Hedgehog Phylogeny (Mammalia, Erinaceidae)—the Reciprocal Illumination of the Quick and the Dead

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ABSTRACT

Over the past decade or so, considerable attention has focused on improving our ability to recover phylogeny. Paleontologists have traditionally relied on the addition of characters for more accurate phylogenies. However, other systematists have shown conclusively that, beyond a certain density of character sampling, the addition of taxa is more likely to improve our ability to identify homoplasy, and in some cases, to elucidate relationships. Although fossils have been shown to be pivotal in the reinterpretation of certain relationships, the question of how extant taxa may affect previous notions of relationships among fossil taxa has yet to be addressed.

This study focuses on the effects of including fossil taxa in a preexisting phylogenetic hypothesis of extant forms and concomitantly reevaluates the historical relationships of the fossil taxa with regard to the extant forms. The Erinaceidae (hedgehogs) were used as the test group. Considerable phylogenetic work has been done on both extant and fossil forms, although these data have never been combined within a cladistic framework. Results suggest that a trenchant reinterpretation of fossil relationships with regard to each other and the living taxa is warranted.

INTRODUCTION

What is the reciprocal effect of fossil and extant taxa on an estimate of phylogeny inferred otherwise solely from living organisms or just the fossil taxa? The investigation of

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fossil taxa has been shown to be instrumental in elucidating the evolution of higher groups of metazoans (e.g., Ostrum, 1975a, 1975b; Gauthier et al., 1988a, 1988b; DeSalle et al., 1992; Novacek et al., 1988; Novacek, 1992; Grimaldi et al., 1993). Specifically, the inclusion of fossil taxa in phylogenetic reconstructions can result in partitioning long stems (Gauthier et al., 1988a, 1988b; Novacek et al., 1988; Novacek, 1992) and resolving certain questions of character homology (e.g., Donoghue et al., 1989; Wheeler, 1990). Despite these observations, there are still those who contend that if characters from extant taxa are identified and interpreted correctly, the inclusion of fossils is superfluous (Ax, 1985, 1987; Patterson, 1977, 1981a, 1981b, 1982; Patterson and Rosen, 1977; Gardiner, 1982; Rosen et al., 1981; Nelson, 1985; Craskse and Jefferies, 1989; Loconte, 1990). Theoretically this must be true, however, one cannot infallibly identify homology or homoplasy (Felsenstein, 1978; Hendy and Penny, 1989; Huelsenbeck, 1991; Novacek, 1992; Novacek et al., 1988; Gauthier et al., 1988a, 1988b).

Regardless, there remains considerable sentiment that paleontology and neontology are distinct fields (as cited above). Neontologists are reluctant to consider fossil taxa because of their inherent missing data (Gardiner, 1982; Rosen et al., 1981; Nelson, 1985; Craskse and Jefferies, 1989; Loconte, 1990), whereas paleontologists are equally reluctant to appreciate the relevance of extant taxa in resolving fossil relationships by their lack of treatment (e.g., Winkler, 1992). Nevertheless, the significance of fossil taxa has been well demonstrated; therefore, they should be included in neontological analyses (Kluge, 1990; Eernisse and Kluge, 1993). The next logical question is the influence, if any, that extant taxa have on fossil taxa relationships. Over the years, paleontologists have reconstructed phylogenies of fossils, giving only cursory attention to the extant members of the group in question. More specifically, for practical reasons there has been a tendency to lump the extant taxa in higher taxonomic groups (i.e., families or genera), while the fossils are treated at the specific level (e.g., Flynn and Galiano, 1982; Novacek, 1985, 1987; Gaffney et al., 1990). Clearly, the principal

reason for such treatment of the extant taxa is the researchers' interest in specific fossil taxa and their phylogenetic position with respect to one another. To a lesser degree, there is some sentiment that fossil taxa will invariably be positioned phylogenetically as plesiomorphic stem lineages (Ax, 1985). With this in mind, one might conclude that the derived states of the extant forms would have little or no effect on the fossils in a phylogenetic study. Given these assumptions, it is reasonable to consider the extant taxa as single terminals at the family or generic level. It has been demonstrated that fossils tend to be plesiomorphic (Donoghue et al., 1989; Gauthier et al., 1988a, 1988b), although this is not universally true. Whether or not the "derivedness" of extant taxa can have an impact on fossils has yet to be adequately tested. Intuitively, the farther back in time a lineage is sampled, the more plesiomorphy one should detect (Huelsenbeck, 1991). However, each lineage is an exclusive chronicle, and one cannot know a priori which taxa will be pivotal in a phylogenetic analysis (Huelsenbeck, 1991).

This brings us back to the question of the relative importance of using extant taxa to help resolve relationships of fossil forms, which I address here.

ERINACEID RELATIONSHIPS

The question of erinaceid monophyly has received considerable attention from both paleontologists and neontologists (Matthew, 1903; Simpson, 1945; Butler, 1948, 1972, 1988; Van Valen, 1967; Rich, 1981; Novacek, 1985; Novacek et al., 1985; Corbet, 1988; Frost et al., 1991), and thus lends itself well for addressing the mutual effects of extant and extinct taxa in a phylogenetic analysis. Early hypotheses of erinaceid relationships were based on overall similarity (Simpson, 1945; Butler, 1948, 1972; Van Valen, 1967). With the advent of cladistic methodology, erinaceomorphs have been reexamined using the rule of synapomorphy in an attempt to discover monophyletic groups. Unfortunately, these studies were restricted predominantly to either fossil taxa (Rich, 1981; Novacek, 1985; Novacek et al., 1985) or only the living forms (Corbet, 1988; Frost et al.,

1991). Despite the paleontological/neontological polarization in erinaceid research, prior work has greatly facilitated the collection of data for this project.

Extant erinaceids are known from Africa, Europe, and Asia. Fossil taxa have also been recovered from these regions, as well as from North American sediments older than the Pleistocene (Butler, 1948, 1972, 1988; Van Valen, 1967; Rich, 1981; Novacek, 1985; Novacek et al., 1985). Currently, the family Erinaceidae is divided into four subfamilies (see table 1): Erinaceinae (spiny hedgehogs), Hylomyinae ([= Galericinae = Echinosoricinae; Frost et al., 1991] gymnures), Tupaiodontinae (Asian fossil forms), and the Brachyericinae, a North American fossil group (Butler, 1948, 1988; Rich, 1981; Novacek, 1985; Novacek et al., 1985; McKenna and Holton, 1967).

The most comprehensive (and most recent) phylogeny of the extant taxa (Frost et al., 1991) recognizes two distinct monophyletic groups; the Hylomyinae and the Erinaceinae. Overall, the findings of Frost et al. corroborate what other systematists have claimed previously (Butler, 1948, 1972, 1988; Rich, 1981; Corbet, 1988). The most significant contribution by Frost et al. (1991) in the understanding of erinaceid phylogeny is a tree well supported by apomorphies discovered through the application of Phylogenetic Analysis Using Parsimony (PAUP) of Swofford (1993), which was unavailable to previous investigators.

The Southeast Asian Hylomyinae (or moonrats) are a monophyletic group comprising the living genera *Hylomys* (including *Neotetracus*), *Podogymnura* and *Echinosorex*. Paleontologists have historically considered the fossil taxa *Galerix* (Europe and Africa), *Lanthanotherium* (Europe and California) and *Neurogymnurus* (Europe) as basal hylomyines (Butler, 1948, 1972, 1988; James, 1963; Novacek, 1985; see table 1). The living Erinaceinae (spiny hedgehogs from Europe, Africa, Asia and the Middle East) are the second monophyletic group recognized. Many fossil taxa have been considered basal members of this group, including several North American fossils (see table 1 for listing). Other than the discord regarding *Proterix*, a North American taxon at different times considered

either a hylomyine (McKenna and Simpson, 1959) or an erinaceine (Gawne, 1968; Bjork, 1975; Rich, 1981), investigators of the erinaceids have generally agreed on the taxonomic positions assigned to the fossil taxa (see table 1).

MATERIALS AND METHODS

The present study mirrors the Frost et al. (1991) analysis of extant erinaceids. Identical outgroup criteria (leptictids + soricoids + tenrecoids) were employed. Briefly, Lipotyphla (soricoids + tenrecoids + erinaceids [+ leptictids]) has been demonstrated to be a monophyletic group (MacPhee and Novacek, 1993), although within-group hierarchy is yet unknown. As such, ancestral states were determined by total congruence of the character states among the three outgroups. Incongruence of states resulted in coding the ancestor as unknown ("?").

All of the Frost et al. (1991) transformation series, except for two arguable characters (their #15 and #43; see below for explanation) were employed in this study. Additional character states were incorporated (see marked transformation series, appendix 1) to accommodate the fossil taxa; an additional 18 transformation series (obtained from the literature) were added (Gawne, 1968; Rich, 1981; Novacek, 1985; MacPhee et al., 1988); and three new transformation series were identified. In addition, a number of transformation series from both Frost et al. (1991) and MacPhee et al. (1988) (refer to appendix 1) were recast to correct ambiguities. Some multistate transformation series were subdivided into binary transformation series to improve detectability of characters along the two main branches (see appendix 1, transformation series 20, 21, 46–51, 97, 98, 100, and 101). In total, 103 transformation series and 26 taxa (not including the three outgroups) were considered in this analysis. The ordering of character states is discussed in appendix 1 for those transformation series in need of explanation. See appendix 3 for a comprehensive list of the ordered multistates.

Analysis of the data was executed using the PAUP program, version 3.1.1 (Swofford, 1993) using the heuristic random stepwise addition option; collapse all zero length

TABLE 1
Current Classification of the Erinaceidae (McKenna, Bell, and others, MS on file)
(−) indicates taxa represented by fragmentary material, specifically jaws and isolated teeth. * indicates taxa not available for this study (i.e., they are on loan to another researcher, or they are type specimens that cannot leave their home institutions).

Order Erinaceomorpha Gregory, 1910
  Family Erinaceidae Fischer de Waldheim, 1817
    Subfamily Tupaiodontinae Butler, 1988
      (−)*Entomolestes* (early Eocene, Europe; middle Eocene, ?; late Eocene, North America)
      (−)*Tupiadon* (middle Eocene, Oligocene, Asia)
      Changlelestes (early Eocene, Asia)
      (−)*Ictopidium* (late Eocene–early Oligocene, Asia)
    Subfamily Galericinae Pomel, 1848 (= Hylomyinae of Frost et al., 1991)
      Tribe Galericini Pomel, 1848
        (−)*Eochinus* (middle Eocene, Asia)
        Galerix (early Oligocene–early Pliocene, Europe; early Miocene, Africa; middle and late Miocene, Asia)
        (−)*Tetracus* (Oligocene, Europe)
        (−)*Ocajila* (late Oligocene–early Pliocene, Europe; early Miocene, Africa; middle and late Miocene, Asia)
        (−)*Pseudogalerix* (early Miocene–late Miocene, Europe)
        Lanthanotherium (Miocene, Africa; middle–late Miocene, Europe; middle–late Miocene, North America)
        Echinosorex (?middle Miocene, Asia [Russia]–present, Asia [Indonesia])
        (−)*Schizogalerix* (middle Miocene–early Pliocene, Asia; late Miocene–?early Pliocene, Africa;
             late Miocene, Europe)
        (−)*Deinogalerix* (late Miocene, Europe)
        Hylomys (= *Neotetracus* and *Neohylomys*) (late Miocene–Recent, Asia; Recent, Asia [East Indies])
        Podogymnura (Recent, Indies, Philippines?)
      Tribe Neurogymnurini Butler, 1948
        Neurogymurus (late Eocene–late Oligocene, Europe)
      Tribe Protericini Butler, 1948
        Proterix (early Oligocene, North America)
    Subfamily Erinaceinae Fischer de Waldheim, 1817
      Tribe Amphechinini Gureev, 1979
        Amphechinus (early–late Oligocene, middle Miocene, Asia; ?early Oligocene, late Oligocene– late
             Miocene, late Pliocene and/or early Pleistocene, Europe; early–middle Miocene, North America)
        (−)*Palaeoscaptor* (late Oligocene, Asia)
        Parvericius (late Oligocene, Asia; early–middle Miocene, North America)
        (−)*Dimylechinus* (early Miocene, Europe)
      Tribe Erinaceini Fischer de Waldheim, 1817
        Gymnurechinus (early Miocene, Africa)
        Stenoechinus (early Miocene, North America)
        Untermannerix (middle–late Miocene, North America)
        Mioechinus (middle Miocene, Asia and Europe)
        Erinaceus (including *Atelerix* and *Mesechinus*) (?late Miocene, early Pliocene–Recent, Asia; ?late
             Miocene, Pleistocene, Recent, Europe; Pleistocene–Recent, Africa; Recent, Mediterranean,
             Atlantic, New Zealand)
        Paraechinus (= *Hemiechinus senus* Frost et al., 1991) (late Pleistocene–Recent, Asia; Recent, Africa)
        Hemiechinus (late Pleistocene–Recent, Asia; Recent, Africa)
    Subfamily Brachyericinae Butler, 1948
      (−)*Exallerix* (Oligocene, Asia)
      (−)*Metexallerix* (late Oligocene and/or early Miocene, Asia)
      Brachyerix (early–late Miocene, Asia)
      Metechinus (late Miocene, North America)
Incertae sedis
      (−)*Litolestes* (middle–late Paleocene, North America)
      (−)*Cedrocherus* (late Paleocene, North America)
      (−)*Scaptogale* (Miocene, Europe)

branches. Both accelerated (ACTRAN) and delayed (DELTRAN) optimizations were considered.

Fossil taxa included in this analysis were chosen based on the following criteria:

1. Taxa were required to be represented by more than jaws or isolated teeth. This criterion is necessary due to the difficulty of resolving relationships when there is a paucity of data (Wible, 1991), a problem compounded by ambiguous character assignment where information is lacking (Platnick et al., 1991). I am not suggesting that fragmentary material should be excluded from a phylogenetic analysis, on the contrary, but for the purpose of this study I attempted to minimize the effects of missing data. *Galerix* is the single fossil incorporated in this analysis that is composed solely of fragmentary material (a palate, almost the entire dentition, and the posterior portion of the maxilla). The reason for its inclusion is that those characters which have historically defined the "galericines" (= hylomyines sensu Frost et al., 1991) are observable in *Galerix* (see Results for discussion of these characters).

2. Taxa chosen are members of the Erinaceidae as currently defined (Butler, 1948, 1972, 1988; Rich, 1981; Novacek, 1985). Note that Tupaiodontinae is excluded from this analysis because it is only represented by dental material.

3. Character evaluation must be based on direct specimen examination. With exceptions noted below, I included only those fossil taxa that could be examined directly. Members of the erinaceine tribe Amphiechinini (Rich, 1981) were unavailable to me at the time of this analysis (see table 1) and were therefore not treated.

Previously reported characters were reviewed on all specimens of the living taxa except for the rare species *Podogymnura aureospinula*, *Hylomys hainanensis*, *Atelerix sclateri*, *A. algirus*, and *Erinaceus amurensis*, for which I relied on the Frost et al. (1991). Many of the fossils included are those figured by Butler (1948), Gawne (1968), James (1963), and Rich (1981 [see table 1]). All the fossils examined were original specimens except *Lanthanotherium* for which only a cast was available. Accordingly, much of the data on foramina and dental roots in this taxon

were taken from James' (1963) descriptions. Auditory characters extracted from MacPhee et al. (1988) could only be observed on those specimens that had been previously prepared (i.e., ingroup figured specimens, see Butler, 1948; Gawne, 1968; Bjork, 1975; Rich, 1981; Frost et al., 1991). Thus, much of the outgroup coding for these auditory characters (46–55, appendix 1) follows the observations of MacPhee et al. (1988). Inaccessibility of the type specimen of *Neurogymnurus* precluded review of the MacPhee et al. (1988) auditory characters. Accordingly, those transformation series were left uncoded for this taxon. In the case of *Metechinus*, positive identification of some characters (47–54, appendix 1) was difficult, and coding was based on available literature (Rich, 1981; MacPhee et al., 1988).

Characters omitted:

Most characters treated in this analysis have been previously addressed in the literature. To avoid duplication of characters because descriptions differ, all characters were reevaluated. Some transformation series of previous authors were not incorporated in this analysis (see discussion below).

Many of the "finer" dental characters (e.g., greatly reduced hypoconulid [Krishtalka, 1976]) were omitted from this analysis because they were obviated by individual variation (personal obs.). Many of these characters (e.g., size of different cusps, [Rich, 1981], presence/absence of cuspules, cingula, etc. [Krishtalka, 1976; Rich, 1981]) have not been addressed adequately in terms of variation (in progress). Without a better understanding of intraspecific variation within extant taxa (e.g., quantitative studies of the transformation series in question), I am reluctant to cite such character states as "potential" apomorphies when fossil taxa are represented by only a few fragmentary specimens.

Frost et al. (1991)—characters excluded from this analysis:

1. Frontal inflation (Butler, 1948; Frost et al., 1991, character #15)—Closer examination of this feature suggests it is a manifestation of another character (#29, Frost et al., 1991), the "height of the frontals relative to parietals." There is a distinct correlation in these two characters: the degree of dorsal inflation of the frontals is proportional to their

height within this group. Deletion of this character had no effect on the Frost et al. (1991) tree topology, but I was reluctant to retain a character that could be redundantly weighting another.

2. Basioccipital condylar foramen location (Novacek, 1986; Frost et al., 1991, character #43)—The conditions in this transformation series are apparently dependent on another Frost et al. (1991) character (#42): whether the condyle has a singular or pleural lobe. The placement of the foramen on the suture is directly related to the emargination of the condyle as observed by Butler (1948).

Fossil erinaceids from North America were reviewed by Butler (1948, 1972, 1988) and more extensively by Rich and Rich (1971) and Rich (1981). Rich's treatment of these fossils established a set of diagnostic features for the North American subfamily and tribes Brachyericinae, Erinaceini, and Amphiechini (the latter not treated in this analysis), based on cladistic methods. All of Rich's characters were reviewed.

Rich (1981) characters excluded from the analysis:

1. Height of P4 hypocone equal to or greater than that of the protocone—My examination of *Metechinus* and *Brachyerix* does not indicate that the hypocone is greater in height than the protocone.

2. Greater reduction of the mandibular angle—I was unable to verify this feature because the ascending ramus is present in only one of the available specimens of *Metechinus* (AMNH F:AM 76698). No ascending rami were preserved in the two specimens of *Brachyerix* available to me.

3. Deep zygomatic arch—Although *Brachyerix* does display this condition, it is unknown whether *Metechinus* also shares this condition. None of the specimens of *Metechinus* examined retain the zygomatic arch.

4. Large size of the I1—Rich noted that an enlarged I1 is shared by both the Amphiechini and Brachyericinae. Only the alveoli of the upper incisors are preserved in the *Metechinus* and *Brachyerix* specimens. Although it is very likely that both taxa had large incisors, other taxa share this feature (*Echinosorex, Hylomys*, some *Atelerix, Hemiechinus*, and *Erinaceus*). Intraspecific vari-

ation and overlapping interspecific variation makes the transformation series difficult to characterize. Also, without access to the amphiechinid material I was unable to investigate this transformation series adequately.

5. Absence of a postcingulum on the lower molars—Presence or absence of the postcingulum shows intraspecific variation in the taxa reviewed. Preliminary investigation of this feature suggests that the condition of the postcingulum is dependent on a number of variables (e.g., extension of the medial cingulum, which tooth, and how much wear).

RESULTS

PAUP discovered 66 most parsimonious trees with a length of 199 (consistency index = 0.593, excluding uninformative characters; retention index = 0.846); figures 1A and 1B represent the strict consensus tree (Sokal and Rolf, 1981; Page, 1981) and Adams tree (Adams, 1972, 1986), respectively, of the 66 most parsimonious trees. For purposes of comparing strict consensus trees among studies (and easy referral for the reader), I have included the strict consensus tree of Frost et al. (1991) representing the living taxa within Erinaceidae (fig. 2).

Of the 66 trees discovered, only 12 reflect topologies that are not dependent on character optimization choices (see figs. 3–7, 9; appendix 2 lists all apomorphies by stem). Of these 12, four tree-pairs (figs. 3B, 4, 6, and 7) are differentiated only on the placement of *Mesechinus* (figs. 8A and 8B, see discussion under section of *Mesechinus*), two are unique (figs. 3A and 5), and finally, there are two differing topologies within the *Hylomys* clade depending on the phylogenetic position of *Lanthanotherium* (figs. 3–7).

As evidenced by the strict consensus tree (fig. 1A), limited resolution of the fossils is obtained. This is primarily due to the conflicting placements of *Galerix* and *Lanthanotherium* with respect to all of the other taxa. A difficulty with consensus trees is that they do not necessarily reflect any of the phylogenetic hypotheses discovered in an analysis (Barrett et al., 1991). An alternative to the strict consensus tree is the Adams tree (Adams, 1972). Adams trees can portray stable
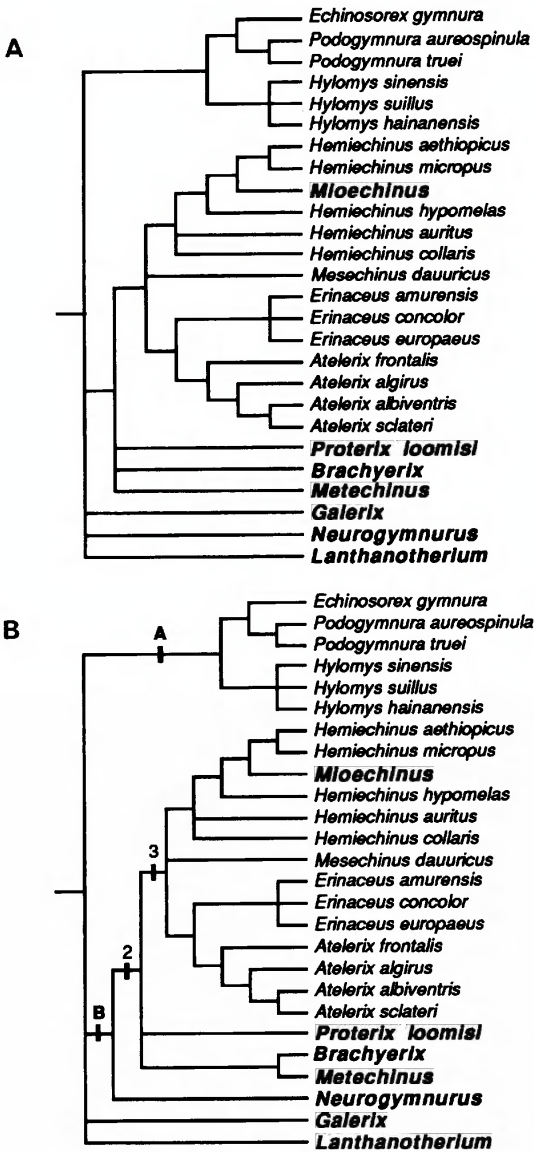
A

B

Fig. 1. (A) The strict consensus tree of the 66 trees discovered; (B) Adams consensus tree. See text for discussion of the indicated stems.

Fig. 2. The single most parsimonious tree discovered in the Frost et al. (1991) analysis. See text for discussion of the indicated stems.

component topologies. In other words, the algorithm identifies those taxa that are phylogenetically unstable and effectively places them as incertae sedis within their most inclusive monophyletic group. Consequently, relationships that are constant in all the discovered topologies are preserved. The strict consensus tr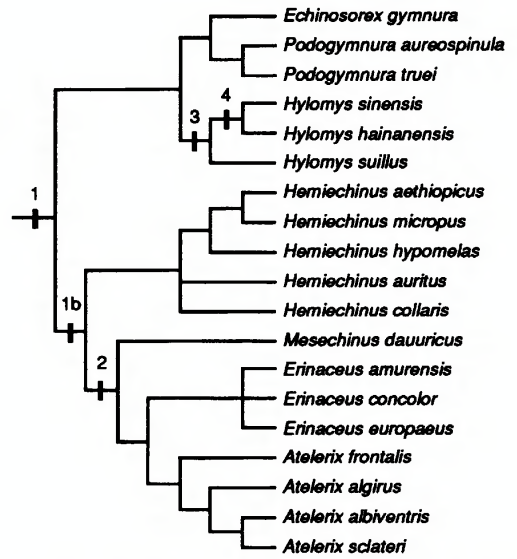ee (fig. 1A) is misleading with respect to some of the fossil taxa; it suggests a lack of resolution among purported basal galericines (*Neurogymnurus*, *Galerix*, and *Lanthanotherium*). The Adams tree (fig. 1B), on the other hand, identifies the two taxa (i.e., *Galerix* and *Lanthanotherium*) responsible for the polytomy at the base of the strict consensus tree (fig. 1A) while retaining the stability of the phylogenetic placement of *Neurogymnurus*. Thus, I have chosen to use the Adams tree to illustrate erinaceid phylogeny.

As shown by a comparison of the Adams tree (fig. 1B; and strict tree, fig. 1A) and the Frost et al. (1991) strict consensus tree (fig. 2) of extant taxa, the fossils had little effect on the relative topology of the extant taxa (see section on *Mesechinus* and *Hylomys* for more discussion). Clade A (fig. 1B), the Hylomyinae, remains stable (however, see discussion of *Hylomys*) as well as clade B, the extant Erinaceinae (+ *Neurogymnurus* + *Proterix* + Brachyericinae), except for *Mesechinus* as mentioned above. Conversely, a trenchant reinterpretation of the historical relationships among fossils is required after consideration of extant material.

In short, the following taxa are discovered to have different phylogenetic affinities than

were previously considered (for further discussion of previous hypothesis, see corresponding sections on the taxa reviewed): (1) *Mioechinus* (from the Miocene of Switzerland) is nested well within *Hemiechinus* (specifically part of the clade previously considered to be the genus *Paraechinus*, figs. 1A and 1B); (2) *Proterix* is placed within clade B (fig. 1B) rather than within the hylomyine (= galericine) clade (fig. 1B, clade A; contra McKenna and Simpson, 1959); (3) *Neurogymnurus* (and sometimes *Galerix*, see discussion below) is more closely related to the extant erinaceines (fig. 1B) than to hylomyines (contra Butler, 1948, 1972, 1988; Novacek, 1985), although the evidence is weak; (4) *Lanthanotherium*, contrary to previous hypotheses regarding its close affinities with the hylomyines (James, 1963), is sometimes considered a sister taxon of clade B (figs. 4–7); (5) some evidence suggests that *Proterix* might be a brachyericine (fig. 7); (6) it is as parsimonious to consider *Mesechinus* as either the sister taxon to the Erinaceinae (defined by Frost et al., 1991), or the sister taxon of the *Erinaceus* + *Atelerix* clade as discovered in the Frost et al. (1991) analysis (figs. 8A and 8B); and finally, (7) the sister-taxa relationship of *Hylomys suillus* and *H. sinensis* (Frost et al., 1991) is suspect (figs. 3A and 3B).

The most problematic aspect of analyzing a matrix with considerable missing data is the difficulty in assigning the evidence to specific stems. Consequently, it is crucial to evaluate all character states that support stems and to recognize if the taxa have been assigned such states by virtue of missing data. That is, character-state assignment may be an artifact of PAUP fulfilling the parsimony criterion by optimizing "unknown" characters a posteriori down the stem until it encounters incongruence. Consequently, I have reviewed all stem assignments and noted those characters that are the products of missing data and therefore subject to misinterpretation.

Following are discussions of the discovered apomorphies. I restrict discussion to those aspects of the Adams tree (fig. 1B) that are depicted as polytomies because of conflicting phylogenetic hypotheses of the taxa in question (except for *Erinaceus*, which was discussed by Frost et al. [1991]). All other stem support is listed in the apomorphy list (appendix 2).

Erinaceidae

The family Erinaceidae is consistently supported by 5 characters in all 12 topologies in this analysis (figs. 3–7, stem 1 [numbers in parentheses refer to character number in Appendix 1]):

(13.1) Fusion of the lacrimal/maxilla suture—This character is not preserved in *Galerix*, *Proterix*, *Lanthanotherium*, and *Mioechinus* and is reversed in *Mesechinus*.

(20.1) Presence of suboptic foramen.

(43.1) A closed basioccipital/petrosal suture—This feature is not preserved in *Galerix*, *Proterix*, and *Lanthanotherium*.

(79.1) P4 lingual roots unfused—The condition of the lingual roots reverses three times; *Galerix* (two roots fused), *Brachyerix* (one root), and the extant erinaceines (two roots fused, figs. 3–7, stem 6). This condition in *Proterix* and *Mioechinus* is not preserved. This transformation series was not recognized as a synapomorphy in the Frost et al. (1991) analysis because it was dependent upon optimization. Both the extant hylomyines and erinaceines exhibit differing derived conditions, thus it was equally parsimonious for either condition to arise along this stem (see fig. 2, stem 1). Consideration of the fossil data suggests that the unfused root condition is synapomorphic not only for the Hylomyinae, but is also shared among some of the fossil taxa found within clade B (fig. 1B).

(80.1) Lower molars with a low trigonid and expanded talonid approximately equal in size to the trigonid—This transformation series was recognized by Novacek (1985) and Frost et al. (1991) as diagnostic for Erinaceidae. There is no data for *Mioechinus*.

See appendix 2 for all other topology-dependent evidence for the monophyly of the Erinaceidae.

Lanthanotherium

The results of this analysis suggest that the hypotheses regarding the phylogenetic position of *Lanthanotherium* within the Erinaceidae is tentative. James (1963) considered *Lanthanotherium* to be a hylomyine (= galericine). His hypothesis is supported here by

two apomorphies related to the condition of the M3 cusps (86.1 ["metastylar spur" present and developed], 87.1 [M3 metacone small], appendix 1; figs. 3A and 3B, stem 10). The metacone is present and small (87.1) in the hylomyines and *Lanthanotherium*; in *Galerix* and *Neurogymnurus* it is well developed (as in the outgroups) and is lost in extant erinaceines (figs. 3A and 3B, stem 6). The M3 is lost in *Brachyerix* and *Metechinus* (87.2, figs. 3A and 3B, stem 9) and unknown in *Proterix*. If *Lanthanotherium* is considered a hylomyine, then the M3 metacone conditions transform in two positions on the cladogram, ancestrally large → small (hylomyines + *Lanthanotherium*), and ancestrally large → absent (extant erinaceines [fig. 3B, stems 10 and 6, respectively]). This transformation series (87.1, appendix 1) was treated as additive in this analysis, although when treated as nonadditive, there was no topological effect on the recovered trees.

The presence of a fourth cusp on the M3 (86.1, appendix 1) is unique to the extant hylomyines and *Lanthanotherium*. If *Lanthanotherium* is considered the sister taxon of clade B (figs. 4–7, see stems 2a or 2b), the presence of the fourth cusp is independently gained twice, or a reversal to the ancestral state in clade B above the level of *Lanthanotherium* is postulated (figs. 4–7, stems 2b or 2c).

The placement of *Lanthanotherium* as a sister taxon of clade B (figs. 4–7, stems 2a or 2b) is supported by two unambiguous transformation series, the posterior extension of the nasals (1.1, appendix 1), and the absence of a posterior spine on the palatal shelf (25.1, appendix 1). The condition of the nasals is unknown in *Galerix* and *Mioechinus,* although all other taxa within clade B (figs. 4–7) exhibit the derived condition of the nasals (posterior extension beyond the antorbital rim). With respect to the absence of a posterior spine on the palatal shelf (25.1), there are no data for *Galerix, Proterix, Metechinus,* or *Mioechinus.* Distribution of this transformation series within the Erinaceidae suggests a reversal to the ancestral condition (25.0) for extant erinaceines (figs. 3–7, stem 6), with the derived condition (25.1) independently arising in *Podogymnura, Hylomys sinensis,* and *Atelerix.*
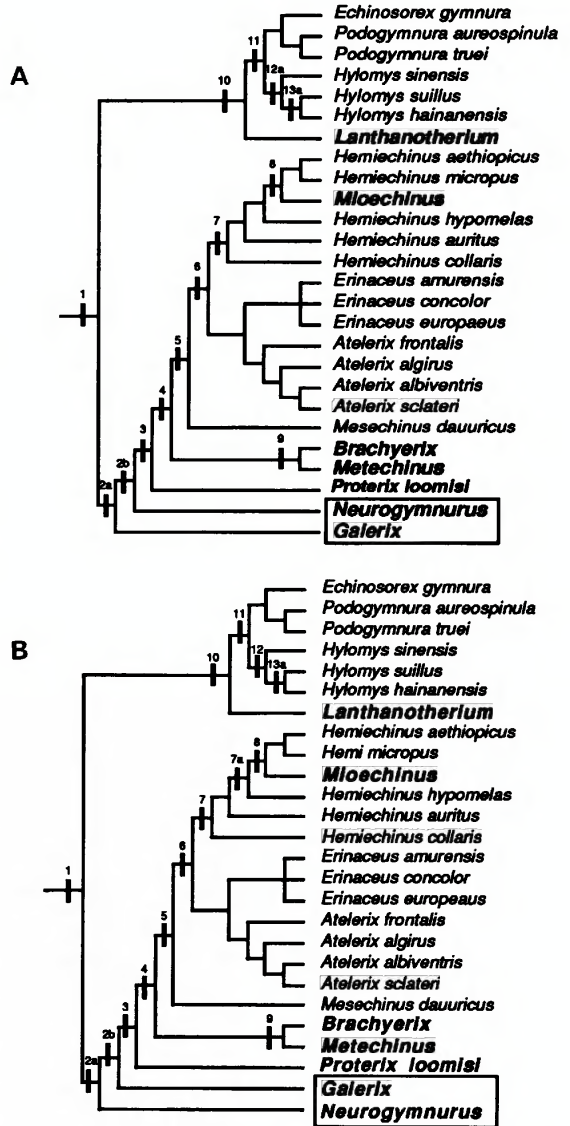

Fig. 3.   A and B are alternative topologies for *Galerix* and *Neurogymnurus,* given the placement of *Lanthanotherium* as the sister taxon to the extant hylomyines (sensu Frost et al., 1991). See text for discussion of the indicated stems.

Clearly the evidence supporting *Lanthanotherium* as either a hylomyine (clade A) or more closely related to clade B is very weak. As noted in the Materials and Methods section, the specimen of *Lanthanotherium* reviewed was a cast and some morphological structures were impossible to see. A critical review of original material is warranted be-
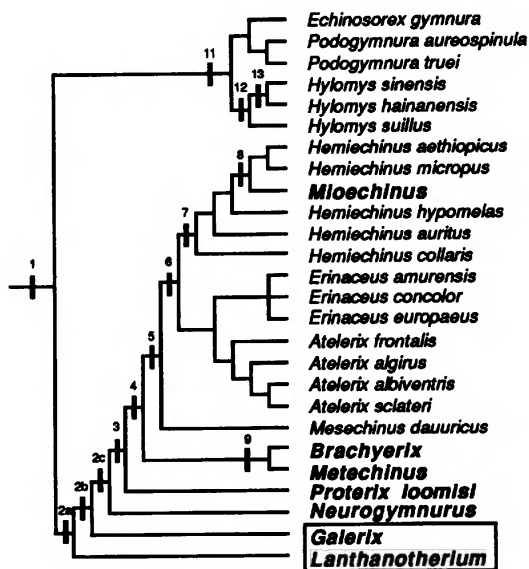
Fig. 4. A discovered phylogenetic hypothesis of *Galerix* and *Lanthanotherium* with respect to clade B (stem 2b). See text for discussion of indicated stems.

fore alternative phylogenetic hypotheses can be pursued further.

Galerix

Of the ten most parsimonious trees discussed in this analysis, there are five alternative placements for *Galerix* (see figs. 3A, 3B, 4, 5, and 6).

Galerix has been identified previously as the most basal of the galericines (= hylomyines [Butler, 1948; Novacek, 1985]). Although this hypothesis is only weakly rejected, a consideration of all the evidence places *Galerix* as either more closely related to clade B (as the sister taxon of *Neurogymnurus*, or the sister taxon of clade B [figs. 3–5, stems 2a or 2b]), or as the sister taxon of the remaining Erinaceidae (fig. 6, stem 1).

The placement of *Galerix* as the sister taxon of clade B (fig. 3A, stem 2a; fig. 4, stem 2b), or as a basal taxon within clade B (fig. 3B, stem 2; figs. 5–7, stem 4) is dependent on two factors: (1) its relationship to *Neurogymnurus* (fig. 3A, stem 2a; fig. 4, stem 2b), and more importantly, (2) on a posteriori character assignment of missing data in the other fossils. The evidence for *Galerix* as the

sister taxon of all the members of clade B (fig. 3A, stem 2a)—fusion of the M1 lingual roots—is admittedly minimal (82.1, appendix 1). On the other hand, all taxa included within this clade possess this feature except *Metechinus*, which exhibits a reversal to the ancestral state—separate roots, as seen in the extant hylomyines. A concern is the effect of *Neurogymnurus* which had been left uncoded for this transformation series because radiographs of the upper and lower jaws were not available, and further preparation on the type specimen was not possible. Therefore, although the fusion of the M1 lingual roots is unique for clade B + *Galerix*, its consideration as evidence for stem support is arguable. Identification of this character state (82.1) as an apomorphy may be an artifact of missing data.

Alternatively, it is equally parsimonious for *Neurogymnurus* to be considered the sister taxon of *Galerix* + clade B (fig. 3A, stem 2b). The evidence in this case (characters 10.2, 30.1, 44.1) is based on a posteriori character assignment of missing cells in the data matrix for *Proterix* and *Galerix*.

The third hypothesis for the phylogenetic position of *Galerix* within clade B is as the sister taxon of *Neurogymnurus* (figs. 5 and 7, stem 2b). The stem uniting *Galerix* + *Neurogymnurus* as the basal group in clade B (figs. 5 and 7, stem 14) is always supported by the fusion of the M1 lingual roots (82.1, appendix 1), as well as an upper canine approximately equal in size to the postcanines (64.2, appendix 1), although the latter is dependent on tree topology.

The relative size of the upper canine (64, appendix 1) is identified as a synapomorphy uniting *Galerix* + *Neurogymnurus* and all the other members of clade B only if *Proterix* is recognized as the sister taxon of *Brachyerix* (fig. 7, stem 9b; see discussion of *Proterix*). I considered this multistate transformation series (64, appendix 1) nonadditive and postulated the ancestral condition according to the outgroup criterion. Despite the lack of constraints (nonadditivity) on this transformation series, its transformation distribution within Erinaceidae is governed by other conflicting data. The net result is that the three-condition transformation series, when placed on the cladogram, is six steps long, which
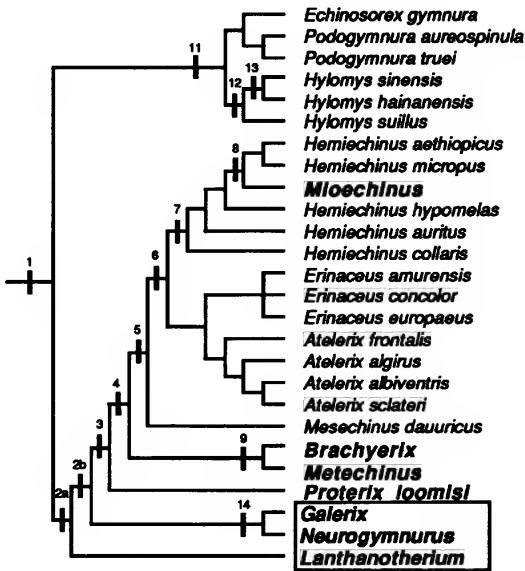
Fig. 5. A discovered phylogenetic hypothesis of *Galerix* and *Lanthanotherium* with respect to clade B (stem 2b). Note that *Galerix* is here considered the sister taxon to *Neurogymnurus*. See text for discussion of indicated stems.
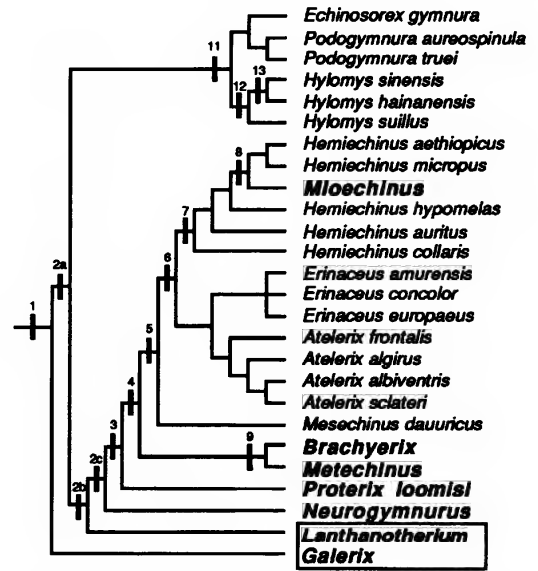
Fig. 6. A discovered phylogenetic hypothesis of *Galerix* as the sister taxon to both clades A and B (stems 11 and 2b, respectively) with *Lanthanotherium* as the sister taxon to clade B (stem 2c). See text for discussion of indicated stems.

seems counter-intuitive to the succession of an ancestrally large canine (with respect to postcanines) → only slightly larger canine → canine equal in size to the postcanines as posited by Frost et al. (1991). In other words, the topology of the tree suggests that the canine reduces and then independently increases in size three times (*Galerix*, *Proterix*, and *Metechinus*).

The sister-taxa relationship of *Neurogymnurus* + *Galerix* depicted in figures 5 and 7 (stem 14) is supported by a reversal to the ancestral condition of a large metacone on the M3 (87.0, appendix 1). As discussed above, homology assessment of this particular dental character within erinaceids is arguable, and I have little confidence for a postulated sister-taxa relationship of these fossils.

The fourth alternative for a phylogenetic position of *Galerix* is that of a sister relationship to Erinaceidae (fig. 6, stem 1). This phylogenetic hypothesis is corroborated by four putatively unambiguous transformation series: (1) the anterior opening of the infraorbital canal is dorsal to P3 (6.1); (2) the antorbital flange is continuous around the

lacrimal canal (9.1); (3) a broad coronoid process (59.1); and (4) c1 is greater in size than the p1 (67.1, appendix 1). Character support is dependent primarily on optimization of the extant hylomyine stem (fig. 6, stem 11). That is, the two clades within the hylomyines exhibit differing conditions for each of the four transformation series. When *Galerix* is considered the sister taxon of Erinaceidae, unambiguous evidence is identified endorsing one of the optimization choices.

Clearly, the phylogenetic position of *Galerix* is elusive with the available data. Thus, I cannot justify favoring one hypothesis over another.

As mentioned previously, Butler (1948) considered *Galerix* a basal galericine (= hylomyine) for a number of interrelated reasons: (1) its possession of characters considered diagnostic of the hylomyines, (2) its age (early Oligocene-late Miocene), and (3) the then-current view that paraphyly was not a significant problem. Following are characters cited by Butler (1948) to support his hypothesis which are addressed in this analysis (those characters not included were shown to be nondiagnostic by Frost et al. [1991]):

1. Condition of M3 metacone (87.1, appendix 1)—Butler (1948) and Frost et al. (1991) hypothesized that the M3 transformation series (relative size of the metacone) was additive and assumed that the well-developed condition of the metacone in *Galerix* and the outgroups were necessarily primitive. Evidence discovered in this analysis suggests that the condition of the M3 metacone in *Galerix* is possibly a reversal to the ancestral state.

2. A strongly developed antorbital flange that obstructs the lacrimal canal from lateral view (8.1, appendix 1)—The development of the antorbital flange, as discussed above, is diagnostic of Erinaceidae, with a reversal occurring in the erinaceine + brachyericine + *Proterix* clade (fig. 1b, stem 2 [Butler, 1948; Rich, 1981]). Butler (1948) assessed the distribution of this character correctly, and cited it as diagnostic of the Hylomyinae (= Galericinae of Butler and most previous authors). Other evidence discovered in this analysis unites the previously believed fossil hylomyines (*Galerix, Neurogymnurus,* and *Lanthanotherium*) more closely to erinaceine + brachyericine + *Proterix* clade suggesting that the transformation of the antorbital flange occurred higher up the stem in clade B (fig. 1B, stem 2).

3. A long snout (2.0, appendix 1)—Frost et al. (1991) refined this character to exact proportions (e.g., percentage of snout length with respect to overall skull length). Even so, the condition of a long snout is shared with the outgroups, and therefore cannot be considered a synapomorphy of Hylomyinae due to the effect of fossils within clade B.

4. Large canines (64–67, appendix 1)—The distribution of this feature is ambiguous, and therefore cannot be regarded as diagnostic.

5. P3 with three roots (75.0, appendix 1)—Three roots is the primitive state. A reduction in the number of roots is convergent in *Hylomys*, and the *Hemiechinus*, as well as the *Atelerix* clades.

Neurogymnurus

Neurogymnurus (figs. 20 and 21) has been considered a hylomyine (= galericine; Butler, 1948) or the sister taxon of the Hylomyinae (Butler, 1988). Recovered evidence in this analysis suggests *Neurogymnurus* to be a member of clade B (fig. 1B); that is, more closely related to the erinaceines + brachyericines than to hylomyines.

Apomorphies discovered in this analysis uniting *Neurogymnurus* with clade B (fig. 1B, stem 1) must be considered within the framework of a possible sister taxa relationship with *Galerix*. As discussed above, much of the evidence to support *Neurogymnurus* (and *Galerix*) is contingent on optimization of missing data. Alternative phylogenetic relationships of *Neurogymurus* as the basal taxon in clade B (figs. 1B, 3A, 3B, 4, and 5, stems 2a, 2b, and 2c) are much the same as those discussed for *Galerix* (transformation series 64.2 and 82.1, appendix 1). The derived condition of an enlarged i1 (60.0, appendix 1) unites *Neurogymnurus* with all other members of clade B (an enlarged i1 is also convergent in *Hylomys sinensis*). The ancestral condition of a small i1 changes at the level of *Neurogymnurus* (fig. 1B, stem B) to an enlarged i1, a condition shared with *Proterix* and the brachyericines. The tooth is then lost in extant erinaceines (fig. 1B, stem 3).

The evidence for the placement of *Neurogymnurus* is minimal, but unlike *Galerix* and *Lanthanotherium*, its position is *always* as a basal taxon in clade B (fig. 3A, 3B, 4, and 5). Although *Neurogymnurus* shares many symplesiomorphies with the hylomyines (and *Lanthanotherium* + *Galerix*), it also shares derived features with clade B (1.1, 30.1, 44.1, appendix 1). Despite the lack of resolution of *Neurogymnurus* in the strict tree (fig. 1A), the given evidence contradicts the previous hypothesis that *Neurogymnurus* is more closely related to the hylomyines (Butler, 1948: figs. 3–7).

Proterix

Proterix has long been considered a primitive erinaceine (Matthew, 1903; Butler, 1948; Gawne, 1968; Bjork, 1975). It has been suggested that *Proterix* might be more closely related to the galericines or the tupaiodontines on the basis that "primitive" erinaceines (i.e., fossils) were otherwise unknown from Eurasia (McKenna and Simpson, 1959, although they acknowledged shared characters with the erinaceines). *Proterix* has also

been placed outside of Erinaceidae proper (i.e., the brachyericines, erinaceines, and hylomyines) and has been considered to be a basal erinaceid (Butler, 1988). In this analysis *Proterix* can alternatively be considered the sister taxon of the extant erinaceine + brachyericines clade (figs. 3–6, stem 3), or the sister taxon of *Brachyerix* (fig. 7, stem 9b). In either interpretation, *Proterix* is consistently supported as a member of clade B by 4 apomorphies: 8.0 (undeveloped antorbital flange), 68.1, 69.1 (absence of P1/p1 respectively), and 71.1 (one P2 root, or 2 roots fused [see appendix 1 for discussion of each transformation series]), although the latter character is suspect because of its homoplastic behavior within the ingroup.

Of the apomorphies supporting the monophyly of Brachyericinae + *Proterix* (see discussion under *Brachyerix* + *Metechinus* below), only one is observable in *Proterix*—the absence of p2 (70.2, appendix 1). All other support is a result of a posteriori character assignment by PAUP.

Synapomorphies postulated for *Proterix* + *Brachyerix* are: (1) the posterior extension of the squamosal resulting in a flangelike structure that projects as far back as the occipital (36.1, appendix 1); and (2) a reversal to the ancestral condition of the presence of an antorbital fossa (7.0, appendix 1). Bjork (1975) reviewed a number of well preserved *Proterix* specimens that were not available to me. He noted that one specimen has a very deep zygomatic arch (an apomorphy postulated by Rich [1981] for Brachyericinae monophyly). I suspect that a more comprehensive review of all the preserved otic regions of *Proterix* would more adequately address the question of *Proterix* + brachyericine monophyly (see below for discussion of auditory characters for brachyericines).

Brachyerix and *Metechinus*

The sister taxa, *Brachyerix* + *Metechinus* (brachyericines, figs. 22 and 24 respectively) and the extant erinaceines are linked by 2 synapomorphies (figs. 3–6, stem 4): (1) the location of the antorbital flange (anterodorsal, 9.2); and (2) double, but separate I3 roots (63.1), which is unknown in *Brachyerix* (see
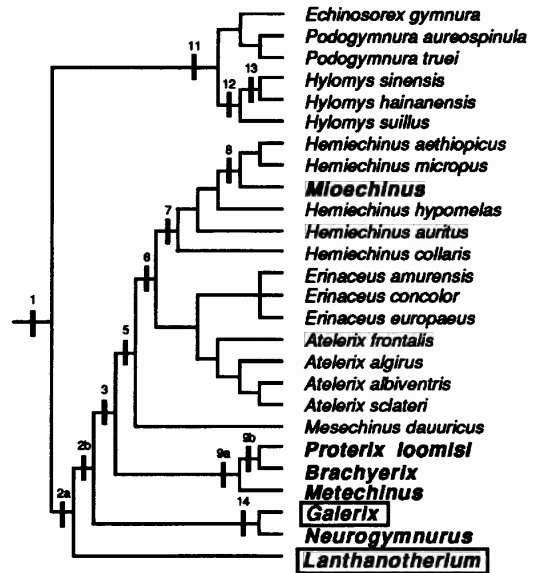

Fig. 7. An alternative phylogenetic hypothesis to that of figure 5. Here *Proterix* is considered the sister taxon to *Brachyerix* (stem 9b). See text for discussion of indicated stems.

appendix 1 for transformation series discussion).

The monophyly of the Brachyericinae is well supported by 10 apomorphies (47.1, 48.1, 50.1, 51.1, 52.1, 53.1, 54.1, 55.1, and 84.1 [appendix 1], the latter [absence of M3]) is dependent on the position of *Proterix*, i.e., *Proterix* must be outside the brachyericines). All of these (except 84.1) are auditory characters unique to the brachyericines.

Mioechinus and the Extant Spiny Hedgehogs

A surprising result of this analysis is the placement of *Mioechinus* (fig. 23) well within the *Hemiechinus* clade (figs. 3–7, stem 8). Originally, this fossil taxon was placed in the genus *Erinaceus* (Thomas, 1918). Butler (1948) found no evidence to place it in any of the genera of recent erinaceines; thus he erected the new genus, *Mioechinus*. Although he identified characters to assign *Mioechinus* within erinaceines (i.e., presence of a nasopharyngeal fossa, palatal perforations, and some dental characters), the small differences in size (and the age of the specimen) led Butler

to conclude that *Mieochinus* must be an intermediate form between the extant and extinct erinaceines. Rich (1981) suggested that *Mioechinus* was closely related to the extant erinaceines, and placed it as the sister taxon of *Erinaceus,* which he identified as the sister group to *Hemiechinus.*

Of the 18 postulated synapomorphies for the extant erinaceine clade (including *Mesechinus* irrespective of its position), only six are observable in *Mioechinus* (2.1, 4.2, 24.1, 28.1, 33.1, 72.1, appendix 1), two of which (24.1 and 28.1) reverse to the plesiomorphic state in *Mioechinus.* The *Hemiechinus* clade (figs. 3–7, stem 7) is supported by four unambiguous characters (3.1, 30.2, 34.1 and 95.1, appendix 1). Of these, two conditions are known in *Mioechinus*: inflation of the basisphenoid (34.1), which is diagnostic of the hemiechinines, and a wide rostrum (3.0 [also seen convergently in *Metechinus*]). The placement of *Mioechinus* within the hemiechinines (figs. 3–7, stems 7a and 8) is further supported by: (1) inflation of the alisphenoid and epiterygoid processes (12.2; figs. 3–7, stem 7a); and (2) a reduction in the P3 roots (75.1; figs. 3–7, stem 8 [convergent in the *Hylomys* and *Atelerix* clades]) (see appendix 1).

It seems indisputable that *Mioechinus* is phylogenetically a hemiechinine. This clade is composed of desert forms found from Pakistan and the Middle East to North Africa, suggesting that: (1) there must have been an arid corridor extending from the Middle East at least to the site in Switzerland (Oeningen) where this specimen was recovered (work in progress); and (2) that this clade is old, as indicated by the occurrence of *Mioechinus* in the middle the Miocene.

Mesechinus

Frost et al. (1991) placed *Mesechinus* as the sister taxon of the *Atelerix* + *Erinaceus* clade (fig. 2, stem 2) based on a shared pelage feature (ventral pelage coarse and sparse [102.1], appendix 1). Nevertheless, Frost et al. (1991) placed little confidence in this result (as depicted in their taxonomic tree, their fig. 10). Figures 8A and 8B show the two parsimonious phylogenetic positions of *Mesechinus* discovered in this analysis: (1) as the sister taxon of the *Atelerix* + *Erinaceus* clade

(fig. 8A, stem 1), or (2) as the sister taxon of all the extant spiny erinaceines (fig. 8B, stem 1). The first topology is supported by the pelage character (102.1) as discovered by Frost et al. (1991). The latter topology is supported by an additional character (23.1, appendix 1), the presence of an alisphenoid bridge in the sphenorbital fissure area (figs. 8B, 12, 18).

The two equally parsimonious placements of *Mesechinus* are dependent on the distribution of the two characters: 23.1 and 102.1. If *Mesechinus* is placed outside the remaining extant erinaceines (fig. 8A, stem 1), both *Hemiechinus auritus* and *H. collaris* are resolved as successive sister taxa to the clade that was previously considered *Paraechinus* (stems 2 and 3: these taxa were not resolved in the Frost et al. analysis). The resolution of these two taxa is a result of *H. collaris* sharing the presence of the alisphenoid bridge with *Mesechinus.* However, if *Mesechinus* is positioned as the sister taxon of the *Erinaceus* + *Atelerix* clade (fig. 8B, stem 1a), there is no stem support to resolve *H. auritus* and *H. collaris.*

When *Mesechinus* is considered the sister taxon of extant erinaceines (fig. 8B, stem 1), the *Hemiechinus* + (*Atelerix* + *Erinaceus*) clade is supported by a reversal to the ancestral feature: the lack of a squamosal component in the bullar roof (39.0, appendix 1). *Mesechinus* exhibits the derived condition (a major squamosal contribution to the bullar roof) like that of the hylomyines and *Neurogymnurus.* At present, the conditions for this transformation series are unknown in brachyericines (the sutures are unobservable). Accordingly, PAUP assigned character states for those taxa as well as *Proterix, Galerix,* and *Lanthanotherium,* thus identifying a reversal to the ancestral state as apomorphic for the extant erinaceines (excluding *Mesechinus*).

Hylomys

The 1991 analysis of Frost et al. (fig. 2, stem 4) identified *Hylomys suillus* and *H. hainanensis* (fig. 13) as a monophyletic group based on the reappearance of the P1 from an absent ancestral state (68.0, appendix 1). The addition of fossil material compromises the

monophyly of these taxa (fig. 1B) due to a posteriori optimization of the unknown ancestral state. That is, the ancestor can sometimes be hypothesized to have retained the P1 with its loss occurring convergently in *Hylomys sinensis, Podogymnura*, and the erinaceines including *Proterix*, and the brachyericines. Subsequently, relationships among *Hylomys* are reconsidered: *H. sinensis* and *H. hainanensis* sometimes constitute a monophyletic group (figs. 3–7, stems 13, 13a). Although this sequence of transformation may seem more reasonable, it is interesting to note that Van Valen (1967) found polymorphism in the series of *Hylomys* he reviewed—some individuals retained four premolars on one side of the maxilla and only three on the other. Luckett (personal commun.) has noted that in some marsupials ontogeny demonstrates the growth of a fifth premolar bud, although the adult dentition only includes four. He has also observed the retention of a milk tooth, accounting for an extra premolar in some marsupials (personal commun.). To my knowledge, the ontogeny of premolars in *Hylomys* has not been studied. In short, I have no confidence in the stability of the recovered phylogenetic arrangement of *Hylomys*.

The alternative hypothesis is the topology found by Frost et al. (1991): *Hylomys suillus* and *H. hainanensis* constitute a monophyletic group. Character support (25.1, appendix 1) results from the presence of *Lanthanotherium* when regarded as a basal hylomyine (figs. 3A and 3B, stem 10); it exhibits the derived feature of a loss of the posterior spine of the palatal shelf (25.1). When *Lanthanotherium* is not positioned along this stem (i.e., stem 10), the optimization on the stem is equivocal because three of the six species in the exant hylomyine clade (*Echinosorex, H. suillus*, and *H. hainanensis*) retain the ancestral condition of a well-developed spine on the palatal shelf.

CONCLUSIONS

The principal purpose of this investigation was to address the question of the relevant importance of extant taxa in recovering phylogenetic histories of extinct taxa, and sec-
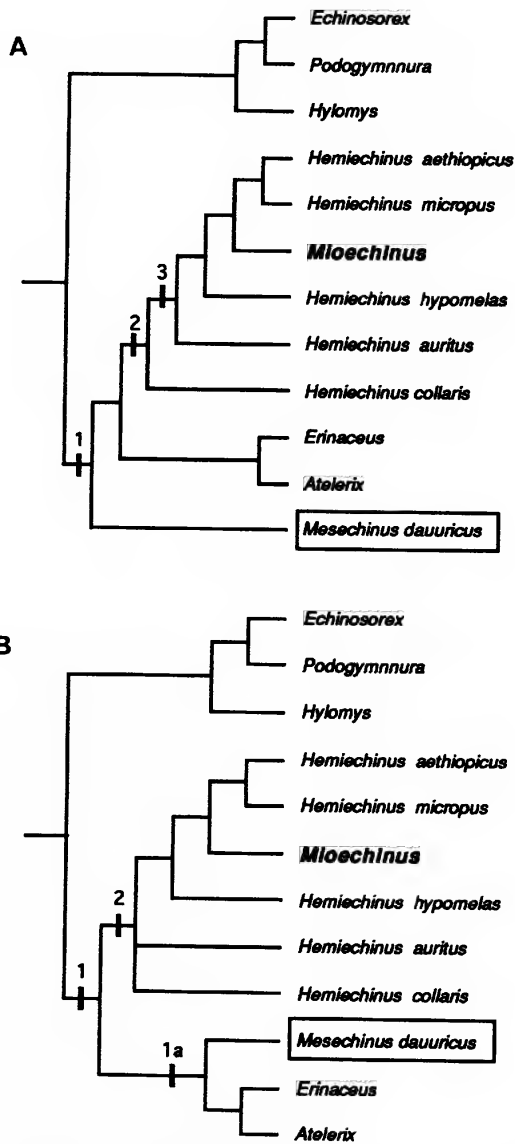

Fig. 8. Recovered phylogenetic hypotheses regarding the placement of *Mesechinus*: (A) as sister taxon to all extant spiny hedgehogs, (B) the sister taxon to *Erinaceus + Atelerix*.

ondarily to see the effect of injecting fossil taxa in a well-resolved phylogeny of extant taxa. The recovered evidence suggests a possible relationship of *Galerix, Lanthanotherium* and *Neurogymnurus* to the Erinaceinae (= clade B; as opposed to the Hylomyinae [= clade A] contradicting previous hypotheses [Butler, 1948; Novacek, 1985]). Also, the placement of a fossil taxon (*Mioechinus*) well

within an extant clade (*Hemiechinus*) strongly demonstrates the importance of considering all taxa within a phylogenetic analysis.

Perhaps the effect of considering extant taxa on our understanding of fossil relationships may seem only interesting from a paleontological perspective. However, this analysis has recovered evidence from the fossil taxa which requires a reinterpretation of relationships among the extant taxa. Systematists who insist that fossils are not required for the recovery of phylogenetic histories (Patterson, 1977, 1981a, 1981b, Gardiner, 1982; Nelson, 1985) apparently reject the growing body of evidence suggesting that fossils may be essential for the identification of character transformations and homologies (Huelsenbeck, 1991; Gauthier et al., 1988a, 1988b) and should be incorporated in phylogenetic analysis as all other taxa (Eernisse and Kluge, 1993; Kluge, 1990; Wheeler, 1990; Gauthier et al., 1988a, 1988b). Other systematists recognize that the inclusion of more taxa (whether fossil or extant) allows for an improved ability to detect homoplasy (Wheeler, 1990; Frost, personal commun.). This study supports the importance of fossils in recovering phylogenetic histories and, concomitantly, the inclusion of extant taxa when considering the phylogenetic relationships of fossils. Granted, in this analysis the impact of adding fossil hedgehogs to a matrix of strictly extant taxa was minor in terms of affecting the topology of the extant tree of Frost et al. (1991). Nevertheless, homologies are reconsidered in light of new evidence (see appendix 2), previous diagnoses of ingroup taxa are challenged (i.e., *Hylomys, Lanthanotherium, Galerix, Neurogymnurus, Proterix*, and *Mioechinus*), and the age of the extant genera has been extended (i.e., *Mioechinus* within the *Hemiechinus* clade).

An additional consideration suggested by this analysis is the a priori assumptions made regarding the directionality of transformation series. This analysis has shown that the confidence level of what appears to be morphological parsimony in one particular transformation (e.g., small i1 → absent i1) can be disrupted with the addition of taxa that partition long stems, such as in the case of the i1 (transformation series 60, appendix 1). The addition of the fossil taxa and the rule of

global parsimony forced the conclusion that the morphological transformation of this tooth within Erinaceidae was missing a step (i.e., large size): small i1 → large i1 → absent i1. That is, the transformation was not: large i1 ← small i1 → absent i1 within the ingroup as suggested by previous authors (e.g., Rich, 1981). Other dental transformation inconsistencies are identified (67, 70, 71, and 73) suggesting that researchers must be careful not to impose a priori directionality on these types of transformation series without hard evidence, and that alternative directions for such transformation series should be entertained.

It is clear, at least for hedgehogs, that a comprehensive analysis of both fossil and extant taxa has shed light on the evolution of the group, but more importantly, on homologies. Undoubtedly, much of the evidence for the phylogenetic placement of the fossils is weak because of missing data. Nonetheless, the recovery of any historical information from depauperate material is worth the effort.

ACKNOWLEDGMENTS

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APPENDIX 1
Transformation Series

The following transformation series follow those of Frost et al. (1991) unless otherwise indicated (see Frost et al. for citations of characters). Numbers in brackets indicated by a pound sign [#] correspond to the numbers of the Frost et al. transformation series. Those indicated by an asterisk [*] are the original numbers of transformation series taken from MacPhee et al. (1988). Transformation series indicated by a single dagger (†) signify those of Frost et al. or other authors (see citations) that have been altered in some fashion (see explanation for each series marked). Those transformation series marked by double daggers (‡) are characters not included in Frost et al. (1991).

Cranial Characters

1. [#1] Nasals, posterior extension: (0) posterior extension anterior to the antorbital rim; (1) posterior extension medial or posterior to antorbital rim.
2. [#2] Rostrum length: (0) long; (1) short.
3. [#3] Rostrum width: (0) wide, anterior incisors adjacent; (1) narrow, anterior incisors not adjacent.
4. [#4] Palatine foramina, size: (0) small; (1) anterior foramina elongated posteriorly; (2) anterior and medial palatine foramina coalesced.
5. [#5] Anterior palatine foramina, location: (0) at the maxilla/palatine suture; (1) anterior to the maxilla/palatine suture.
6. [#6] Position of the anterior opening of the infraorbital canal: (0) dorsal or posterodorsal to P4-M1; (1) dorsal to P3-P4.
7. [#7] Antorbital fossa: (0) present; (1) absent. (Note: this character was mislabeled in Frost et al. [1991: fig. 12]. The fossa is located immediately ahead of the anterior root of the zygoma on the facial maxilla, not anterodorsal to the orbit as depicted in their illustration.)
8. [#8] Antorbital flange and lacrimal canal: (0) lacrimal canal visible from lateral view; (1) lacrimal canal obstructed from lateral view by antorbital flange.
‡9. Location of antorbital (= prelacrimal) flange: (0) anteroventral to lacrimal canal; (1) continuous around the anterior rim of the lacrimal canal; (2) anterodorsal to lacrimal canal; (3) absent.
10. [#9] Postventral process of the zygoma (maxilla): (0) absent; (1) small; (2) large.
11. [#10] Jugal size: (0) large, reaches lacrimal; (1) small, does not reach lacrimal; (2) vestigial, confined to lateral rim of zygoma; (3) absent.
†12. [#11] Pterygoid/alisphenoid and epiterygoid processes: (0) epiterygoid processes absent, alisphenoid not inflated; (1) epiterygoid processes present, alisphenoid not inflated; (2) epiterygoid processes present, alisphenoid inflated; (3) epiterygoid processes present, alisphenoid and epiterygoid processes inflated. Frost et al. coded leptictids as not having epiterygoid processes. This is incorrect (Novacek, 1986; personal obs.). Nevertheless, outgroup analysis is inconclusive (both tenrecoids and soricoids lack epipterygoid processes), therefore the transformation series is considered unpolarized.
13. [#12] Lacrimal/maxilla suture: (0) unfused; (1) fused.
14. [#13] Supraorbital process, a frontal process on the parietal/frontal suture: (0) absent or poorly defined; (1) sharp.
15. [#14] Supraorbital foramen (frontal): (0) present; (1) absent.
16. [#16] Anterior process of the parietal: (0) absent or very weak; (1) extends anteriorly along the supraorbital rim to form the base of the supraorbital process.
17. [#17] Anterior process of the alisphenoid: (0) absent; (1) present.
18. [#18] Anterior opening of the inferior stapedial foramen (alisphenoid): (0) inferior ramus of the stapedial artery emerges from the bulla via a groove; (1) artery emerges from a foramen in the alisphenoid.
†19. [#19] Cranio-orbital foramen (frontal): (0) closely associated or joined with the ethmoid foramen; (1) ethmoid and cranio-orbital foramen widely separated. The cranio-orbital (= sphenofrontal) foramen was misidentified as the ophthalmic foramen by Butler (1948). This foramen is the opening for the superior ramus of the stapedial artery, which runs from the auditory region (Evans and Christensen, 1979; MacPhee, 1980, personal commun.) to the orbital temporal region via the interior of the cranium, behind a wing of the alisphenoid bone.
†20. [#20] Suboptic foramen (orbitosphenoid): (0) absent; (1) present. This character from Frost et al. (1991) is treated here as two characters: presence/absence, and relative position (see character 21). Note that Butler (1956) described a skull of *Leptictis* as possessing a suboptic foramen that opened onto the medial wall of the sphenorbital fissure. Although this condition could not be verified by Novacek (1986) in the specimens that he reviewed (Butler's material was not included in his anal-

ysis), he accepted Butler's findings and coded all leptictids as possessing a suboptic foramen within the medial wall of the sphenorbital fissure, and erinaceids as having an anteriorly placed suboptic foramen with respect to the fissure (see character 21). Closer inspection showed the latter supposition by Novacek (regarding erinaceids) not to be the case. Frost et al. (1991) disregarded Butler's findings, and apparently Novacek's (1986) argument as well, and coded leptictids as absent for this character. Due to the ambiguity of outgroup comparison, I have left this character unpolarized. See figures 14–19.

†21. Suboptic foramen (orbitosphenoid), relative position: (0) anterior to sphenorbital fissure; (1) present in the medial wall of the sphenorbital fissure; (2) present in medial wall of sphenorbital fissure but hidden within fissure. This transformation series seems to be related to the shortening of the skull in erinaceids. As the skull shortens, the alisphenoid overlaps the orbitosphenoid, creating a strong alisphenoid "wing" (see character 17). The degree of overlap seems directly related to the visibility of the suboptic foramen from lateral view. With increasing overlap, the suboptic foramen ultimately becomes confluent with the foramen rotundum (as seen in *Erinaceus europeaus* [MacPhee, 1980]). As mentioned above, Novacek (1986) identified leptictids as probably possessing this foramen in the medial wall of the sphenorbital fissure. This condition seems to be characteristic of Lipotyphla (sensu MacPhee and Novacek, 1993; McDowell, 1958), although I cannot be certain that this position is homologous with that seen in erinaceids. Accordingly, I have left this transformation series unordered and without an ancestral condition posited. See figures 14–19.

‡22. Alisphenoid canal (Butler, 1948, 1988; MacPhee and Novacek, 1993): (0) present; (1) absent or weakly developed (only exhibited on one side of the cranium). This feature was dismissed by MacPhee and Novacek (1993) and Butler (1988) as difficult to characterize. Expression of the alisphenoid canal appears to be related to the shortening of the skull (as is the position of the suboptic foramen, see character 21). Shortening of the orbitotemporal region concomitantly reduces the length of the alisphenoid canal until the canal disappears. In *Hemiechinus*, the alisphenoid canal, if present, is generally expressed only on one side of the skull. In *Erinaceus*, which displays the most pronounced cranial shortening, the alisphenoid canal is absent. Because of the

ambiguity of the state in *Hemiechinus* I have lumped "absent or weakly developed" as a single condition. See figures 14–19.

‡23. Alisphenoid/orbitosphenoid bridge: (0) absent or incomplete; (1) present, strongly developed. This character is related to character 17, although not all species within Erinaceidae that possess the anterior alisphenoid process also possess the developed bridge mentioned by Frost et al. See figures 16 and 17.

24. [#21] Sphenopalatine foramen (palatine): (0) anterodorsal or slightly posterodorsal to palatine transverse torus; (1) decidedly posterodorsal to palatine transverse torus.

25. [#22] Palatal shelf and spine: (0) well-developed spine on posterior palatal shelf; (1) posterior spine absent or vestigial.

26. [#23] Palatine, lateral fossa, anterodorsal to the palatine transverse torus: (0) absent; (1) present.

27. [#24] Zygomatic process of the squamosal: (0) not elevated posteriorly; (1) elevated posteriorly.

28. [#25] Postglenoid foramen (squamosal): (0) separated from the glenoid fossa by entoglenoid process; (1) not separated from the glenoid fossa.

29. [#26] Suprameatal fossa composition (squamosal): (0) mastoid and squamosal contributions equal; (1) mastoid and squamosal contributions subequal to predominantly mastoid. In error, Frost et al. (1991) coded those taxa that lacked a suprameatal fossa (see character 30 [#27]) as having the (0) condition, i.e., equal contributions of mastoid and squamosal. I have recoded those taxa lacking a suprameatal fossa as (?) to avoid inadvertently weighting the (0) condition.

30. [#27] Suprameatal fossa depth: (1) absent; (1) shallow; (2) moderately developed; (3) deep; (4) very deep.

31. [#28] Suprameatal fossa shape: (0) normal, anterior and posterior borders widely separated; (1) compressed, anterior and posterior borders widely separated. As with character 29, I have recoded those taxa that lack a suprameatal fossa as (?).

32. [#29] Relative height of skull: (0) parietals relatively higher than frontals; (1) frontals more elevated than parietals.

33. [#30] Nasopharyngeal fossa (basisphenoid): (0) absent; (1) present.

34. [#31] Inflation of the basisphenoid: (0) absent; (1) present.

‡35. Temporal/sagittal crest extend to frontal bones (Novacek, 1986): (0) present; (1) absent or weak. Sagittal crests are observed in only some taxa within tenrecoids and soricoids, but

universally within leptictids (Novacek, 1986). By virtue of outgroup ambiguity, this transformation series is unpolarized. Within erinaceids, only three taxa exhibit an anterior extension of the sagittal crest to the frontals (i.e., *Neurogymnurus, Brachyerix,* and *Metechinus*). Novacek (1986) noted that leptictids vary in the number of crests (one or two), although he did not treat this variation as phylogenetically significant within *Leptictis. Neurogymnurus* also varies in the number of crests present, suggesting that this feature might be diagnostic among the species. Treatment of intraspecific variation within the fossil taxa is outside the scope of this review; therefore the conditions were left untreated.

‡36. Extreme flattening and lateral extension of posterior region of the zygoma (Matthew, 1903; Gawne, 1968): (0) absent; (1) present. The derived character state is apparently autapomorphic for *Proterix,* although it has been noted in *Apternodus* (McDowell, 1958), a North American fossil soricoid. In both cases, this very unusual structure is composed of a pronounced mastoid exposure on the occipital bone (McDowell, 1958; Gawne, 1968; Bjork, 1975) which Gawne (1968) refers to as a "lambdoidal plate."

‡37. Exostosis (= rugosity) on squamosal and parietal (Butler, 1948): (0) absent; (1) present. This is an interesting autapomorphy for *Neurogymnurus* and could very well be a function of increased surface area for muscle attachment. Gawne (1968) noted exostosis on *Proterix.* I have examined the two cited specimens of Gawne (1968) and have been unable to verify her observations. *Brachyerix* specimens studied show a slight modeling on the parietals which is reminiscent of *Neurogymnurus,* without approaching the magnitude observed in *Neurogymnurus.* For this reason I have coded *Brachyerix* as absent for this condition. See figure 20.

38. [#32] Ectotympanic: (0) slender, ring-shaped, loosely attached with a small anterior process; (1) broader, sometimes engulfing anterior process, firmly attached. (*Metechinus* and *Brachyerix* have been left uncoded for this transformation series. Refer to transformation series 54 for further discussion.)

39. [#33] Petrosal: (0) promontorium predominantly confined to bullar (= tympanic) roof, squamosal does not participate in bullar roof; (1) promontorium forms posteromedial wall, squamosal is major component of bullar roof.

40. [#34] Inflation of the mastoid region between the exoccipital and squamosal: (0) absent; (1) present.

†41. [#35] Mastoid portion of suprameatal fossa: (0) not inflated; (1) inflated. As with the previous suprameatal fossa characters, I have recoded those taxa that lack this structure as (?).

42. [#36] Ventral process of the petrosal: (0) not inflated; (1) inflated.

43. [#37] Basioccipital/petrosal suture: (0) narrow slit exposing portion of the interior petrosal sinus; (1) closed with a well-defined posterior lacerate foramen.

44. [#38] Stapedial foramen (petrosal): (0) posterior to squamosal/alisphenoid suture and posterior to postglenoid foramen; (1) located on squamosal/alisphenoid suture and close to the postglenoid foramen.

45. [#39] Epitympanic recess, lateral wall: (0) formed partially by squamosal; (1) formed entirely by mastoid.

‡46. [*1] Rostral tympanic process (RTP): (0) absent; (1) present. MacPhee et al. (1988) suggest that the presence of a small rostral tympanic is primitive. Due to outgroup ambiguity, I have left this transformation series unpolarized.

‡47. [*1] Size of rostral tympanic process: (0) small; (1) large. The presence of a large rostral tympanic is autapomorphic for brachyericines. Despite outgroup ambiguity of its presence or absence, all outgroup taxa which do possess an RTP possess a small one. Therefore, I have polarized these RTP conditions.

‡48. [*1] Position of rostral tympanic process: (0) restricted to medial aspect of promontorium; (1) situated on promontorium, but medially inflated; (2) situated medial to promontorium from which it spreads as a wide sheet to ossify all of the tympanic floor except for variable ectotympanic contribution. This transformation series is polarized in accordance with the observations of MacPhee et al. (1988), but it is unordered.

‡49. [*1] Articular surface of the rostral tympanic process: (0) absent; (1) present. Outgroup ambiguity within Lipotyphla does not allow for assertions (as by MacPhee et al. [1988]), which state that the presence of an articular surface on the RTP is "morphotypic."

‡50. [*1] Contribution of rostral tympanic process to the external auditory meatus: (0) absent; (1) present.

‡51. [*2] Caudal tympanic process of petrosal: (0) absent or insignificant; (1) present; small, incompletely encloses fossula of fenestra cochleae; (2) present; extensive, delimits or forms apertures for the facial nerve (VII) and internal carotid artery. MacPhee et al. (1988) suggested that condition (1) is the primitive condition. Polarization and ordering of this trans-

formation series is not possible due to the ambiguity in the outgroups.

‡52. [*3] Tympanic process of basisphenoid: (0) absent; (1) present; large; (2) present; large, coalesces with alisphenoid tympanic wing and forms the anteroinferior floor of meatus. Outgroup ambiguity requires that this transformations series be left unordered and unpolarized.

‡53. [*4] Tympanic process of alisphenoid: (0) small; does not completely form tubal foramen in combination with the basisphenoid, little or no pneumatization; (1) large; completely forms tubal foramen in combination with the basisphenoid, strongly pneumatized.

‡54. [*5] Ectotympanic: (0) crura expanded relative to ontogenetically early condition; ectotympanic phaneric (= hidden) or semiphaneric; (1) crura not expanded relative to ontogenetically early condition; ectotympanic aphaneric or highly semiphaneric. The authors of this transformation series predict that the fossil forms do not expand the crura relative to their early ontogenetic condition. This is an assumption based on adult material. I have included this character, but have left it unpolarized. MacPhee et al. considered the derived state to be condition (1).

‡55. [*15] Arterial canals, intratympanic: (0) absent, or enclose only a stem of unreduced internal carotid at its entrance into tympanic cavity; (1) present, enclose stem of unreduced internal carotid and its major intratympanic divisions. Rich (1971) observed arterial canals in *Paraechinus*. MacPhee et al. (1988) acknowledged this condition in *Paraechinus*, but differentiated these occurrences based on the extent to which these canals were developed. I am following MacPhee et al. in the assumption that the different conditions observed in *Paraechinus* and the brachyericines are not homologous (see MacPhee et al., 1988, p. 36 for a more detailed discussion). See figure 22.

56. [#40] Paroccipital processes: (0) small; (1) robust.

57. [#41] Exoccipital: (0) not expanded; (2) expanded.

58. [#42] Occipital condyle: (0) condyle emarginated, lobed; (1) no emargination.

59. [#44] Coronoid process: (0) narrow, pointed; (1) broad, rounded.

Dental Characters

†60. [#45 & #46] i1: (0) present, enlarged; (1) present, small; (2) absent. Frost et al. divided this transformation series into two binary series. I have simplified these by treating them as one series and polarizing it on (1), the ancestral condition. The (0) state is autapomorphic for *Hylomys sinensis* (note: Rich [1981] has suggested that *Brachyerix* and *Metechinus* also share enlarged I1/i1, although this has not been reasonably demonstrated on available material).

†61. [#47] i2 relative size (Butler, 1948; Novacek, 1986; Frost et al., 1991): (0) greatly enlarged; (1) nearly equal to other incisors; (2) smaller than other incisors (this condition was added to accommodate *Metechinus*). I have reordered and rooted this character on state (1) under the assumption that the tooth must pass through a transitory state (Luckett, personal commun.).

62. [#48] I2: (0) greater than I3; (1) less than or equal to I3.

63. [#49] I3, number of roots: (0) one root; (1) two roots, separate; (2) two roots, fused.

64. [#50] C1 size: (0) significantly larger than adjacent postcanine teeth; (1) slightly larger than adjacent postcanine teeth; (2) approximately equal in size to adjacent postcanine teeth.

65. [#51] C1, number of roots: (0) two roots; (1) one root or two roots fused.

66. [#53] C1, relative size: (0) equal to, or larger than I3; (1) subequal or slightly smaller than I3.

67. [#52] c1, relative size: (0) approximately equal to, or smaller than p1; (1) significantly larger than p1.

68. [#54] P1: (0) present; (1) absent.

69. [#55] p1: (0) present; (1) absent.

‡70. p2 (Rich, 1981; Novacek, 1986): (0) moderate size, two roots; (1) small, peglike, procumbent, one root; (2) absent. Outgroup ambiguity requires that this transformation series be left unordered and unpolarized.

†71. [#56] P2 roots: (0) two roots; (1) one root or two roots well fused; (2) absent. Absence of P2 is autapomorphic for *Brachyerix*. Luckett (personal commun.) has suggested that a decrease in the number of roots, or the fusion of roots is "generally" indicative of a trend to lose the tooth. Although this argument is intuitive, I alternatively considered this character transformation (as with character 62) both nonadditive and additive. Neither optimization effects the topology of the tree.

72. [#57] p3: (0) two roots present; larger in size than p2; (1) one root present, nearly equal in size to p2; (2) absent.

†73. [#58] P3 lingual lobe (= protocone): (0) present, well developed; (1) vestigial or absent. Frost et al. (1991) noted that *Echinosorex* and most extant erinaceines exhibit a P3 lingual lobe. I consider this lobe to be a protocone

based on the four-cuspid P3 in *Galerix*. The fourth cusp is presumably the hypocone (see discussion under character 86).

74. [#59] P3 size: (0) normal; (1) reduced.

75. [#60] P3 roots: (0) three roots; (1) fewer than three roots.

‡76. P3 hypocone: (0) absent; (1) present.

‡77. p4 (Novacek, 1986): (0) with elongate talonid and talonid basin; (1) with short, bicuspid or unicuspid heel. This character is uniformly present in all taxa reviewed, although it has been reported to be homoplastic within erinaceomorphs (Novacek, 1986).

†78. [#61] P4 shape and presence of hypocone: (0) quadrate, hypocone present; (1) triangular, hypocone absent or vestigial. Frost et al. (1991) claimed, in error, that leptictids lack a hypocone. Novacek's (1986) identification of a hypocone on the P4 is correct. Regardless, outgroup ambiguity requires this transformation series to be treated as unpolarized.

79. [#62] P4 lingual roots: (0) one lingual root; (1) two unfused roots; (2) two lingual roots, fused.

80. [#63] Trigonid height: (0) high (significantly taller than talonid), talonid short or vestigial; (1) low (nearly equal in height with talonid), talonid expanded, large.

‡81. m1 (Novacek, 1986): (0) trigonid moderate; (1) marked elongation of prevallid shear on m1. Transformation state (1), the P4/m1 shear, has historically diagnosed the Erinaceidae (Butler, 1948, 1988; McDowell, 1958; Krishtalka, 1976; Schwartz and Krishtalka, 1976), although Butler (1988) suggested that this character is primitive for mammals. It should be noted here that his supposition is based on the presence of the P4/m1 shear in Cretaceous eutherians and soricomorphs, not in erinaceomorphs. However, based on occlusal patterns, Butler concluded that the P4/m1 shear seen in soricids is not homologous with the erinaceid shear because the paraconids of m2–3 do not participate in the shear, as is the case in soricids. Regardless, the fact that soricids have dilambdodont teeth, makes it difficult to homologize many of the dental characters. On the basis of occlusal differences presented by Butler (1948) and the differences in gross dental morphology (zalambdodonty vs. tribosphenty), I support Butler's position that the erinaceid prevallid shear is unique.

82. [#64] M1 lingual roots: (0) separate; (1) fused for most of the length.

‡83. Distinct ectocingulum on labial side of m1 and m2 (Novacek, 1986): (0) absent; (1) present. Novacek (1986) observed that "erinaceomorphs" have a much broader ectocingulum than leptictids. In a previous paper Novacek coded the presence of an ectocingulum only

in the "erinacines, brachyericines and hylomyines" and convergently in *Cedrocherus* and *Litolestes* (Novacek, 1985). Although this character is present in leptictids, it is absent in tenricoids and soricoids, and in all of the erinaceomorphs reviewed by Novacek (1985), except for the two abovementioned taxa. Because of the ambiguity of this character, I consider it unpolarized.

‡84. M3 (Rich, 1981; Novacek, 1986): (0) present; (1) absent.

85. [#65] M3 roots: (0) three roots; (1) two roots.

†86. [#66] M3 metastylar spur (referred to as a hypocone): (0) absent or weak; (1) present, well developed on buccal side. The posterolingual cusp has been identified by previous authors (Butler, 1948; Novacek, 1985, 1986; Novacek et al., 1985; Frost et al., 1991) as a hypocone, based solely on topographical position. A reinterpretation of this lingually directed cusp suggests that it is not homologous with the hypocone identified in erinaceomorphs, and that it should be interpreted as an expanded metastylar spur or metaconule. Evidence in support of this conclusion is: 1) There is no loph that unites the protocone and hypocone as seen in both the M1 and M2 in all taxa (R. Tedford and J. J. Hooker, personal commun.) (see fig. 25). 2) The alveoli of the metacone and the cusp in question are confluent, not separate as seen in the M1 and M2 (see fig. 25 and Butler, 1948, p. 460, his fig. 13). 3) The only taxon in which the fourth cusp can be considered singular is *Echinosorex*—the cusp in question is literally stuck onto the side of the metacone. All other hylomyines have a condition in which these two cusps share a common base cone, but are doublecusped at the apex. 4) The occlusal pattern of the fourth cusp in *Echinosorex* shows that it occludes posterobuccally (like a metacone) rather than posterolingually as generally seen in hypocones.

Novacek (1985) characterized hypocones in some early erinaceomorphs as "weak or absent," but regarded the Galericinae (= Hylomyinae) as regaining the hypocone (with the exclusion of *Galerix*). The hypocones identified by Novacek (1985; Novacek et al., 1985) all sit upon a cingulum, which is not the condition seen in the hylomyines. Although a reidentification of this cusp in no way affects the tree topology of Frost et al. (1991), it does bring to the front lines the problem of some dental homologies with respect to adult dentition.

87. [#67] M3 metacone conditions: (0) well developed; (1) small; (2) absent.

88. [#68] m3 talonid: (0) present; (1) absent.

Postcranial Characters

89. [#69] Axis, postventral keel: (0) absent; (1) present.
90. [#70] Axis, neural spine: (0) low; (1) high.
91. [#71] Scapula, metacromion process: (0) deltoid, amorphous projection; (1) long, fusiform projection.
92. [#72] Sacral vertebrae, neural spines: (0) not fused into continuous longitudinal plate; (1) fused into continuous longitudinal plate.
93. [#73] Ischium, postdorsal process: (0) not greatly elongated; (1) greatly elongated. (Note: Frost et al. incorrectly referred to this species as "postventral," although it is labeled "postdorsal" on their illustration.)
94. [#74] Tibia, lateral flange on anterosuperior margin: (0) absent or only weakly present; (1) strongly developed.

Nonskeletal Characters

95. [#75] External pinnae, length relative to condyloincisive length (Thomas, 1918; Corbet, 1974, 1988; Robbins and Seltzer, 1985; Frost et al., 1991): (0) short; (1) long.
96. [#76] Hallux: (0) normal, (1) reduced, claw not reaching base of second digit; (2) absent.
†97. Pelage spines: (0) absent; (1) present. Frost et al. (1991) characterized the presence/absence and condition of the spines as one transformation series. I have split their transformation series in order to identify the acquisition of spines along the main stem.
†98. [#77] Pelage condition: (0) smooth spines; (1) spines papillate, not grooved; (2) spines papillate and grooved. As with Frost et al. (1991), this transformation series is unordered, and has been left unpolarized because of outgroup ambiguity.
99. [#78] Pelage, completely white spines among dark spines: (0) absent; (1) present.
†100. Spines on top of head: (0) absent; (1) present. As with transformation series 97 and 98, I have broken Frost et al.'s series into two separate transformation series (100, 101).
†101. [#79] Pelage, medial tract on crown: (0) spineless, medial crown tract narrow; (1) spineless, medial crown tract wide; (2) spineless, medial crown tract absent. This transformation series has been left unordered, but is unpolarized as a result of recasting the transformation series of Frost et al. (see above).
102. [#80] Pelage, condition on ventral side: (0) soft and densely furred; (1) coarse and relatively sparsely haired.
103. [#81] Pelage, body underfur: (0) absent; (1) present.
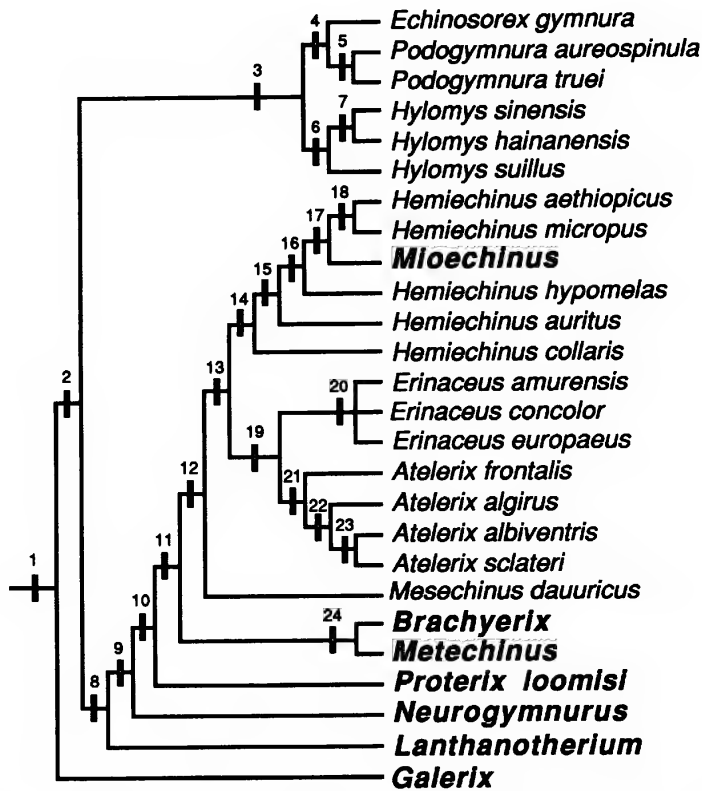
Fig. 9. One of the discovered trees with its accompanying apomorphy list. For alternative character-supported stems see text.

APPENDIX 2

Apomorphy List

Character states dependent on optimization are indicated by an asterisk (*). Those characters that are dependent on the position of *Lanthanotherium* as the sister taxon to the Hylomyinae are indicated by (‡). These characters *are not* considered as stem support if *Lanthanotherium* is united to the hylomyines. Characters already considered ambiguous based on optimization were not marked if they were also dependent on the location of *Lanthanotherium*. This apomorphy list was generated from tree #47 of this analysis (fig. 9). This tree was chosen because it closely approximated the distribution of apomorphies of the Adams tree.

Stem	Character	Steps	CI	Change
Stem 1	6	1	0.500	$1 \rightarrow 0$
	8	1	0.500	$1 \rightarrow 0$
	9	1	0.667	$1 \rightarrow 0$
	59	1	0.333	$1 \rightarrow 0$
	67	1	0.333	$1 \rightarrow 0$
	80	1	1.000	$1 \rightarrow 0$
Stem 2	*10	1	0.667	$0 \rightarrow 1$
	*13	1	0.500	$0 \rightarrow 1$
	*20	1	0.500	$0 \rightarrow 1$
	*39	1	0.500	$0 \rightarrow 1$
	*43	1	1.000	$0 \rightarrow 1$
	*73	1	0.167	$0 \rightarrow 1$
	*79	1	0.500	$0 \rightarrow 1$

APPENDIX 2—(*Continued*)

Stem	Character	Steps	CI	Change
	*86	1	0.500	0 → 1
	‡87	1	0.667	0 → 1

If *Lanthanotherium* is the sister taxon to the extant Hylominae, there is no unambiguous evidence to support this stem.

Stem	Character	Steps	CI	Change
Stem 3	35	1	0.500	0 → 1
	70	1	0.667	0 → 1
	71	1	0.400	0 → 1
	89	1	1.000	0 → 1
	*90	1	1.000	0 → 1
	*91	1	1.000	0 → 1
	*92	1	1.000	0 → 1
	93	1	1.000	0 → 1
	94	1	1.000	0 → 1

If *Lanthanotherium* is the sister taxon to the hylomyines, the only unambiguous synapomorphy to unite them is character 86.1. Subsequently, characters 70.1 and 71.1 are the only unambiguous character support for the extant Hylomyinae.

Stem	Character	Steps	CI	Change
Stem 4	5	1	1.000	0 → 1
	6	1	0.500	1 → 0
	9	1	0.667	1 → 0
	*10	1	0.667	1 → 0
	15	1	0.500	0 → 1
	103	1	1.000	0 → 1
Echinosorex gymnura	7	1	0.250	0 → 1
	21	1	0.667	1 → 0
	26	1	1.000	0 → 1
	73	1	0.167	1 → 0
Stem 5	22	1	0.333	0 → 1
	‡25	1	0.200	0 → 1
	62	1	0.500	0 → 1
	68	1	0.333	0 → 1
	69	1	0.333	0 → 1
Podogymnura truei	40	1	0.333	0 → 1
	57	1	0.500	0 → 1
Stem 6	4	1	0.667	0 → 1
	14	1	1.000	0 → 1
	16	1	1.000	0 → 1
	19	1	0.500	0 → 1
	40	1	0.333	0 → 1
	57	1	0.500	0 → 1
	64	1	0.333	0 → 1
	67	1	0.333	1 → 0
	72	1	0.400	0 → 1
	‡74	1	0.200	0 → 1
	75	1	0.333	0 → 1

If *Lanthanotherium* is considered the sister taxon to the Hylomyinae, character 59.0 is considered supporting evidence on this stem.

Stem	Character	Steps	CI	Change
Stem 7	69	1	0.333	0 → 1
Hylomys sinensis	1	1	0.500	0 → 1
	‡25	1	0.200	0 → 1
	60	1	0.500	1 → 0
	64	1	0.333	1 → 2

APPENDIX 2—(*Continued*)

Stem	Character	Steps	CI	Change
	66	1	0.500	$0 \rightarrow 1$
	68	1	0.333	$0 \rightarrow 1$
Stem 8	1	1	0.500	$0 \rightarrow 1$
	*7	1	0.250	$0 \rightarrow 1$
	‡25	1	0.200	$0 \rightarrow 1$
	*30	1	0.571	$0 \rightarrow 1$
	*38	1	1.000	$0 \rightarrow 1$
	*44	1	1.000	$0 \rightarrow 1$
	*96	1	0.667	$0 \rightarrow 1$
	*97	1	1.000	$0 \rightarrow 1$
	*100	1	1.000	$0 \rightarrow 1$
	*102	1	0.500	$0 \rightarrow 1$

If *Lanthanotherium* is the sister taxon to the Hylomyinae, character states, 10.2, 60.0, and 64.2 are here considered supporting evidence on this stem.

Stem	Character	Steps	CI	Change
Stem 9	60	1	0.500	$1 \rightarrow 0$
	*61	1	0.500	$1 \rightarrow 0$
	64	1	0.333	$0 \rightarrow 2$
	*82	1	0.333	$0 \rightarrow 1$
	*86	1	0.500	$1 \rightarrow 0$
Stem 10	8	1	0.500	$1 \rightarrow 0$
	*18	1	1.000	$0 \rightarrow 1$
	*22	1	0.333	$0 \rightarrow 1$
	*58	1	0.500	$0 \rightarrow 1$
	68	1	0.333	$0 \rightarrow 1$
	69	1	0.333	$0 \rightarrow 1$
	70	1	0.667	$0 \rightarrow 2$
	71	1	0.400	$0 \rightarrow 1$
	*72	1	0.400	$0 \rightarrow 1$
	*73	1	0.167	$1 \rightarrow 0$
	*87	1	0.667	$1 \rightarrow 2$
	*88	1	1.000	$0 \rightarrow 1$
Stem 11	9	1	0.667	$1 \rightarrow 2$
	*15	1	0.500	$0 \rightarrow 1$
	*62	1	0.500	$0 \rightarrow 1$
	63	1	1.000	$0 \rightarrow 1$
	*67	1	0.333	$1 \rightarrow 0$
	*74	1	0.200	$0 \rightarrow 1$
	*85	1	1.000	$0 \rightarrow 1$
Stem 12	2	1	1.000	$0 \rightarrow 1$
	4	2	0.667	$0 \rightarrow 2$
	11	1	1.000	$2 \rightarrow 1$
	17	1	1.000	$0 \rightarrow 1$
	21	1	0.667	$1 \rightarrow 2$
	23	1	0.333	$0 \rightarrow 1$
	24	1	0.333	$0 \rightarrow 1$
	25	1	0.200	$1 \rightarrow 0$
	27	1	1.000	$0 \rightarrow 1$
	28	1	1.000	$0 \rightarrow 1$
	33	1	1.000	$0 \rightarrow 1$
	35	1	0.500	$0 \rightarrow 1$
	45	1	1.000	$0 \rightarrow 1$

APPENDIX 2—(*Continued*)

Stem	Character	Steps	CI	Change
	56	1	1.000	0 → 1
	59	1	0.333	1 → 0
	60	2	0.500	0 → 2
	61	2	0.500	0 → 2
	70	1	0.667	2 → 1
	72	1	0.400	1 → 2
	79	1	0.500	1 → 2
Stem 13	39	1	0.500	1 → 0
Stem 14	3	1	0.500	0 → 1
	30	1	0.571	1 → 2
	34	1	1.000	0 → 1
	95	1	1.000	0 → 1
	*98	1	1.000	0 → 2
	*102	1	0.500	1 → 0
Stem 15	23	1	0.333	1 → 0
Stem 16	12	1	1.000	1 → 2
	30	1	0.571	2 → 3
	41	1	1.000	0 → 1
	42	1	1.000	0 → 1
	101	1	1.000	2 → 1
Stem 17	*30	1	0.571	3 → 4
	75	1	0.333	0 → 1
Stem 18	73	1	0.167	0 → 1
Hemiechinus aethiopicus	12	1	1.000	2 → 3
Hemiechinus micropus	22	1	0.333	1 → 0
	23	1	0.333	0 → 1
Mioechinus	24	1	0.333	1 → 0
	58	1	0.500	1 → 0
	71	1	0.400	1 → 0
	72	2	0.400	2 → 0
	74	1	0.200	1 → 0
Stem 19	32	1	1.000	0 → 1
	101	1	1.000	2 → 0
Stem 20	63	1	1.000	1 → 2
	65	1	1.000	0 → 1
	96	1	0.667	1 → 0
Erinaceus amurensis	99	1	0.500	0 → 1
Erinaceus europaeus	20	1	0.500	1 → 0
Stem 21	25	1	0.200	0 → 1
	29	1	1.000	0 → 1
	71	1	0.400	1 → 0
Atelerix frontalis	99	1	0.500	0 → 1
Stem 22	21	1	0.667	2 → 1
	75	1	0.333	0 → 1
Stem 23	73	1	0.167	0 → 1
Atelerix albiventris	96	1	0.667	1 → 2
Mesechinus dauuricus	13	1	0.500	1 → 0

APPENDIX 2—(Continued)

| Stem	Character	Steps	CI	Change
	31	1	1.000	0 → 1
	*98	1	1.000	0 → 1
Stem 24	47	1	1.000	0 → 1
	48	1	1.000	0 → 1
	50	1	1.000	0 → 1
	51	1	1.000	1 → 3
	52	1	1.000	1 → 2
	53	1	1.000	0 → 1
	54	1	1.000	0 → 1
	55	1	1.000	0 → 1
	*66	1	0.500	0 → 1
	*73	1	0.167	0 → 1
	84	1	1.000	0 → 1
Brachyerix	*7	1	0.250	1 → 0
	12	1	1.000	1 → 0
	30	1	0.571	1 → 0
	36	1	0.500	0 → 1
	37	1	0.500	0 → 1
	40	1	0.333	0 → 1
	71	1	0.400	1 → 2
	*74	1	0.200	1 → 0
	79	1	0.500	1 → 0
Metechinus	3	1	0.500	0 → 1
	30	2	0.571	1 → 3
	64	1	0.333	2 → 0
	82	1	0.333	1 → 0
Proterix	*7	1	0.250	1 → 0
	36	1	0.500	0 → 1
	64	1	0.333	2 → 1
Neurogymnurus	19	1	0.500	0 → 1
	37	1	0.500	0 → 1
	‡87	1	0.667	1 → 0
Lanthanotherium	24	1	0.333	0 → 1
	‡74	1	0.200	0 → 1
Galerix	61	1	0.500	1 → 2
	64	1	0.333	0 → 1
	76	1	1.000	0 → 1
	*79	1	0.500	0 → 2
	‡82	1	0.333	0 → 1
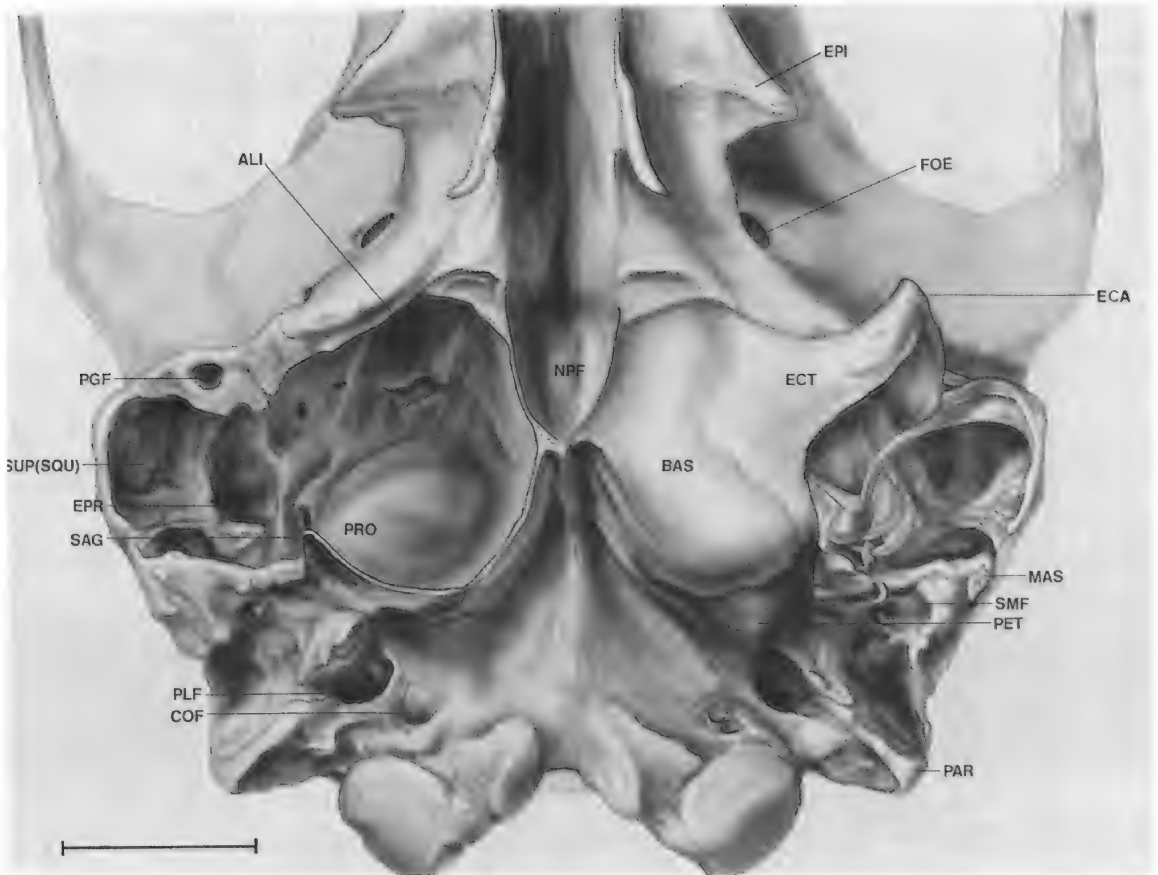
Fig. 10. *Hemiechinus hypomelas* (= *Paraechinus*) ventral view of basicranium. Right auditory bullae removed. Taken from Frost et al. (1991). Scale = 5 mm. Abbreviations used in figures 10–25: AC arterial canals; ALI alisphenoid; ALIB alisphenoid bridge; ALIC alisphenoid canal; ANT antorbital fossa; ANTF antorbital flange; APF anterior palatine foramen; BAS basisphenoid, tympanic wing; COF condylar foramen; CR crest (hypocone-protocone); EAM external auditory meatus; ECA ectotympanic, anterior process; ECT ectotympanic; EPI epipterygoid process; EPR epitympanic recess; ETF ethmoid foramen; EUS eustachian tube; EX exostosis; FOE foramen ovale; HYPC hypocone; INF incisive foramina; LP lambdoidal plate; M1 first upper molar; M3 third upper molar; MAS mastoid process of the petrosal; METS metastylar spur; MPF middle palatine foramen; NPF nasopharyngeal fossa; PAG promontory artery groove; PAR paroccipital process; PET petrosal, tympanic wing; PGF postglenoid foramen; PLF postlacerate foramen; PPF posterior palatine foramen; PRC protocone; PRO promontorium; SAG sta-pedial artery groove; SCA sinus canal, anterior opening; SMF stylomastoid foramen; SOF suboptic foramen; SPHF sphenorbital fissure; SQU squamosal; STM stapedius muscle; SUP suprameatal fossa; TYM tympanohyal.
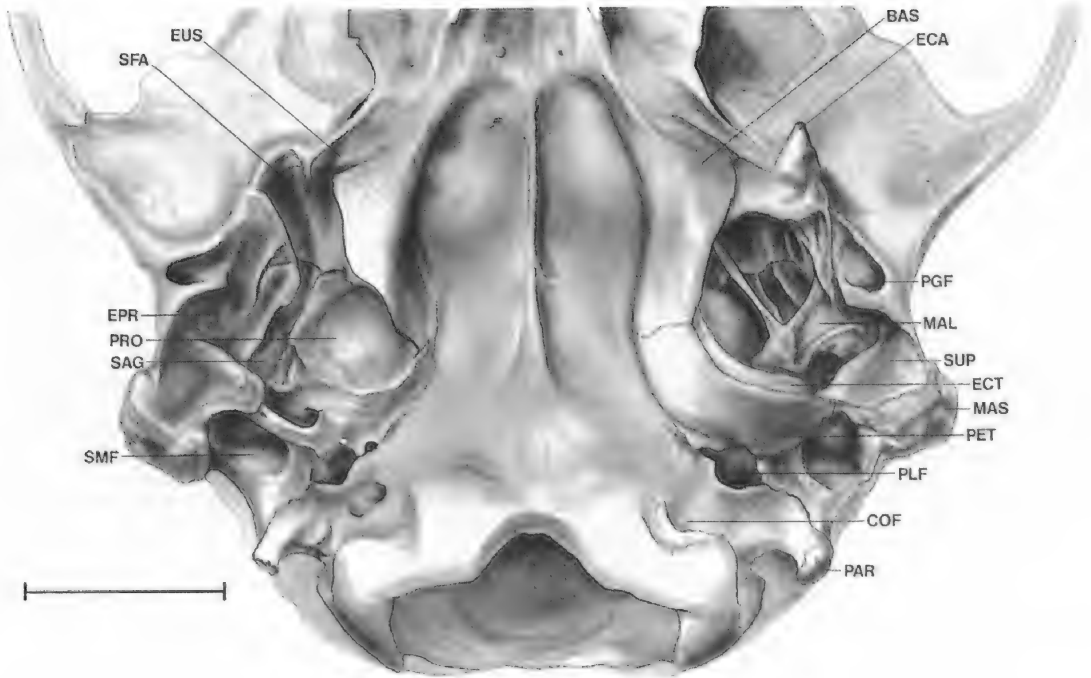
Fig. 11. *Podogymnura aureopinula*, ventral view of basicranium. Right auditory bullae removed. Taken from Frost et al. (1991). Scale = 5 mm.
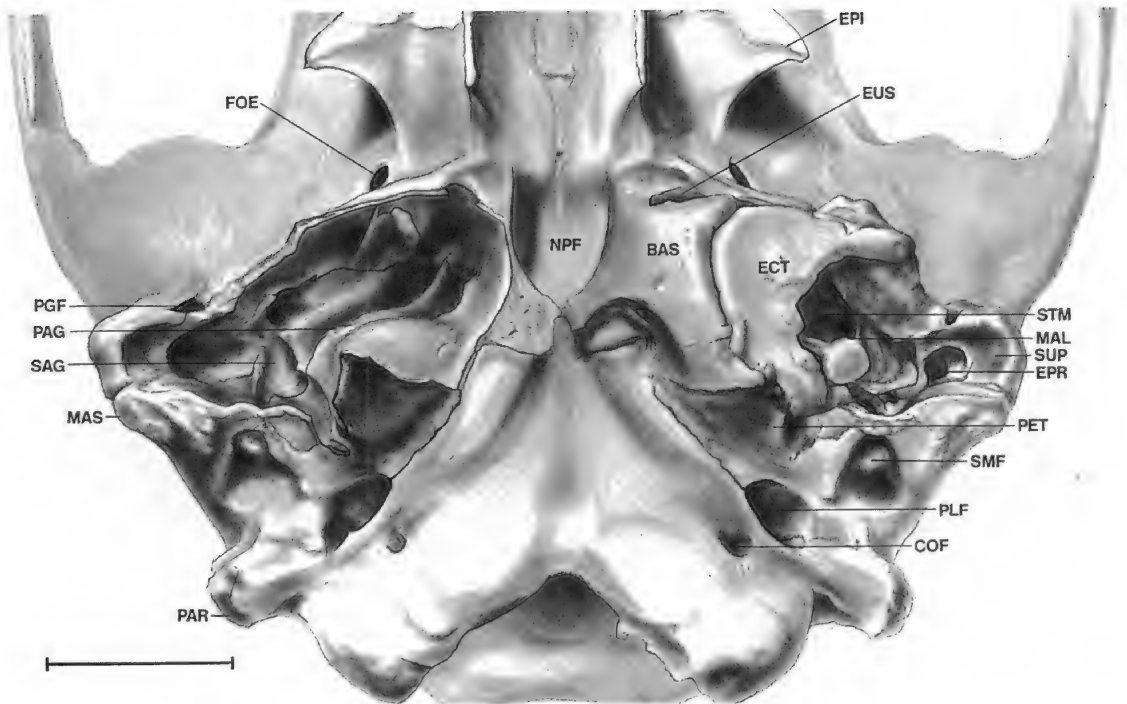

Fig. 12. *Mesechinus dauuricus* (= *Hemiechinus*) ventral view of basicranium. Right auditory bullae removed. Taken from Frost et al. (1991). Scale = 5 mm.
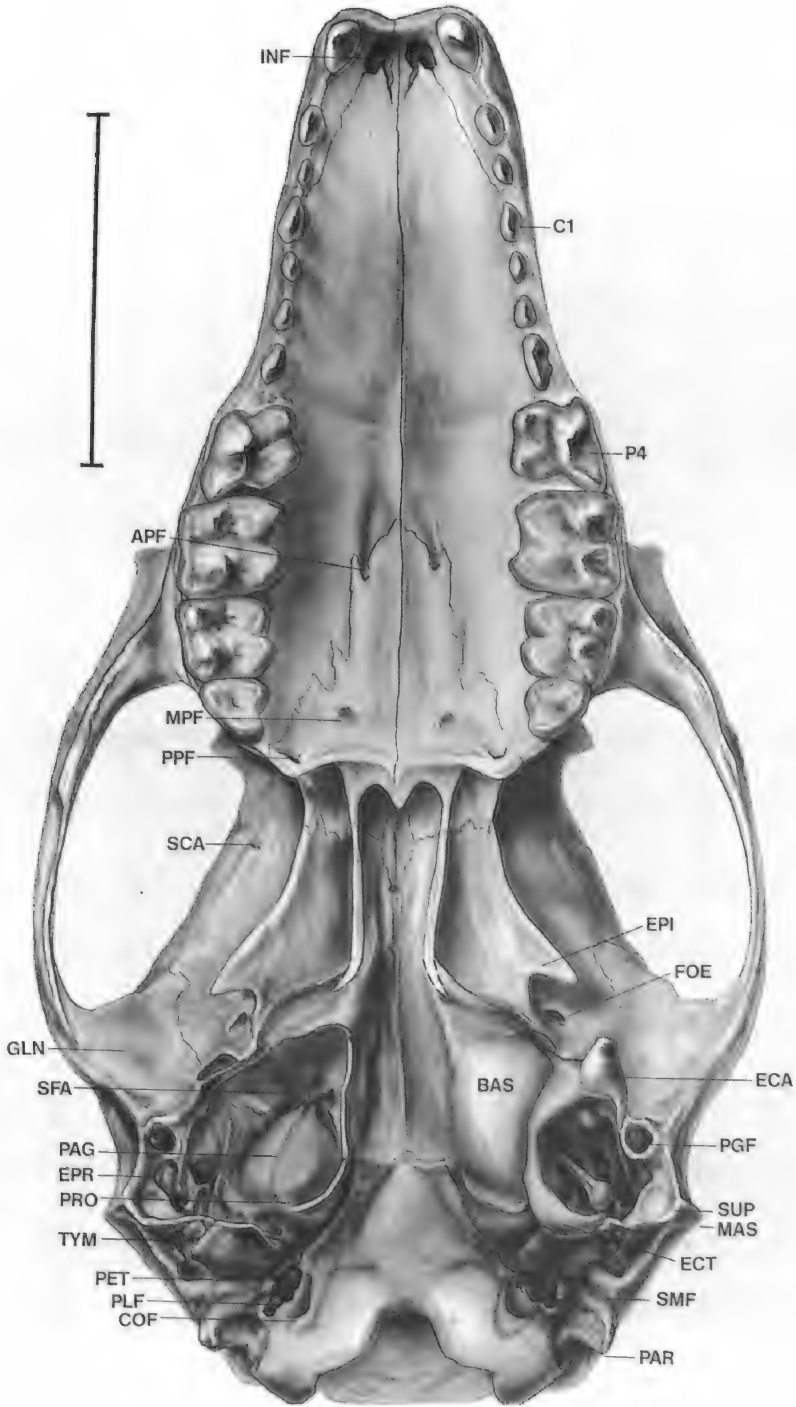
Fig. 13. *Hylomys hainanensis*, ventral view of skull. Right auditory bullae removed. Taken from Frost et al. (1991). Scale = 10 mm.
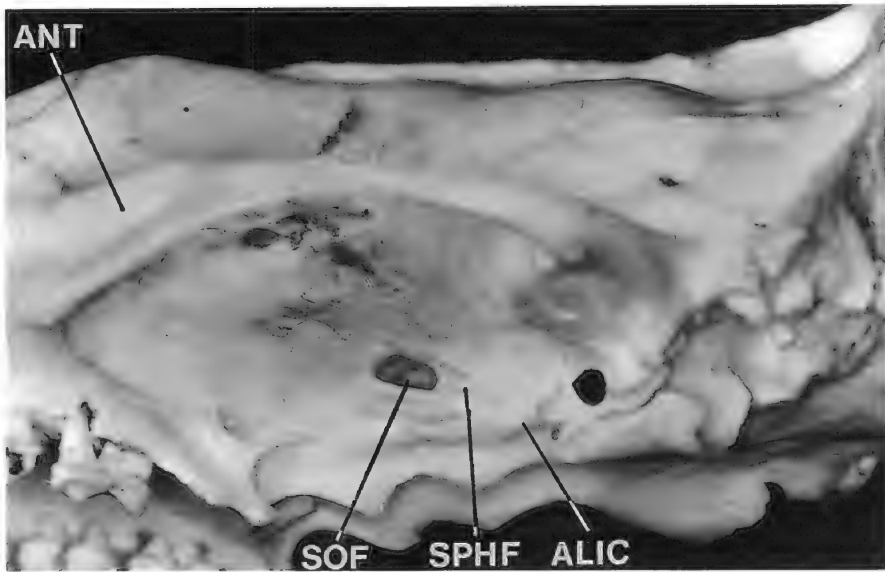
Fig. 14.   *Echinosorex gymnurus* (USNM 487891), lateral view of left orbitotemporal region.
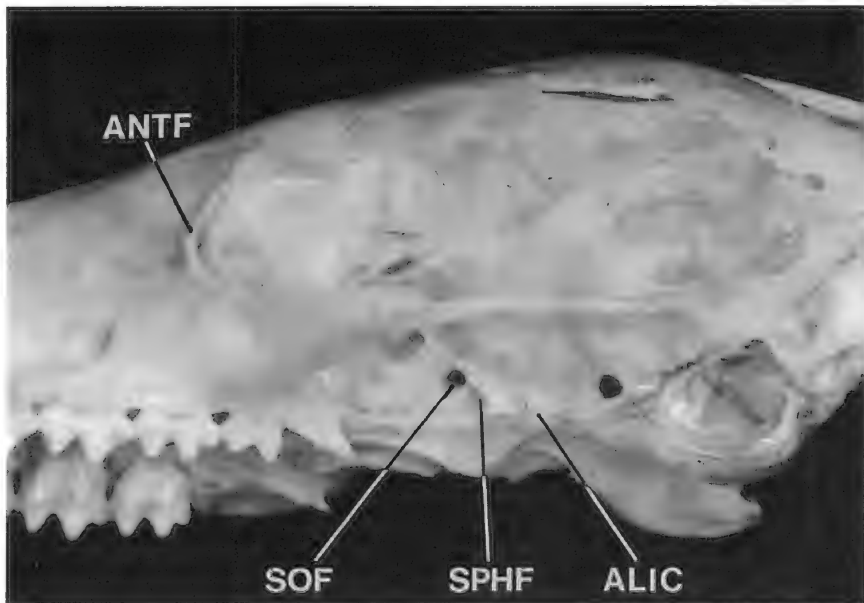
Fig. 15.   *Podogymnura truei* (AMNH unnumbered), lateral view of right orbitotemporal region (negative reversed for comparative purposes). See text for comments.
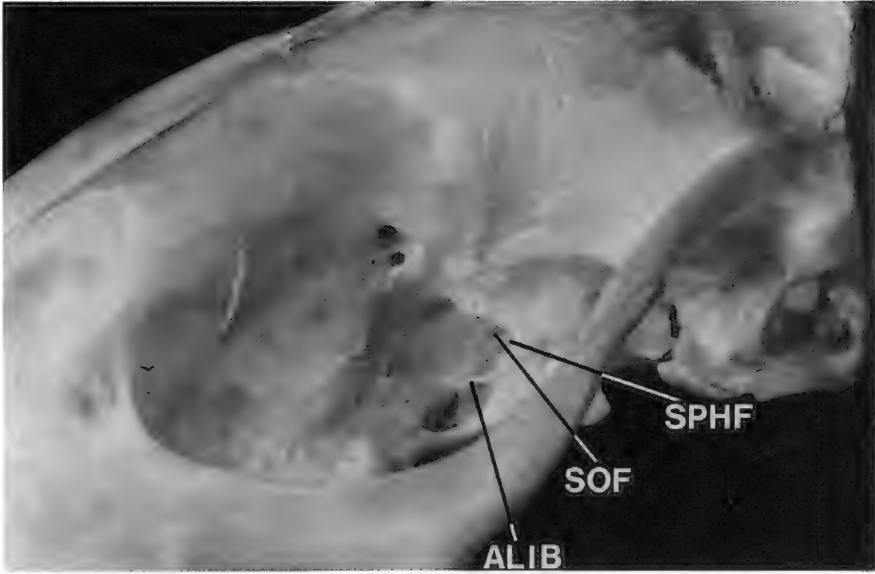
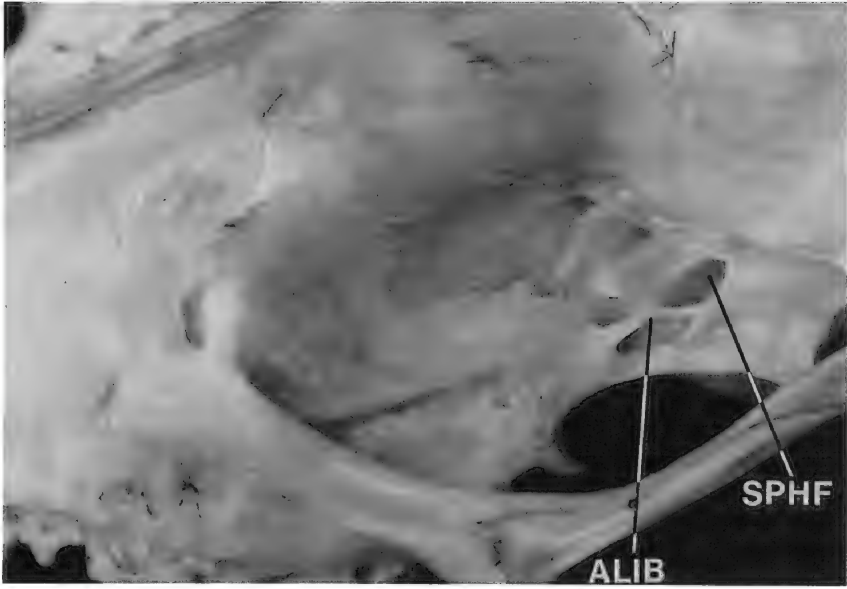Fig. 16. *Atelerix frontalis* (= *Aethechinus* [USNM 267653], lateral view of left orbitotemporal region.

Fig. 17. *Erinaceus concolor* (USNM 369533), lateral view of left orbitotemporal region. See text for comments.
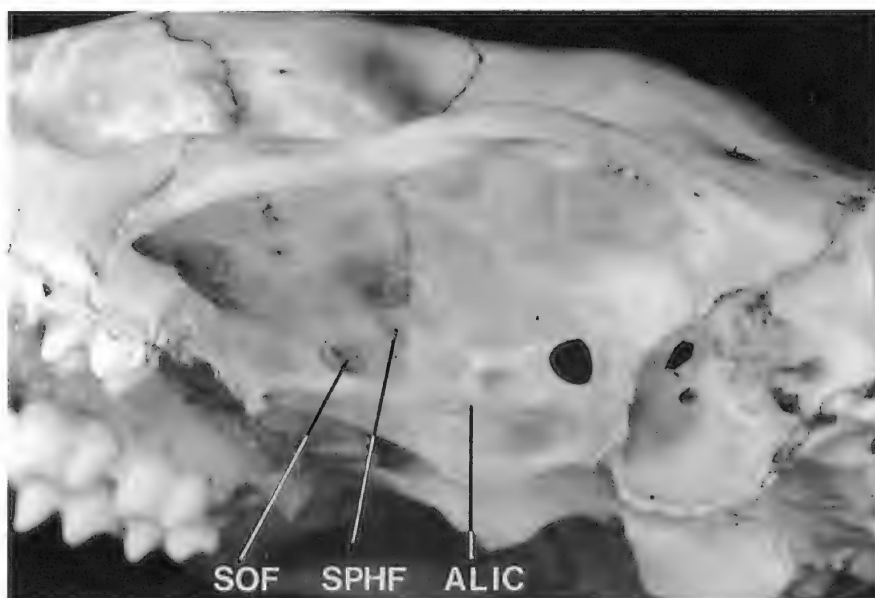
Fig. 18.   *Mesechinus dauuricus* (= *Hemiechinus* [USNM 270538]), lateral view of left orbitotemporal region.
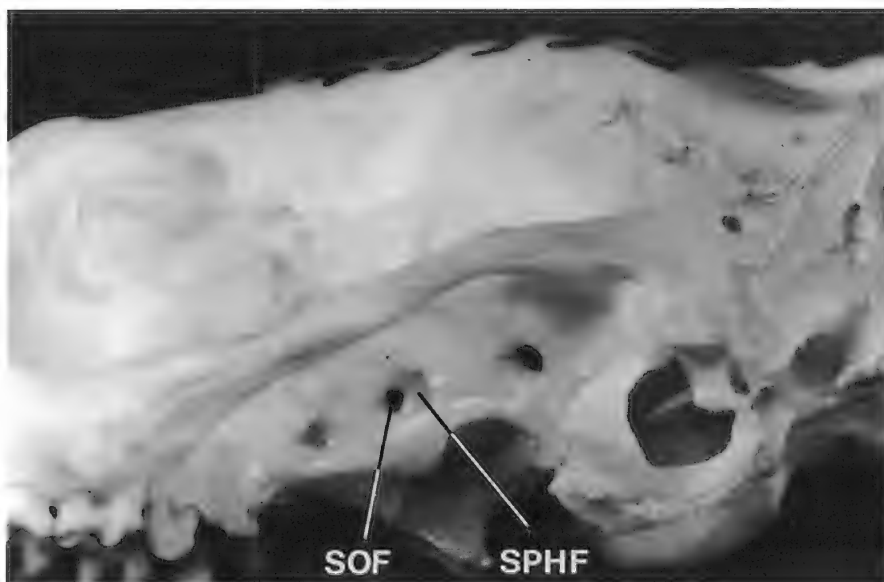

Fig. 19.   *Hemiechinus auritus* (USNM 340933), lateral view of left orbitotemporal region. See text for comments.
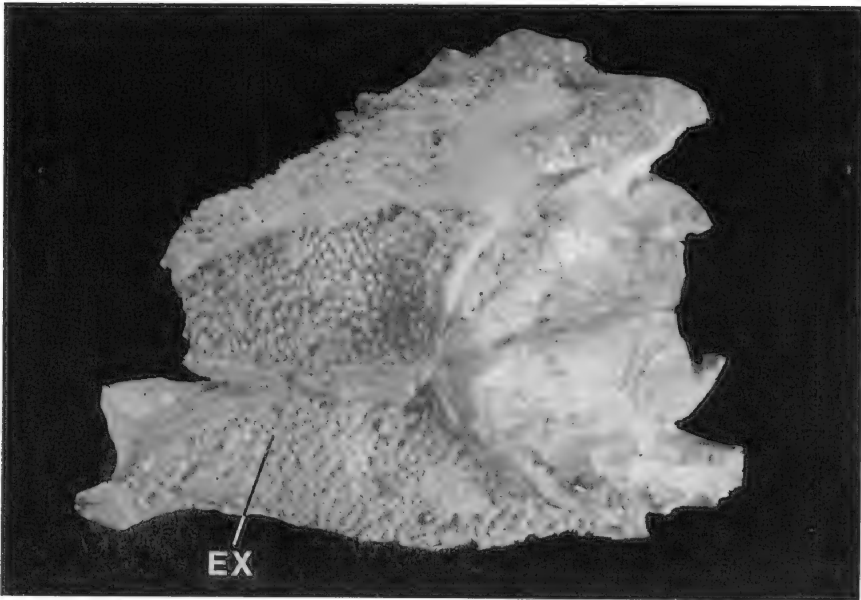
Fig. 20.   *Neurogymnurus* (BM M9653) dorsal view of skull. See text for comments. Measurements unavailable.
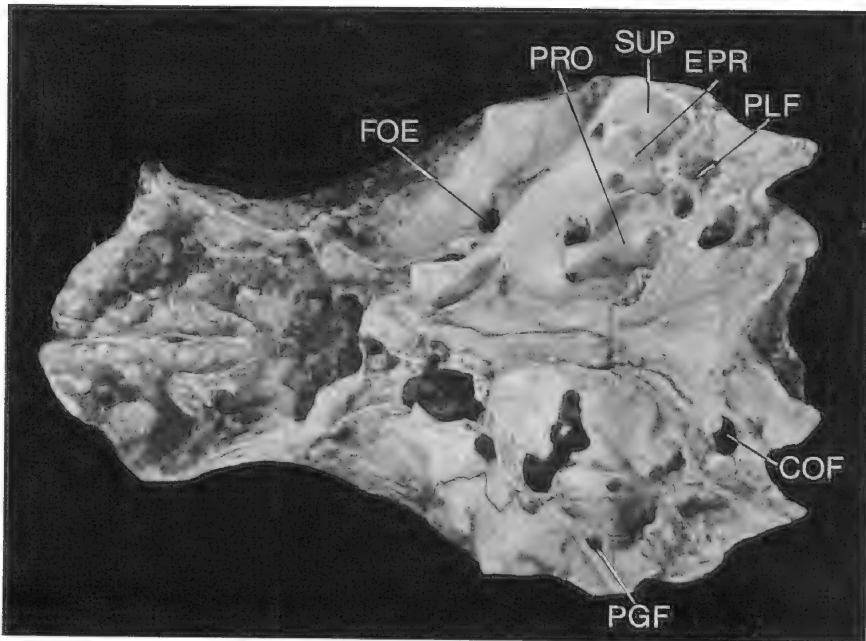

Fig. 21.   *Neurogymnurus* (BM M3752), ventral view of skull. See text for comments. Measurements unavailable.
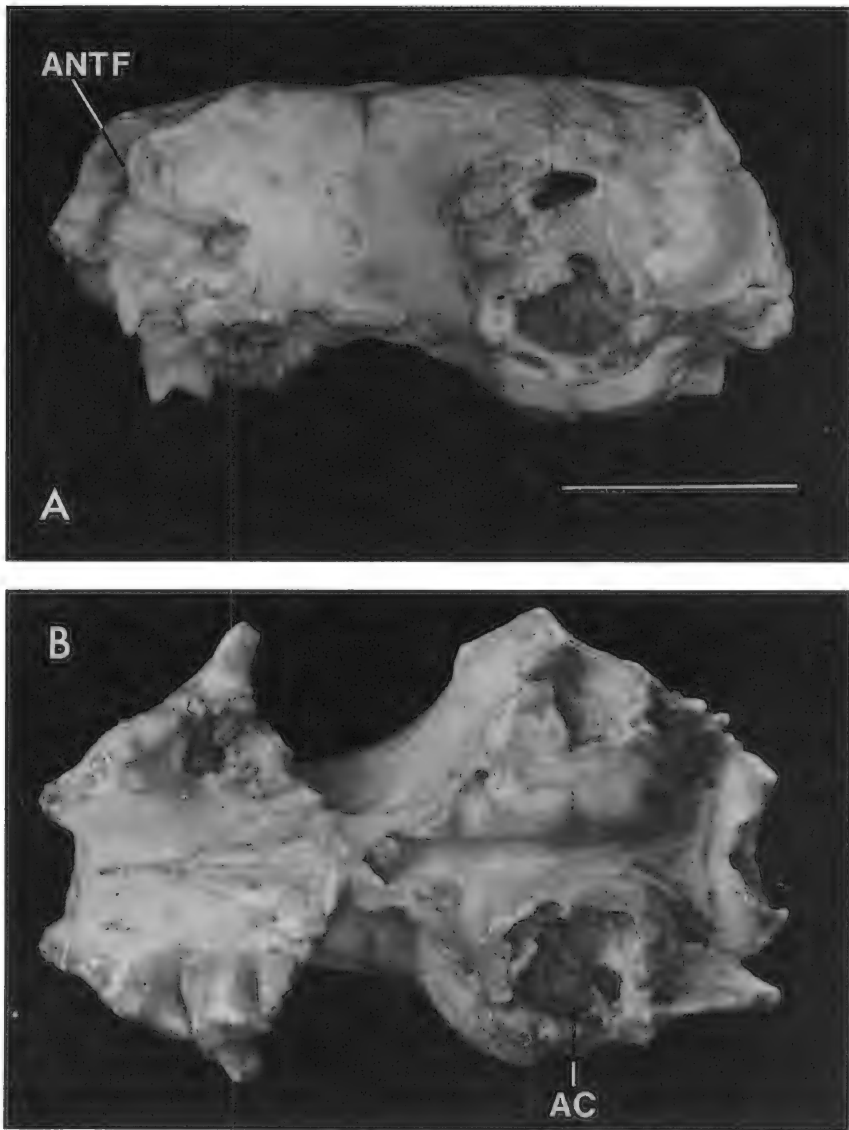
Fig. 22. *Brachyerix macrotis* (AMNH 21335 type): **(A)** right lateral view of skull (negative reversed for printing); **(B)** ventral view of skull. Scale = 10 mm.
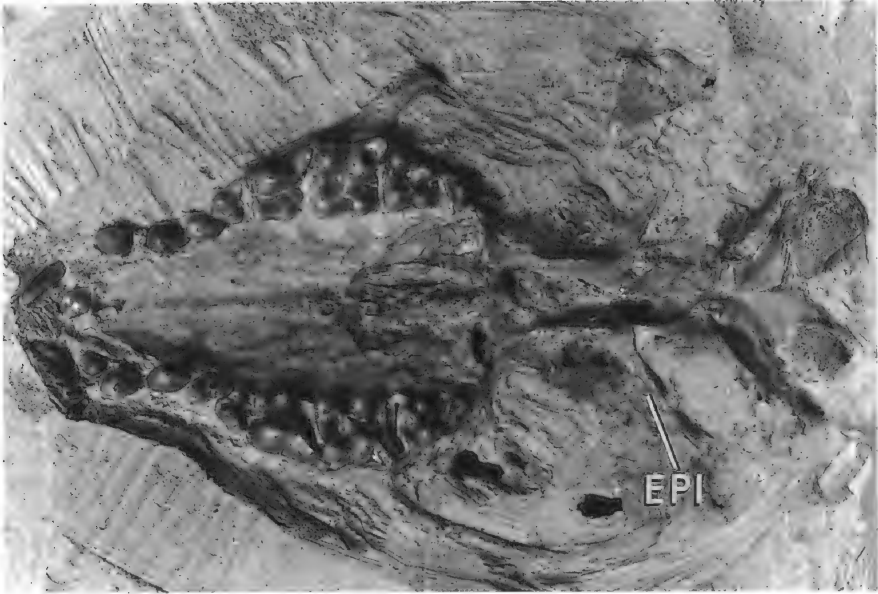
Fig. 23. *Mioechinus oengensis* (BM unnumbered type), ventral view of skull. No measurements available; see text for comments.
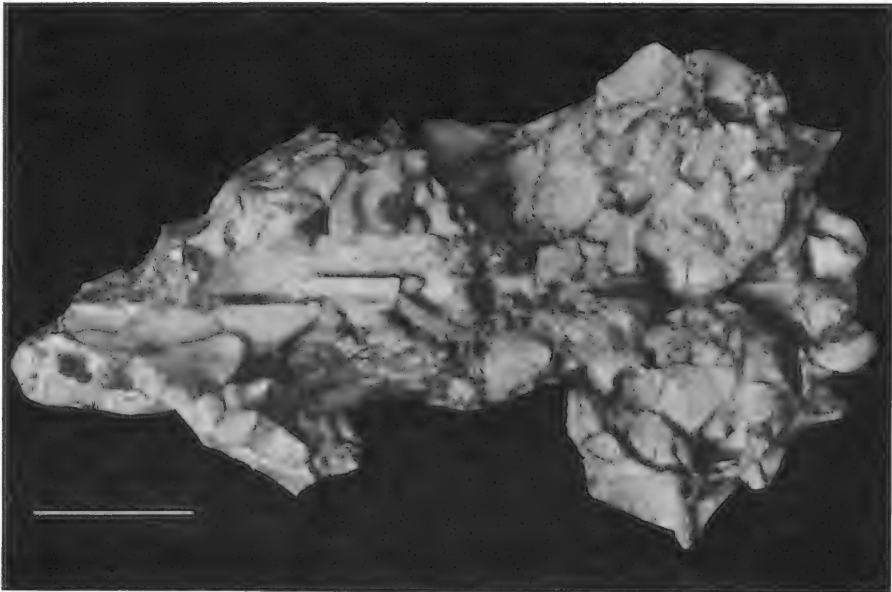

Fig. 24. *Metechinus nevadensis* (F:AM 76706) ventral view of skull. Scale = 1 cm.
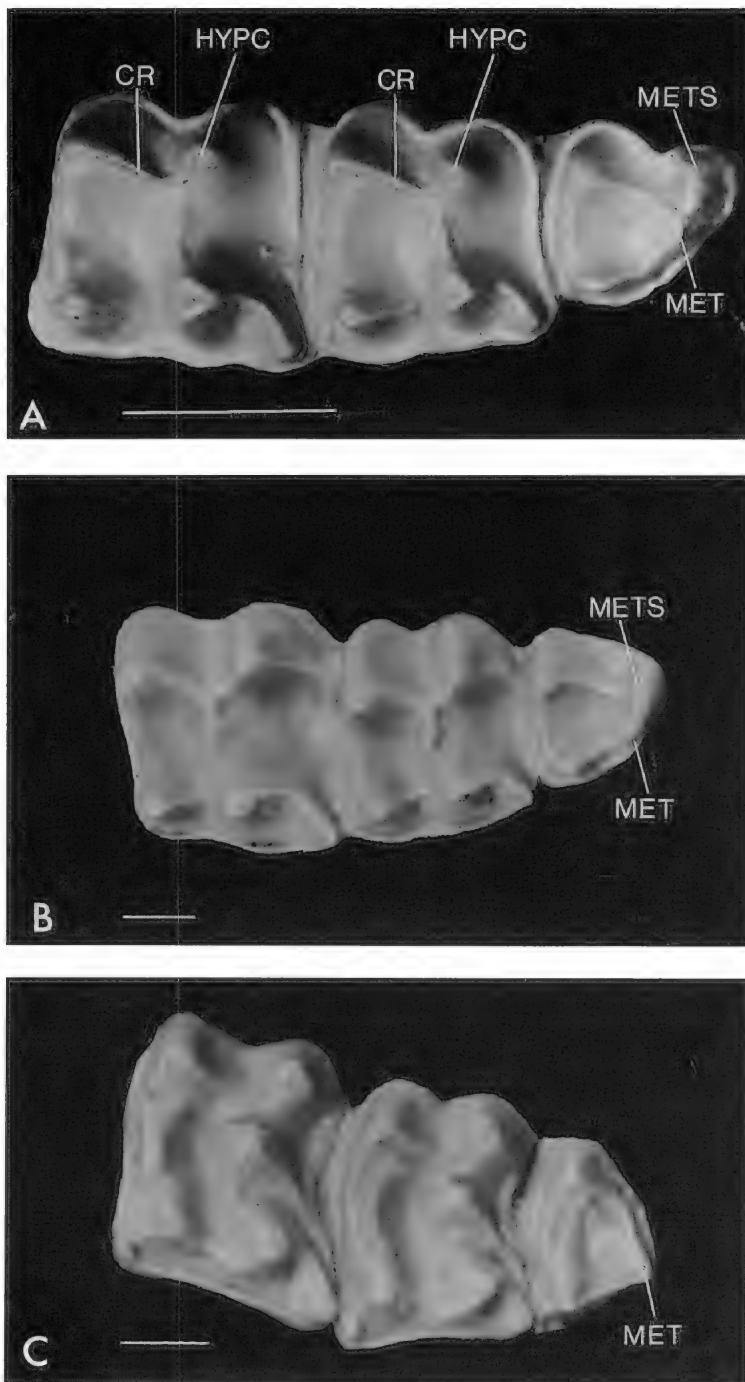
Fig. 25. Comparative study of the M1-M3 of: **(A)** *Echinosorex gymnurus* (AMNH 106069, right side; scale = 5 mm); **(B)** *Hylomys suillus* (USNM 282347, right side; scale = 1 mm); and **(C)** *Galerix* (BM M4845, right side; scale = 1 mm). See text for comments.

Data Matrix

27 taxa including ancestor (not including outgroups: lepictids, soricoids, and tenrecoids, 103 transformation series. The following transformation series are unpolarized: 11, 12, 15, 22, 31, 41, 46, 49–52, 54, 65, 58, 70, 73, 75, 77, 78, 81, 83, 90–92, 97, 98, 100, 101, 105. The following transformation series are unordered: 11, 21, 48, 51, 52, 63, 70, 79, 98, 101.

Echinosorex gymnura
0000101100 2110100001 0000010000 ?000010010 1100000011 1000001001 1000001111 1010011011 1111000?00 ?01

Podogymnura aureospinula
0000100100 2110100001 1100100000 ?000100?10 ?010010010 1100000011 1100001111 1010011011 1010011011 1111000?00 ?01

Podogymnura truei
0000100100 2110100001 1100100000 ?010010010 1100001011 1100001111 1010011?? 1111000?00 ?01

Hylomys sinensis
1001010111 2111010011 1000100000 ?000100011 ?010010010 1100001000 1002010111 1111101111 1010011011 1111000?00 ?00

Hylomys suillus
0001010111 2111010011 1000000000 ?000100011 ?010010010 1100001001 1001000001 1111101111 1010011011 1111000?00 ?00

Hylomys hainanensis
0001010111 2111010011 1000000000 ?000100011 ?010010010 1100001001 1001000011 1111101111 1010011?? 1111000?00 ?00

Hemiechinus aethiopicus
1112011022 1310101101 2101001104 0011100100 1111110010 1100010102 2112000111 1211101121 1110102100 0000111201 100

Hemiechinus hypomelas
1112011022 1210101101 2101001103 0011100100 1111110010 1100010102 2112000111 1201001121 1110102100 0000111201 100

Hemiechinus micropus
1112011022 1210101101 2011001104 0011100100 1111110010 1100010102 2112000111 1211101121 1110102100 0000111201 100

Hemiechinus auritus
1112011022 1110101101 2101001102 0011100100 0011110010 1100010102 2112000111 1201001121 1110102100 0000111201 200

Hemiechinus collaris
1112011022 1110101101 2111001102 0011100100 0011110010 1100010102 2112000111 1201001121 1110102100 0000111201 200

Mesechinus dauuricus
1102011022 1100101101 2111001101 1010100110 0011110010 1100010102 2112000111 1201001121 1110102100 0000011101 210

Erinaceus amurensis
1102011022 1110101101 21?1001101 0110100100 0011110010 1100010102 2122100111 1201001121 1110102100 0000001011 010

Erinaceus concolor
1102011022 1110101101 2111001101 0110100100 0011110010 1100010102 2122100111 1201001121 1110102100 0000001001 010

APPENDIX 3–(Continued)

Erinaceus europaeus
1102011022 1110101100 0110100100 0011110010 1100010102 2122100111 1201001121 1110102100 0000010?1 010

Atelerix frontalis
1102011022 1110101101 0110100100 0011110010 1100010102 2112000111 0201001121 1110102100 0000011011 010

Atelerix algirus
1102011022 1110101101 2111101111 0110100100 0011110010 1100010102 2112000111 0201101121 1110102100 0000011001 010

Atelerix albiventris
1102011022 1110101101 1111101111 0110100100 0011110010 1100010102 2112000111 0201101121 1110102100 0000011001 010

Atelerix sclateri
1102011022 1110101101 1111101111 0110100100 0011110010 1100010102 2112000111 0211101121 1110102100 0000021001 010

Galerix
??????1??? 1110101101 ?1?1101111 0110100100 0011110010 1100010102 2112000111 0211101121 1110102100 0000011001 010

????1?11? ?????????? ?????????? ?????????? 2??10?1000 0000011121 111000?? ?????????? ???

Proterix loomisi
10?0?1001? ??0??????? ??0?10???? ?????????0 ?001001112 1?00??1?1 ?1?00????? ?????????? ???

Brachyerix
1000?10022 2010?00101 1100100?00 ?000011??1 ?011?1111 3211110?110 ?1200?1101 1111?1?? ?????????? ???

Neurogymnurus
10????1112 2110000011 1000100001 0000001?10 ?????00010 0??2001000 0010??1111 1?10000??? ?????????? ???

Metechinus
1010011102? ?110?0?1?? ?????????003 000?000??0 ??1?011111 3211100?00 0?100??112 1111?0?1111 10?1?????? ?????????? ???

Mioechinus
?112?1???? ?2???????? ??0???1?? 0?11?????? ?????????? ?????????0?? ?11200?1?? 0000101?1?? ?110101?1?? ?????????? ???

Lanthanotherium
10?0?1???? ?????????1 ?001101?? ?????00??? ?????????? ?????????1 1000001000 0?110?1111 1010011??? ?????????? ???

ancestor
0000000000 ??00?00000 1?00000000 ?000000000 ?000000000 ??000?00?? ??0?000001 1000?0?0? 0?0?0??00 ??0000??0? ?00

tenrecoids
0000000030 3000100000 1000000000 ?0{01}0{01}00000 ?0000{01}001? {12}100000001 1000?00100 0000001000 ?000000000 0000000000 ?00

soricoids
0000000030 3000100000 1000000000 ?0000{01}{01}000 ?0000{01}}000? 1000000001 1000?0010{12} 0010001000 ?000000000 0000000?00 ?00

leptictids
0000000020 0100000000 1100000000 ?000001000 ?0000100{01}? 0001000001 1000000000 0000000100 0010000000 ?0000?????? ???

APPENDIX 4

List of Specimens Examined

Abbreviations: AMNH = American Museum of Natural History; F:AM = Frick Collection, American Museum of Natural History; BM = British Museum (Natural History); MNHNP = Museum National D'Historie Naturelle; UCMP = University of California Museum of Paleontology; USNM = United States National Museum, Smithsonian Institution.

Atelerix albiventris

AMNH	16581
AMNH	210385
USNM	181442

Atelerix algirus

AMNH	31247
USNM	476058

Atelerix frontalis

AMNH	87639
AMNH	87640
AMNH	207247
USNM	267653

Brachyerix macrotis

AMNH	21335
F:AM	74965
F:AM	74964
F:AM	76695

Echinosorex gymnura

AMNH	102781
AMNH	102782
AMNH	103736
AMNH	103737
AMNH	103883
AMNH	103886
AMNH	106068
AMNH	106069
BM	34698
BM	76.5.2.7
BM	87.178
BM	87.179
BM	6.10.4.13
BM	71.2613
BM	55.12.24.35
BM	60.5.14.73
BM	14.12.8.104
BM	91.10.7.45
BM	0.3.30.31
BM	8.7.1.7.9
BM	51.181
BM	12.24.90
BM	55.1453
BM	51.180
BM	14.12.8.102
BM	61.1157
USNM	487891

Entomolestes

AMNH	105393
AMNH	98742

Eolestes

AMNH	un-numbered

Erinaceus concolor

AMNH	149412
USNM	369533

Erinaceus europeaus

AMNH	35304
AMNH	10735
USNM	153410

Galerix

AMNH	10516 A–H
BM	M4845
BM	M5380
BM	M5383

Hemiechinus aethiopicus

USMN	470566

Hemiechinus auritus

AMNH	22876
AMNH	22889
USNM	340933
BM	80021

Hemiechinus hypomelas

USNM	326697

Hylomys parvus

BM	19.11.5.8
BM	19.11.5.9
BM	19.11.5.10
BM	19.11.5.11

Hylomys sinensis

USNM	241402
BM	11.2.1.21
BM	11.2.1.22
BM	82.205
BM	33.4.1.117
BM	33.4.1.124
BM	33.4.1.132
BM	11.2.1.15
BM	11.2.1.18
BM	11.8.61
BM	11.2.1.19

Hylomys suillus siamensis

BM	2610439
BM	2610436

Hylomys suillus dorsalis

USNM	292347

APPENDIX 4—(Continued)

BM	55.66.1
BM	712614
BM	712615
BM	712616
BM	712617
BM	712618
BM	92.9.64
BM	95.10.4.3
BM	95.10.4.4

Hylomys suillus maxi

BM	62.711
BM	71.26.14
BM	71.26.17
BM	71.26.18

Lanthanotherium gigantum

BM	M16335

Lanthanotherium sawini

UCMP	54600
UCMP	82731

Litolestes

AMNH	33938
AMNH	33941
AMNH	33947
AMNH	33831

Mesechinus dauuricus

USNM	270539

Metechinus

F:AM	74925
F:AM	76698
F:AM	76707

Metechinus nevadensis

F:AM	74925

Mioechinus oeningensis

BM	un-numbered

Neurogymnurus

BM	M7509
BM	M9653
BM	M9655
BM	M2388
BM	9654
BM	5109
MNHN	QU8680
MNHN	QU8691
MNHN	QU8692
MNHN	QU8693
MNHN	QU8694
MNHN	QU8695
MNHN	QU8697
MNHN	QU8698
MNHN	QU10700

Podogymnura truei

BM	53.660
BM	53.659
BM	65.660
AMNH	un-numbered

Proterix

F:AM	74961
F:AM	9756
AMNH	un-numbered

Pseudogalerix

BM	M15810 mult.

Leptictids

Leptictis

F:AM	108194
AMNH	62369

Tenrecoids

Echinops teifairi

AMNH	17060
AMNH	170601

Microgale dobsoni

AMNH	31261

Oryzorictes tetradactylus

AMNH	31257

Potomogale velox

AMNH	120250
AMNH	240968

Setifer setosus

AMNH	100749
AMNH	170538
AMNH	170540
AMNH	100762

Tenrec ecaudatus

AMNH	170512
AMNH	100733

Solenodontidae

Solenodon paradoxus

AMNH	28270
AMNH	18502

Soricids'

Anourosorex squamipes

AMNH	3830

Paracrocidura maxima

AMNH	82484

Myosorex varius

AMNH	168050

APPENDIX 4—(*Continued*)

Solisorex pearsoni
     AMNH   240937

Syvisores granti
     AMNH   180969

Scutisorex samereni congicus
     AMNH   48455

Nectogale elegans
     AMNH   114844

Chimarrogale
     AMNH   114825

Suncus murina
     AMNH   44758

Talpa europaea
     AMNH   70790
     AMNH   42558

Talpa romana
     AMNH   160455

Uropsilus soricipes
     AMNH   110591