |  | 11 | 8 | 811 |  |  |  | 1 | 20 | 25 |  |  |  |  |  | 25 | 13 | 4 |  |  |  | 17 | 13 | 3 |  |  |  | 2 | 18 |
| 202 |  | 11 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 | 25 |  |  |  |  | 25 | 18 |  |  |  |  |  | 18 |
| 203 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 |  | 713 | 1 |  |  | 1 | 22 |  | 25 |  |  |  | 25 | 13 | 3 |  |  |  |  | 16 |
| 204 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 | 11 | 4 |  |  |  | 419 |  | 19 |  |  |  |  | 19 |
| 205 |  | 11 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 206 | 11 | 1 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 207 | 11 | 1 |  |  |  |  | 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 |  | 24 |  |  |  |  | 25 |  | 1 | 24 |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 213 |  | 10 |  |  |  |  | 10 | 1 | 9 |  |  |  | 4 | 20 |  | 1 | 7 |  |  | 2 | 24 | 3 | 11 |  |  |  | 418 | 13 | 3 |  |  |  | 1 | 17 |
| 214 |  |  | 11 |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 5 | 7 |  |  |  | 12 |  | 7 | 1 |  |  | 8 |  | 18 |  |  |  |  | 18 |
| 215 |  | 11 |  |  |  |  | 11 |  | 23 |  |  |  |  | 24 |  | 14 |  |  |  |  | 14 |  | 9 |  |  |  | 9 |  | 5 |  |  |  |  | 5 |
| 216 |  | 29 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 16 | 9 |  |  |  | 25 |  | 9 | 12 |  |  | 21 |  | 4 | 13 |  |  |  | 17 |
| 217 |  | 11 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 23 | 1 |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 17 |  |  |  | 1 | 18 |
| 218 |  |  | 10 |  |  | 1 | 11 |  |  | 21 |  |  |  | 21 |  | 16 | 4 |  |  | 2 | 24 | 1 |  | 16 |  |  | 118 | 1 | 2 | 13 |  |  | 2 | 18 |
| 219 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  |  | 25 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 220 | 7 | 74 |  |  |  |  | 11 | 11 | 6 |  |  |  |  | 17 |  | 45 |  |  |  | 1 | 20 |  | 25 |  |  |  | 25 | 6 | 6 |  |  |  | 1 | 13 |
| 221 | 11 | 1 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 | 25 |  |  |  |  | 25 |  | 15 |  |  |  |  | 15 |
| 222 | 11 | 1 |  |  |  |  | 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 |  |  |  |  | 25. |  | 5 |  |  |  |  | 5 |
| 225 |  | 11 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 226 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  |  | 25 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 227 | 9 | 91 |  |  |  |  | 10 | 15 | 4 |  |  |  |  | 19 |  | 24 |  |  |  |  | 24 |  | 21 |  |  |  | 22 |  | 16 |  |  |  |  | 16 |
| 228 | 11 | 1 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  |  | 25 |  | 25 |  |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 229 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  |  | 25 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 230 | 8 | 82 |  |  |  |  | 10 |  | 20 |  |  |  |  | 24 |  | 14 |  |  |  |  | 21 |  | 10 | 1 |  |  | 16 | 7 | 9 |  |  |  |  | 16 |
| 231 |  | 17 |  |  |  |  | 8 | 4 | 4 |  |  |  |  | 4 |  | 4 |  |  |  |  | 5 |  | 3 |  |  |  | 4 | 5 | 1 |  |  |  |  | 6 |
| 232 |  | 11 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 19 |  |  |  | 1 | 22 |  | 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 |  |  |  |  | 16 |
| 236 |  |  |  | 11 |  |  | 11 | 24 |  |  |  |  |  | 24 |  |  |  | 21 |  |  | 21 | 25 |  |  |  |  | 25 |  |  | 16 |  |  |  | 16 |
| 237 |  | 11 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  | 25 |  | 9 |  |  |  |  | 19 |
| 238 | 11 | 1 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 24 |  |  |  |  | 24 |  | 25 |  |  |  | 25 |  | 9 |  |  |  |  | 19 |
| 239 |  | 11 |  |  |  |  | 11 |  | 24 |  |  |  |  | 24 |  | 23 |  |  |  | 1 | 24 |  | 25 |  |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 240 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 241 |  | 11 |  |  |  |  | 11 |  |  | 24 |  |  |  | 24 |  | 19 |  |  |  |  | 19 |  | 25 |  |  |  | 25 |  | 19 |  |  |  |  | 19 |
| 242 |  | 110 |  |  |  |  | 11 |  | 618 |  |  |  |  | 24 |  | 10 | 11 |  |  | 1 | 24 |  | 8 | 12 |  |  | 20 |  |  | 12 |  |  |  | 17 |
| 243 | 11 | 1 |  |  |  |  | 11 | 24 |  |  |  |  |  | 24 | 24 |  |  |  |  |  | 24 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 244 |  |  | 11 |  |  |  | 11 |  |  | 24 |  |  |  | 24 |  |  | 20 |  |  |  | 20 |  |  | 25 |  |  | 25 |  |  | 19 |  |  |  | 19 |
| 245 | 11 | 1 |  |  |  |  | 11 | 23 | 1 |  |  |  |  | 24 | 20 |  |  |  |  |  | 20 | 25 |  |  |  |  | 25 | 19 |  |  |  |  |  | 19 |
| 246 |  | 47 |  |  |  |  | 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 |  |  |  |  |  | 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 .

| PA\# | TS\# | Transformation series | Taxon |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 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 | [2: (0) present; (1) absent | 0 | 0 | 0 | 0 | 0 | $0 / 1$ | 0 | $0 / 1$ | 0 | $0 / 1$ |
| 4 | 8 | I2, size: $(0)>$ 13; (1) $=13 ;(2)<13$ | 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 ) $1 / 2$ 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; <br> (1) crescentic | 0 | 0 | 0 | 0/1/2 | 0 | 1 | 0 | 0 | 0 | 0 |
| 13 | 46 | P3, centrocrista (paracone-metacone): <br> (0) present; (1) absent | 1 | 1 | 1 | 1 | NA | NA | NA | NA | na | 1 |
| 14 | 47 | P3, hypocone: (0) present; <br> (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 | P 4 , hypocone height: $(0)<$ protocone; <br> (1) $\approx$ protocone | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 56 | P4, hypocone gross size: ( 0 ) < protocone; $(1) \approx$ protocone | 0 | 0 | 1 | $0 / 1$ | 0 | 0 | 1 | 0 | 0 | 1 |
| 18 | 57 | P4, protocone position (to paracone): <br> (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; <br> (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; <br> (1) conical | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25 | 78 | M1, protocone position (paracone): <br> (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 | MI, 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; <br> (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 | , | $0 / 1$ | 1 | 1 |
| 36 | 117 | M2, metastyle: (0) present; (1) absent | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

APPENDIX 4
Continued

| PA\# | TS\# | Transformation series | Taxon |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | ECHG | HLYS | HYLU | ATXA | ATXG | ERIA | ERIAE | HEME | HEMA | HEMH |
| 37 | 121 | M2, posthypocrista: (0) to postcingulum; <br> (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; <br> (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: $(0)=i 2 ;(1)>i 2$ | 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 | i 2 , 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; <br> (1) equal; (2) larger | 0 | 0/2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 52 | 152 | lower canine, size: $(0)=\mathrm{pl}$; $(1)>\mathrm{pl}$ | 1 | NA | 1 | NA | NA | NA | NA | NA | NA | NA |
| 53 | 153 | lower canine, morphology: (0) like i2/p2; <br> (1) not | 1 | $0 / 1$ | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| 54 | 160 | pl: (0) present; (1) absent | $0 / 1$ | 1 | 0 | 1 | 1 | 1 | 1 | 0/1 | 0 | 1 |
| 55 | 161 | pl, 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 | p 3 , 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 | p 3 , posterolingual cusp: (0) prominent; <br> (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 | p 4 , talonid: $(0)$ greatest breadth of tooth; <br> (1) not | 0 | 1 | 0 | 1 | 1 | 1 | 1 | $0 / 1$ | 1 | 1 |
| 67 | 183 | p4, posterolabial cuspule to protoconid: <br> (0) present; (1) absent | 0/1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 68 | 185 | p 4 , paraconid height: $(0)=$ protoconid; <br> (1) < protoconid | 1 | NA | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 69 | 189 | p 4 , protoconid size: $(0)>$ metaconid; <br> (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 | p 4 , size: $(0)=\mathrm{ml}$; (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 | ml, trigonids: (0) high; (1) low | NA | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 74 | 205 | ml, lingual wall: (0) markedly concave; <br> (1) not | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 75 | 206 | ml , talonid: (0) enclosed lingually by entocristid; (1) not | 1 | 1 | 1 | NA | 1 | 0 | 1 | 1 | 1 | 1 |
| 76 | 207 | ml , talonid: (0) opens posteriorly; <br> (1) closed | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 77 | 208 | ml, hypoconid: (0) isolated; (1) not | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| 78 | 209 | ml , entoconid size: $(0)>$ hypoconid; | 2 | 0 | 0 | 0/3 | 2 | 3 | 3 | 0 | 3 | 3 |

(1) $>$ paraconid; (2) $=$ cusps;
(3) $>$ than both

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 | ml , paraconid to protoconid: (0) lingual; <br> (1) labial; (2) aligned | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 81 | 220 | m 1 , paracristid: $(0)$ terminates at midanterior; (1) not | 1 | 1 | 1 | 1 | $0 / 1$ | 0 | 1 | 1 | 0 | 1 |
| 82 | 222 | m 2 , size: ( 0 ) shorter than m 1 ; <br> (1) larger than ml | 0 | 0 | 0 | NA | 0 | 0 | 0 | 0 | 0 | 0 |
| 83 | 223 | m 2 trigonids: (0) high, short talonid; <br> (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 | m 2 , paraconid shelf: ( 0 ) present; (1) absent | 0 | 0 | 0 | NA | 0 | 0 | 0 | 0 | 0 | 0 |
| 86 | 228 | m 2 , paracristid lingual extension (to ml ): <br> (0) equal; (1) labial; (2) lingual | 1 | 1 | 1 | 0/1/2 | 1 | 0 | 1 | 1 | 1 | 1 |
| 87 | 229 | m 2 , entostylid: (0) absent; (1) weak; <br> (2) strong | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 88 | 233 | m 2 , paraconid to metaconid: (0) lingual; (1) labial; (2) aligned | 1/2 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 89 | 234 | m 2 , paraconid to protoconid: (0) lingual; <br> (1) labial; (2) aligned | 0 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 90 | 235 | m 2 , hypoconid to protoconid: (0) lingual; <br> (1) labial; (2) aligned | 2 | 1 | 1 | 0 | 2 | 2 | 2 | 1 | 0 | 0/1/2 |
| 91 | 236 | m 2 , entoconid size: $(0)=$ protoconid; <br> (1) tallest cusp; (2) = hypoconid; <br> (3) = metaconid | 2 | 0 | 0 | $2 / 3$ | 0 | 3 | 0 | 3 | 0 | 2 |
| 92 | 237 | m 2 , talonid: (0) posteriorly narrow; <br> (1) not | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 93 | 238 | m 2 , talonid basin: (0) lingually enclosed; <br> (1) not | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| 94 | 240 | m 2 , cristid obliqua contact point: <br> (0) base of protoconid; (1) higher | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 95 | 241 | m2, entocristid: (0) high; (1) low; <br> (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; <br> (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 | m 3 , trigonids: (0) high; (1) short; <br> (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.

| Echinosorex gymnurus | $\{01\} 100000000 \quad ? 01\{012\} 000010 \quad 2000\{01\}\{01\}\{01\} 010 \quad 0211\{01\} 0 ? 001 \quad\{01\} 000100020$ $011\{01\} 0\{01\} 0001 \quad 0 ? 1\{012\} 10\{01\} 10\{01\} \quad 10 ? 1100210 \quad 1011010\{12\} 02 \quad 2110\{12\} 02001$ |
| :---: | :---: |
| Hylomys sinensis | $000001 ? 001 \quad ? 011000010 \quad 2000021000 \quad 021\{12\} 100000 \quad 1\{01\} 101010\{01\} 0$ \{02\}?\{01\}1?00011 1\{01\}11111??? 1001101010 1011010??1 0110202000 |
| Hylomys suillus | $010\{01\} 0\{01\}\{01\} 001 \quad ? 011001010 \quad\{12\} ? 00011010 \quad 02 ? 110 ? 010 \quad 10101000 ? 0$ $01100000\{012\}\{012\} \quad 11\{01\} 1101100 \quad 1011100010 \quad 1011010 ? ? 1 \quad 0110102001$ |
| Atelerix albiventris | $010201 ? 0\{01\} 1 \quad 1\{012\} 11\{01\} 0\{01\}\{01\} 10 \quad 21\{01\} 0\{02\} 11010 \quad 02 ? ? 10 ? 00\{01\}$ <br> 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 $2100011010 \quad 020110 ? 000 \quad 11 ? ? ? 00010$ 0?11?001?? ????1111?? $1\{01\} 01101210 \quad\{01\} 011010 ? ? 20110102011$ |
| Erinaceus amurensis | $01\{01\} 20\{01\} 0000 \quad 11 ? 1000010 \quad 2100011000 \quad 020210 ? 000 \quad 11 ? ? ? 00010 \quad 1 ? 11 ? 001 ? ?$ ???? $111100 \quad 1101001310 \quad 0011000 ? ? 23100102011$ |
| Erinaceus europaeus | $0102\{01\} 1 ?\{01\}\{01\} 1 \quad 10 ? 1001010 \quad 2100011000 \quad 020210 ? 001 \quad 11 ? ? ? 00010 \quad 0 ? 11 ? 001 ? ?$ ???? $111100 \quad 1001101310 \quad 1011010 ? ? 2 \quad 0110202\{01\} 10$ |
| Hemiechinus aethiopicus | $01\{01\} 201 ? 0\{01\} 1 \quad ? 0 ? 1000010 \quad 21\{01\} 001\{01\} 000 \quad 0201\{01\} 0 ? 011 \quad 11 ? ? ? 00010$ $0 ? 1\{01\} ? 0\{01\} 1 ? ?$ ????1\{01\}1100 $1011100010 \quad 1011010 ? ? 1 \quad 311010201$ ? |
| Hemiechinus auritus | 010201?00\{01\} \{01\}0?1000010 $2100011000 \quad 020210 ? 001 \quad 11 ? ? ? 00020$ 0?10?001?? ????1111?? 1001101310 0011010??0 0110102010 |
| Hemiechinus hypomelas | $01\{01\} 201 ? 00\{01\} \quad 1011\{01\} 01010 \quad\{12\} ? 00011010 \quad 02 ? 010 ? 001 \quad 11 ? ? 900010$ 0?01?\{01\}01?? ????11110\{01\} 1011101310 1011010??\{012\} 211010201? |
| Outgroups: Tenrecoids | $0\{01\} 0\{01\} 01 ? 0\{01\} 0 \quad 10111 ? ? 111 \quad 321$ ??????? ? $32 ? ? ? ? 0 ? ?$ ? $\{01\}\{01\} 000\{01\}\{01\} 20$ $\{02\} ?\{01\}\{01\}\{02\}\{01\} 0\{01\}\{01\} 0 \quad 1\{01\}\{01\}\{12\} 11\{01\} 10\{01\} \quad 11\{01\} 02 ?\{02\} 410$ 1100?\{02\}0\{12\}0\{23\} 42??201?10 |
| Soricoids | $0\{01\}\{01\} 1\{01\} 01001 \quad 20111 ? ? 21\{01\} \quad\{23\} 2102\{13\} 100\{01\}$ ?20\{02\}\{12\}\{02\}10\{01\}\{01\} $10\{01\} 0\{01\} 01070 \quad\{01\} 1110\{01\} 0001 \quad 1 ? 1\{01\} 111 ? ? 2$ 1110111210 ? $120 ?\{02\} 020\{012\}$ 311\{01\}201?02 |

## APPENDIX 5

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


Apomorphy list

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

## 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 2 a ( 19 extant taxa). The second apomorphy list (d) was generated from tree 1 in analysis 2 b (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 | 12: (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 | Cl size: ( 0 ) significantly larger than adjacent post-canine teeth; (1) slightly larger than postcanine teeth; (2) approximately equal in size to adjacent postcanine teeth. |
| 6 | [65] | TS\# | 19 | Cl , 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 13. |
| 8 | [67] | TS\# | 152 | c1, relative size: (0) approximately equal to, or smaller than P1; (1) significantly larger than p 1 . |
| 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 | ml : (0) trigonid moderate; (1) marked elongation of prevallid shear on ml . |
| 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) smali; (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 | 111110111 | 110100110 |
| Hylomys suillus | 1100100000 | 1111110111 | 110100110 |
| Hylomys hainanensis | 1100100001 | 1111110111 | 110100110 |
| Hemiechinus aethiopicus | 2211200011 | 1121110112 | 11101021 |
| Hemiechinus hypomelas | 2211200011 | 1120100112 | 111101021 |

## APPENDIX 6

Continued
(b) Data matrix extracted from Gould (1995) (continued)
$\left.\begin{array}{llll}\text { Hemiechinus micropus } & 2211200011 & 1121110112 & 111101021 \\ \text { Hemiechinus auritus } & 2211200011 & 1120100112 & 111101021 \\ \text { Hemiechinus collaris } & 2211200011 & 1120100112 & 111101021 \\ \text { Mesechinus dauuricus } & 2211200011 & 1120100112 & 111101021 \\ \text { Erinaceus amurensis } & 2212210011 & 1120100112 & 111101021 \\ \text { Erinaceus concolor } & 2212210011 & 1120100112 & 111101021 \\ \text { Erinaceus europaeus } & 2212210011 & 1120100112 & 111101021 \\ \text { Atelerix frontalis } & 2211200011 & 1020100112 & 111101021 \\ \text { Atelerix algirus } & 2211200011 & 1020110112 & 111101021 \\ \text { Atelerix albiventris } & 2211200011 & 102110112 & 111101021 \\ \text { Atelerix sclateri } & 2211200011 & 1021110112 & 111101021 \\ \text { Outgroups: Tenrecoids } & 11000 ? 0010 & 000000100 & 0 ? 000000\{01\} \\ & \text { Soricoids } & 11000 ? 0010 & \{12\} 001000100\end{array}\right) 0 ? 0000000\{01\}$
(c) Phylogenetic Analysis 2a, Tree Number 1: Length $=41$; consistency index $(\mathrm{CI})=0.756$; homoplasy index $(\mathrm{HI})=0.244$; Cl excluding uninformative characters $=0.744$; HI excluding uninformative characters $=0.256$; retention index $(\mathrm{RI})=$ 0.917 ; rescaled consistency index $(R C)=0.694$.


Apomorphy list


## APPENDIX 6

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

|  | Branch | PA\# | Steps | Cl | Change | Branch | PA\# | Steps | CI | Change |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| node 4 | $\rightarrow$ node 7 (contd.) | 20 | 1 | 1.000 | $1 \Rightarrow 2$ | node $7 \rightarrow$ node 8 | 12 | 1 | 0.333 | $1 \Rightarrow 0$ |
|  |  | 23 | 1 | 1.000 | $0 \Rightarrow 1$ | node $8 \rightarrow$ node 9 | 14 | 1 | 0.333 | $1 \Rightarrow 0$ |
|  |  | 26 | 1 | 1.000 | $0 \Rightarrow 1$ | node $9 \rightarrow$ node 10 | 16 | 1 | 0.500 | $1 \Rightarrow 0$ |
|  |  | 27 | 1 | 0.500 | $1 \Rightarrow 0$ | $\rightarrow$ node $\rightarrow$ node 11 | 12 |  |  |  |
|  |  | 28 | 1 | 1.000 | $1 \Rightarrow 2$ | node $10 \rightarrow$ node 11 | 12 | 1 | 0.333 | $0 \Rightarrow 1$ |
|  |  | 29 | 1 | 1.000 | $0 \Rightarrow 1$ | node $11 \rightarrow$ node 12 | 4 | 1 | 1.000 | $1 \Rightarrow 2$ |
|  |  |  |  |  |  |  | 6 | 1 | 1.000 | $0 \Rightarrow 1$ |

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


Apomorphy list

| Branch |  | PA\# | Steps | CI | Change | Branch |  |  | PA\# | Steps | CI | Change |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| node 1 | $\rightarrow$ Echinosorex | 8 | 1 | 1.000 | $0 \Rightarrow 1$ | node 4 | $\rightarrow$ | node 5 | 14 | 1 | 0.333 | $1 \Rightarrow 0$ |
| node 1 | $\rightarrow$ node 2 | 5 | 1 | 1.000 | $0 \rightarrow 1$ | node 5 | $\rightarrow$ | node 6 | 16 | 1 | 0.500 | $1 \Rightarrow 0$ |
|  |  | 13 | 1 | 1.000 | $0 \Rightarrow 1$ | node 6 | $\rightarrow$ | node 7 | 4 | 1 | 1.000 | $1 \Rightarrow 2$ |
|  |  | 14 | 1 | 0.333 | $0 \rightarrow 1$ |  |  |  | 6 | 1 | 1.000 | $0 \Rightarrow 1$ |
|  |  | 15 | 1 | 1.000 | $0 \Rightarrow 1$ | node 5 | $\rightarrow$ | Atelerix algirus | 12 | 1 | 0.333 | $1 \Rightarrow 0$ |
|  |  | 16 | 1 | 0.500 | $0 \Rightarrow 1$ |  | $\rightarrow$ |  | 12 |  |  | $1 \Rightarrow 0$ |
| node 2 | $\rightarrow$ node 3 | 5 9 | 1 | $1.000$ | $1 \rightarrow 2$ |  |  | albiventris |  |  |  |  |
|  |  | 9 10 | $\begin{aligned} & 1 \\ & 1 \end{aligned}$ |  | $\begin{aligned} & 0 \rightarrow 1 \\ & 0 \Rightarrow 1 \end{aligned}$ |  |  |  |  |  |  |  |
| node 3 | $\rightarrow$ Hylomys sinensis | 1 | 1 | 1.000 | $1 \Rightarrow 0$ |  |  |  |  |  |  |  |
|  |  | 7 | 1 | 1.000 | $0 \Rightarrow 1$ |  |  |  |  |  |  |  |
| node 3 | $\rightarrow$ node 4 | 1 | 1 | 1.000 | $1 \Rightarrow 2$ |  |  |  |  |  |  |  |
|  |  | 2 | 1 | 1.000 | $1 \Rightarrow 2$ |  |  |  |  |  |  |  |
|  |  | 3 | 1 | 1.000 | $0 \Rightarrow 1$ |  |  |  |  |  |  |  |
|  |  | 4 | 1 | 1.000 | $0 \Rightarrow 1$ |  |  |  |  |  |  |  |
|  |  | 13 | 1 | 1.000 | $1 \Rightarrow 2$ |  |  |  |  |  |  |  |
|  |  | 20 | 1 | 1.000 | $1 \Rightarrow 2$ |  |  |  |  |  |  |  |
|  |  | 23 | 1 | 1.000 | $0 \Rightarrow 1$ |  |  |  |  |  |  |  |
|  |  | 26 | 1 | 1.000 | $0 \Rightarrow 1$ |  |  |  |  |  |  |  |
|  |  | 27 | 1 | 0.500 | $1 \Rightarrow 0$ |  |  |  |  |  |  |  |
|  |  | 28 | 1 | 1.000 | $1 \Rightarrow 2$ |  |  |  |  |  |  |  |
|  |  | 29 | 1 | 1.000 | $0 \Rightarrow 1$ |  |  |  |  |  |  |  |


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