

Phylogenetic Relationships  
of Hedgehogs and Gymnures  
(Mammalia: Insectivora:  
Erinaceidae)

DARREL R. FROST,  
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and  
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## ABSTRACT

Frost, Darrel R., W. Chris Wozencraft, and Robert S. Hoffmann. Phylogenetic Relationships of Hedgehogs and Gymnures (Mammalia: Insectivora: Erinaceidae). *Smithsonian Contributions to Zoology*, number 518, 69 pages, 12 figures, 19 plates, 8 tables, 1991.—Using 81 transformation series containing 172 characters of osteology, dentition, and external morphology, the phylogeny of Recent erinaceids is investigated using standard phylogenetic techniques. For this analysis, we used as the first taxonomic outgroup of Erinaceidae, Soricidae + Tenrecoidea; and as the second taxonomic outgroup, †Leptictidae. Supraspecific monophyletic groups identified from this analysis are Erinaceidae; Hylomyiinae; *Podogymnura* (*aureospinula*, *truei*); *Echinosorex* + *Podogymnura*; *Hylomys* (*sinensis*, *suillus*, *hainanensis*); Erinaceinae; *Hemiechinus*; subgenus *Paraechinus* (*aethiopicus*, *micropus*), *hypomelas* + *H. auritus* + *H. collaris*; *Mesechinus dauuricus* + (*Erinaceus* + *Atelerix*); *Erinaceus* (*europaeus*, *concolor*, *amurensis*); and *Atelerix* (*albiventris*, *sclateri*, *algirus*, *frontalis*). Evidence does not support the monophyly of *Hemiechinus* (as recognized by Honacki et al., 1982) or of *Hemiechinus* excluding *H. dauuricus*. *Mesechinus* is elevated from subgeneric status (under *Hemiechinus*) to generic status to contain *dauuricus* and *hughi*. *Paraechinus* is considered a subgenus of *Hemiechinus*. *Neohylomys* and *Neotetracus* are considered synonyms of *Hylomys*. Diagnoses and taxonomic accounts of genera are presented along with comments on the taxonomy of and variation within species. *Hemiechinus aethiopicus*, *H. deserti*, and *H. dorsalis* are provisionally regarded as subspecies of *H. aethiopicus*.

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# Phylogenetic Relationships of Hedgehogs and Gymnures (Mammalia: Insectivora: Erinaceidae)

*Darrel R. Frost, W. Chris Wozencraft,  
and Robert S. Hoffmann*

## Introduction

Erinaceomorphs are known from the lower Eocene (Novacek et al., 1985) with characteristics of the family already well established by the Early Oligocene (Butler, 1948). The Erinaceidae is a relatively plesiomorphic family of lipotyphlan insectivores that has its Recent distribution in the tropical and temperate zones of Eurasia and Africa. Current taxonomy divides the Recent members of the family into two nominally monophyletic subfamilies (Butler, 1948, 1956, 1988; Novacek, 1985, 1986; Corbet, 1988), Hylomyiinae (= Galericinae = Echinisoricinae) (with 3–5 genera and 6 species) of the Southeast Asian tropics, and Erinaceinae (with 3–5 genera and 14 species), of Africa, Europe, and arid regions of Asia (Honacki et al., 1982; Nowak and Paradiso, 1983; Corbet, 1988). For purposes of discussion, we will use the nomenclature of Corbet (1988) (see Table 7), that is, 5 genera of hylomyiines and 4 genera of erinaceines.

Because of their important position in larger questions of insectivore classification, erinaceids have been the object of considerable previous investigation. Leche (1902), Butler (1948, 1956, 1988), and McDowell (1958) studied the anatomy, and Novacek (1986) reviewed the relationships of the subfamilies within the framework of larger questions of erinaceomorph relationships. In an attempt to resolve the controversy surrounding generic distinctions in erinaceines, Robbins and Setzer (1985) evaluated the phenetic similarities

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of the erinaceine genera. More recently, Corbet (1988) reviewed the taxonomy, phylogeny, ecology, and zoogeography of Erinaceidae.

What has not been attempted is a rigorous approach to inferring the phylogenetic relationships of extant taxa of erinaceids from Recent material. In this paper we attempt such a phylogenetic analysis. More specifically, the questions asked are: (1) Are all of the nominal taxa within Erinaceidae monophyletic? (2) What is the most parsimonious hierarchical arrangement (= hypothesized historical relationships) of these discovered monophyletic taxa? (3) What taxonomy best reflects our knowledge of the relationships of these taxa?

Although the recent paper by Corbet (1988) might be considered an example of what we are trying to accomplish, we have reservations about his phylogenetic methods and taxonomy. Additionally, we could not verify some of the characters he used (see below). Because comparisons between our study and that of Corbet (1988) are unavoidable, we will highlight differences between our approaches, both philosophically and methodologically.

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### Methods and Materials

We employed outgroup comparison, independent polarization of transformation series, and formation of the most parsimonious explanation of the data, a cladogram (Watrous and Wheeler, 1981; Wiley, 1979). For analysis, 81 transformation series containing 172 characters of external morphology, dentition, and osteology were collected from specimens of erinaceids of all nominal species, except *Hemiechinus hughii* (of which we have only seen the unique skull-less holotype), *Paraechinus intermedius*, and *P. nudiventris* (see Appendix 1, "Specimens Examined"). We used species for the operational taxonomic units (OTU) of our phylogenetic analyses to avoid problems resulting from unsuspected genus-level paraphyly.

Characters were initially drawn both from the literature (e.g., Butler, 1948, 1956, 1988; McDowell, 1958; MacPhee, 1981; Novacek, 1985, 1986; Corbet, 1988) and from our own observations. For purposes of outgroup comparison with Recent taxa, the arrangement of Novacek (1986) was accepted; that is, Soricoidea (Soricidae + Solenodontidae + Talpidae) + Tenrecoidea (Tenrecidae + Chrysochloridae) was considered the first taxonomic outgroup (sensu Watrous and Wheeler, 1981). Novacek (1985) and Butler (1988) noted a number of fossil erinaceomorphs that would normally be the nearest presumptive outgroups of erinaceids. Although fossil erinaceomorphs were not utilized directly as outgroups for our analysis, published information was used, when available (e.g., Novacek, 1985), for some polarity decisions. A fossil taxon, †Leptictidae († denotes fossil taxon), was considered the second taxonomic outgroup for our analysis. This choice was made because of the extensive summary of anatomy available (Novacek, 1986), and because second outgroup possibilities among Recent mammals demonstrated such an array of variation as to make comparisons unhelpful. Because of the taxonomic diversity in Soricoidea and Tenrecoidea, only the plesiomorphic conditions are noted for those taxa in the data matrix.

Much of the following discussion revolves around decisions made concerning the determination of polarity or the manner in which morphological variation is described that might influence the character placement on the tree. We attempted to describe the morphology involved in each transformation series

in such a manner that it would be as unambiguous as possible. Where a particular morphological feature could be broken down into many recognizable components, we did so, and only considered reuniting those components when the correlation of their distribution was perfect. After a pattern of variability was described, each OTU was categorized to one state of that pattern, usually by the assignment of a letter code that implied no polarity decision. Finally, after all OTU's had been coded, the polarity was assigned to each letter code by comparison to the outgroups. Generally, when both first and second outgroups agree in the polarity assigned to a transformation series, our rationale for adopting a particular polarity will not be discussed. Although polarity decisions are discussed with some transformation series, we have included data lines in our matrix (Appendix 2) for the plesiomorphic conditions found in Soricoidea, Tenrecoidea, and †Leptictidae to help in the understanding of our polarity decisions. Rooting of the cladogram was determined by using a hypothetical ancestor deduced from the distribution of characters in the outgroups.

Some character transformations could not be polarized adequately, due to ambiguous outgroup comparison. These features were used in the analysis as unpolarized (i.e., additivity retained) or unordered transformations (i.e., additivity not retained); that is, no polarity of transformation was assumed except those determined by correlation with the remaining characters. These transformations cannot affect the rooting of the calculated tree, but do serve to enhance stem definition within the rooted tree. Characters for all transformation series are presented in the data matrix for all outgroups (Appendix 2). In the following list, in the polarized transformation series, zero (0) denotes the plesiomorphic character and one (1) and two (2) denote progressively more derived characters; where the character was initially drawn from the literature, we have included that reference, although we do not necessarily code or state the character in the same manner. In unordered transformations the particular order of integers carries no information. In unpolarized transformations, additivity is retained although the ancestral condition was coded as "unknown," allowing the polarity of the transformation to be determined by correlation with the otherwise most parsimonious solution of the data.

Analysis of data was completed using the PAUP (Phylogenetic Analysis Using Parsimony) program, version 2.4.1 (Swofford, 1984). The data matrix was analyzed using the multiple parsimony (MULPARS) and global swapping options. Global swapping allows the program to search for more parsimonious trees by global (as opposed to "nearest neighbor") swapping of branches. MULPARS allows the swapping procedure to be performed on all topologically distinct trees of a given length rather than the first found of any particular length. Although the default option (FARRIS), used for optimization of character placement, prefers reversal over convergence, by using the CSPOSS and BLRANGE options (which note ambiguous placement of characters), as well as comparing results with DELTRAN outputs (an option that



prefers convergence to reversal), and taking into account the distribution of "unknown" character assignments, evidence corroborating stems could be restricted to characters of unambiguous placement.

We have not employed differential character weighting. This practice has been argued against convincingly by Patterson (1982) and Novacek (1986). In short, character weighting assumes that in the absence of evidence from congruence of character distribution, one can "know" how "plastic" (in an a posteriori sense) a particular transformation is. Additionally, a posteriori weighting assumes that there are discoverable "natural" classes of transformations. Although we admit that pretests of homology are grounded in perceptions of similarity, we deny that injecting assumptions about the undetected levels of non-homology can increase the rigor of the analysis. Basically, weighting removes any objective grounds for discussion of character incongruence. Recently, Corbet (1988) has approached the systematics of erinaceids using subjective weighting of characters (see below).

In a number of features our observations disagree with previous authors. Although earlier studies were usually careful, the specimens available were (and in some cases still are) few and sampling errors were common. More unfortunate has been the tendency for some authors to refer to published literature and not to specimens. Many features that looked promising in our literature search did not survive specimen examination; we have tried to point out these discrepancies in our discussions. Because many of these features did not play central roles in previous discussions of phylogeny or identification, we have tended to ignore these for brevity's sake. Before the reader assumes that we have missed a character noted by earlier authors we suggest that specimens be examined. However, following our list of transformation series is a section, "Characters Not Utilized in Analysis," in which we discuss some of the features that have figured prominently in earlier studies.

We did not attempt to exclude apparent synapomorphies of Erinaceidae or interesting autapomorphies of terminal taxa from the analysis. Although such inclusion elevates the consistency index (CI), the only concern this could raise would rest on the belief that the consistency index is a measure of topological stability, or that it allows comparison between data matrices. Both of these beliefs are unfounded. We have used the consistency index as it was intended, only as a measure for comparing trees derived from the same data matrix (Kluge and Farris, 1969).

### Character Transformation Series

#### CRANIAL CHARACTERS

We follow the nomenclature of Jayne (1898), McDowell (1958), MacPhee (1981), and Novacek (1986).

1. Nasal, posteriormost extension: (0) posteriormost por-

tion of the nasals anterior to the level of the antorbital rim; (1) posteriormost portion of nasals extends medial or posterior to the level of the antorbital rim. This transformation is most likely related to rostral length (Transformation Series #2); however, the relationship is not necessarily a direct one as shown by the difference between *Neotetracus sinensis* (Plate 5) and *Hylomys suillus* (Plate 6).

2. Rostrum, length (Butler, 1948): (0) long (42% or more of skull length); (1) short (35% or less of skull length). Rostrum length is measured from the nasolacrimal foramen to the premaxilla midline. Although outgroup comparison is ambiguous, in that many tenrecoids and soricoids have relatively short rostra, fossil erinaceomorphs have relatively long rostra (Novacek, 1986). We are therefore confident that, within Erinaceidae, we have characterized the transformation correctly. Butler (1956), Rich and Rich (1971), and Novacek (1986) also considered a long snout to be plesiomorphic within this clade. Corbet (1988) conversely considered the short snout of the erinaceines to be primitive and distinguished between the length of the rostrum in *Podogymnura* and *Echinosorex* on one hand and *Hylomys*, *Neotetracus*, and *Neohylomys* on the other. Our measurements of these taxa do not support Corbet's separation into two rostrum length classes (Table 1).

3. Rostrum, width: (0) rostrum wide, anterior incisors not closely adjacent; (1) rostrum narrow, anterior incisors closely adjacent. In the plesiomorphic condition there is a distinctive diastema between the anteriormost incisors (e.g., compare *Hemiechinus auritus*, Plate 15, with *Erinaceus europaeus*, Plate 13).

4. Palatine foramina, size (Butler, 1948; Novacek, 1986): (0) small; (1) anterior foramina elongated posteriorly; (2) anterior foramina elongated to include middle palatine foramina. There is no reason to assume that the palatal perforations found in many erinaceids are homologous with those found in marsupials (Butler, 1972). Corbet (1988) did not distinguish among the anterior, middle, and posterior palatine foramina,

TABLE 1.—A comparison of selected skull measurement ratios, mean (range), of hylomyines and *Erinaceus europaeus* to the character state groups of Corbet (1988).

Specimens (N)	Rostrum/ Skull length	Interorbit/ Mastoid width
<i>Podogymnura</i> (2)	0.453–0.457 <sup>1</sup>	0.561–0.593 <sup>4</sup>
<i>Echinosorex</i> (15)	0.455(0.438–0.480) <sup>1</sup>	0.502(0.437–0.541) <sup>5</sup>
<i>Neotetracus</i> (4)	0.418(0.395–0.439) <sup>2</sup>	0.606(0.583–0.644) <sup>6</sup>
<i>Hylomys</i> (14)	0.467(0.441–0.507) <sup>2</sup>	0.630(0.542–0.678) <sup>6</sup>
<i>Neohylomys</i> (1)	0.434 <sup>2</sup>	0.535 <sup>6</sup>
<i>Erinaceus</i> (10)	0.376(0.367–0.391) <sup>3</sup>	0.603(0.545–0.659) <sup>6</sup>

<sup>1</sup>Corbet coded these as having long rostra.

<sup>2</sup>Corbet coded these as having short rostra.

<sup>3</sup>Corbet coded these as having very short rostra.

<sup>4</sup>Corbet coded these as having slight interorbital constriction.

<sup>5</sup>Corbet coded these as having pronounced interorbital constriction.

<sup>6</sup>Corbet coded these as having minimal interorbital constriction.

and referred to "palatal perforations" as being absent, small, or large. His transformation series and distribution of characters would coincide with our series.

5. Anterior palatine foramina, location: (0) at the maxilla/palatine suture; (1) anterior to the maxilla/palatine suture. Corbet (1988) drew attention to the presence of long grooves in the palate for the major palatine artery in those taxa that have the anterior palatine foramina located anterior to the palatine/maxilla suture. The major palatine artery emerges ventrally from the anterior palatine foramen and continues anteriorly along a groove in the maxillary. These grooves are associated with the forward placement of the foramina (our Character 5.1); their distinctiveness and length are correlated with the age of the individual. There are faint, nondescript grooves in those taxa that have the foramina located at the suture, and these run forward in the palate, although not as distinctly as in the taxa with condition 5.1. We could not verify on our specimens Corbet's contrasting of *Hylomys* and *Neotetracus* with short grooves and *Podogymnura* and *Echinosorex* with long grooves and suspect that this is individually variable with age.

6. Infraorbital canal, position of the anterior opening (Butler, 1948; Rich and Rich, 1971; Novacek, 1986): (0) dorsal or posterodorsal to the P4-M1 area; (1) dorsal to the P3-P4 region. Although most taxa coded as having the plesiomorphic condition have the anterior opening above P4-M1, *Podogymnura truei* has the opening more posterior, dorsal to the M1-M2 region (see Plate 3). For purposes of this analysis this species was coded as having condition "0." In many soricoids and tenrecoids the position of the infraorbital foramen is set even farther posterior. We have refrained from considering *P. truei*

as having a condition other than "0," simply because of the ambiguity of outgroup comparison. This transformation reflects the relative shortening of the rostrum; the correlation is not perfect, however, so this transformation was retained as distinct from Transformation Series #2 (rostrum length).

7. Antorbital fossa (Butler, 1948, 1956; Novacek, 1986): (0) present; (1) absent. The antorbital fossa serves for the origin of the snout muscles and is located lateral and posterior to the infraorbital foramen on the anterior surface of the zygoma. Butler (1956) noted some structural differences between the antorbital fossa of †*Leptictis* and those found in tenrecoids, soricoids, and erinaceomorphs. Without evidence to the contrary, however, we regard these features as homologous. Although antorbital fossae are variably absent among some soricoids and tenrecoids, we regard presence to be the plesiomorphic condition. Subadults and most adults of *Echinosorex* do not exhibit the presence of an antorbital fossa, although some older individuals may develop an indistinct shallow fossa. Corbet (1988:123) referred to "horizontal crests behind infraorbital foramen" in his analysis of the hylomyines. If we interpret his transformation series correctly, he referred to the deeply excavated antorbital fossa on the zygoma. In *Hylomys*, *Neotetracus*, *Neohylomys*, and *Podogymnura* the excavation of this fossa is reflected in the two ridges that surround it and meet posteriorly. In the erinaceines the fossa is absent and in those *Echinosorex* where a shallow fossa is present, it lacks a distinct lower rim.

8. Antorbital (= prelacrima) flange (Butler, 1948, 1956): (0) not developed, so the lacrimal foramen is visible from the lateral view; (1) developed to a degree that the lacrimal

TABLE 2.—Abbreviations of morphological features used in figures and legends.

ACM	Acromion	MET	Metacromion
ALI	Alisphenoid	MPF	Middle palatine foramen
ANT	Antorbital fossa	NAF	Nasolabialis fossa
APF	Anterior palatine foramen	NPF	Nasopharynx fossa
BAS	Basisphenoid, tympanic wing	NSV	Neural spine of vertebrae
CBL	Condylbasal length	PAG	Promontory artery groove
C/c	Upper/lower canine	PAR	Paroccipital process
COF	Condylar foramen	PET	Petrosal, tympanic wing
DEN	Dens	PGF	Postglenoid foramen
EAM	External auditory meatus	PLF	Posterior lacerate foramen
ECA	Ectotympanic, anterior process	P/p	Upper/lower premolar
ECT	Ectotympanic	PPF	Posterior palatine foramen
EPI	Epipterygoid process	PRO	Promontorium
EPR	Epitympanic recessus	SAG	Stapedial artery groove
ETF	Ethmoid foramen	SCA	Sinus canal, anterior opening
EUS	Eustachian tube	SFA	Stapedial foramen, anterior opening
FIB	Fibula (fused)	SMF	Stylomastoid foramen
FOE	Foramen ovale	SQU	Squamosal
GLN	Glenoid fossa	STM	Stapedius muscle fossa
INF	Incisive foramina	SUP	Suprameatal fossa
KEL	Postventral keel of axis	TIB	Tibial crest or flange
M/m	Upper/lower molar	TRA	Transverse process
MAL	Manubrium of malleus	TYM	Tympanohyal
MAS	Mastoid process of the petrosal		



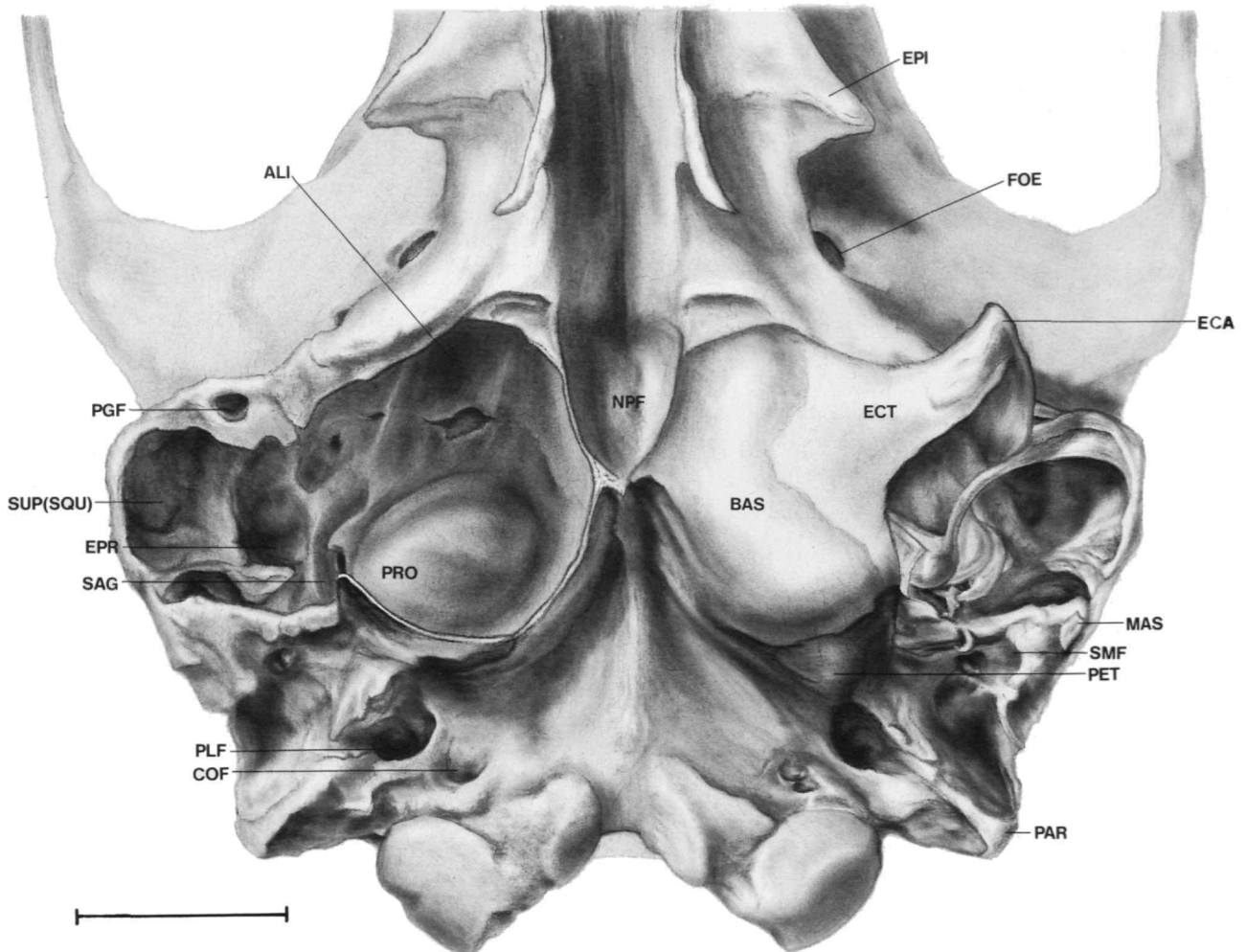


FIGURE 1.—The basicranium of *Paraechinus hypomelas* (ventral view). Left auditory bullae cut away. (Scale = 5 mm; key to abbreviations in Table 2.)

foramen is hidden from lateral view. Butler (1948, 1956) discussed this feature from the viewpoint of the direction of the opening of the nasolacrimal foramen. Because the orientation of the nasolacrimal duct is merely a reflection of the development of the antorbital (= prelacrima) flange we have cast the description of this feature in that light.

9. Maxilla, posteroventral process on zygoma: (0) absent; (1) present, small and indistinct; (2) present, large and distinct.

10. Jugal, size (Butler, 1956; Novacek, 1985, 1986): (0) large, reaches lacrimal; (1) smaller, does not reach lacrimal, reaches posteroventral process of zygoma; (2) vestigial, confined to lateral rim of zygomatic process of maxilla; (3) absent. Even though a large jugal is clearly plesiomorphic for mammals, "local" outgroup comparison is uninformative in this case; therefore, this transformation must be treated as

unordered. According to Butler (1972), the general reduction of the jugal can be considered evidence of monophyly of the lipotyphlans.

11. Pterygoid/alisphenoid and epipterygoid processes (parapterygoid of Osborn and Helmy, 1980) (Novacek, 1986): (0) epipterygoid processes absent, alisphenoid not inflated; (1) epipterygoid processes present, alisphenoid not inflated; (2) epipterygoid processes present, alisphenoid inflated; (3) epipterygoid processes present, alisphenoid and epipterygoid processes inflated. In *Paraechinus* the hypotympanic cavity of the middle ear is extended anteriorly into the base of the pterygoid/alisphenoid complex (Figure 1); in *P. aethiopicus* alone, it is expanded even farther into the epipterygoid process (Plate 14).

12. Lacrimal/maxilla suture (Butler, 1956): (0) unfused

and/or distinct in adults; (1) fused and indistinct in young adults.

13. Frontal, supraorbital processes (Butler, 1948): (0) absent or poorly defined and blunt; (1) sharp, readily identifiable processes present. Our characterization of this transformation series differs from Corbet (1988) only in considering *Neohylomys* to share the derived condition with *Hylomys* and *Neotetracus*, rather than treating it as plesiomorphic. Corbet reported that the process in *Neohylomys* was not as well developed as those in the other taxa. Our examination of the type series leads us to believe that the process in *Neohylomys* is developed as well as or better than the process in the other taxa.

14. Frontal, supraorbital foramen (Novacek, 1986): (0) present; (1) absent. The absence of these foramina in the tenrecoids and soricoids makes outgroup comparison ambiguous. This transformation was therefore treated as unpolarized in our analysis.

15. Frontal inflation (Butler, 1948): (0) no inflation; (1) variable degrees of inflation. Butler (1948:450) noted that in this feature, *Paraechinus* and *Hemiechinus* resemble hylomyines. We could not characterize the difference in the degree of inflation of the frontals between *Paraechinus*, *Hemiechinus*, and the remaining erinaceines because of the difficulty in measuring and the apparent amount of individual variation. However, see Transformation Series #29 (skull height). Related directly to this feature, Corbet (1988) distinguished among the hylomyines by interorbital width. Our measurements do not support his division of the hylomyines into three distinct groups (Table 1).

16. Parietal, anterior process (Butler, 1948): (0) absent or very weak; (1) extends anteriorly along the supraorbital rim to form the base of the supraorbital process. The parietal has an anterolateral process that forms part of the postorbital rim and participates in the formation of the supraorbital process.

17. Alisphenoid, anterior process (Butler, 1948): (0) absent; (1) present. This character, related to the location of the sphenopalatine foramen, is apparently involved with the shortening of the orbitotemporal region. The orbital wing of the alisphenoid has a narrow, fusiform anterior process that sometimes fuses with a similar posterior process from the maxilla. The degree of formation seems to be individually variable. With the formation of this "bridge," a narrow, short shelf is formed between the sphenopalatine and sphenorbital foramina.

18. Alisphenoid, inferior stapedia foramen, anterior opening (Corbet, 1988): (0) stapedia artery emerges from the auditory bulla in a groove in the alisphenoid; (1) stapedia artery emerges from the auditory bulla in a foramen in the alisphenoid. The inferior ramus of the stapedia artery emerges from the hypotympanic sinus on the anterior edge of the auditory bullae, slightly ventral and lateral to the foramen ovale. In hylomyines, this occurs in a groove in the alisphenoid (e.g., *Podogymnura*, Figure 2). In the erinaceines, there is a

completely or incompletely formed foramen (e.g., *Hemiechinus*, Figure 3; *Paraechinus*, Figure 1). Corbet (1988) distinguished *E. amurensis* and *E. concolor* from all other erinaceines by the incomplete development of the inferior stapedia foramen. However, specimens we have examined of these and other erinaceine taxa reveal both conditions occurring, although the incomplete condition may be more prevalent in *E. amurensis* than in any other erinaceine taxon, as pointed out by Corbet (1988).

19. Frontal, ophthalmic foramen (Butler, 1948): (0) joined with, or closely adjacent to, the ethmoid foramen; (1) the foramina widely separated from the ethmoid foramen (e.g., see Figure 12).

20. Orbitosphenoid, suboptic foramen (Butler, 1948; Novacek, 1986): (0) absent; (1) present, in medial wall of sphenorbital fissure; (2) present, anterior to sphenorbital fissure. The "0" condition is unknown in erinaceids, which exhibit conditions "1" and "2." Novacek (1986) has hypothesized implicitly 0→1→2, but we refrain from accepting this without sufficient outgroup comparison, and have treated this transformation as unordered in our analysis.

21. Palatine, sphenopalatine foramen (= orbitonasal foramen of Butler, 1948; sphenoid foramen of Novacek, 1986): (0) anterodorsal or slightly posterodorsal to the palatine transverse torus; (1) decidedly posterodorsal to palatine transverse torus. This transformation is difficult to visualize because it depends upon what horizontal plane is used for the skull. Therefore, we do not distinguish between those that are slightly anterior or posterior to the bisecting torus line.

22. Palatal shelf and spine (Corbet, 1988): (0) posterior palatal shelf with well-developed spine; (1) posterior spine absent or vestigial. In most taxa the palate extends posteriorly over the pterygoids (= mesopterygoid fossa) beyond the palatine transverse torus. Thomas (1918), Butler (1948), Robbins and Setzer (1985), and Corbet (1988) considered *Atelerix* to have a mesopterygoid fossa distinctly longer ("broader" in their terminology) than other erinaceines. We find variation of this feature in erinaceines to be so extensive as to be difficult to characterize, and polarized only ambiguously in comparison with outgroups. At least one specimen of *Echinosorex* (USNM 145584) has a decidedly long mesopterygoid fossa. In general, however, it appears that erinaceines have longer mesopterygoid fossae than hylomyines. A detailed analysis of this feature would likely document that there is a gradual statistical increase in the length of the mesopterygoid fossa as one progresses through the cladogram from hylomyines through erinaceines, finding its greatest development in specimens of *Atelerix*. Moreover, in specimens we have examined, *Atelerix* is easily distinguishable from other erinaceines on the absence of a well-developed posterior palatal spine (= posterior nasal spine of Jayne, 1898).

23. Palatine, lateral fossa, anterodorsal to the palatine transverse torus: (0) absent; (1) present. Development of a lateral fossa behind the palatal torus may be a reflection of the

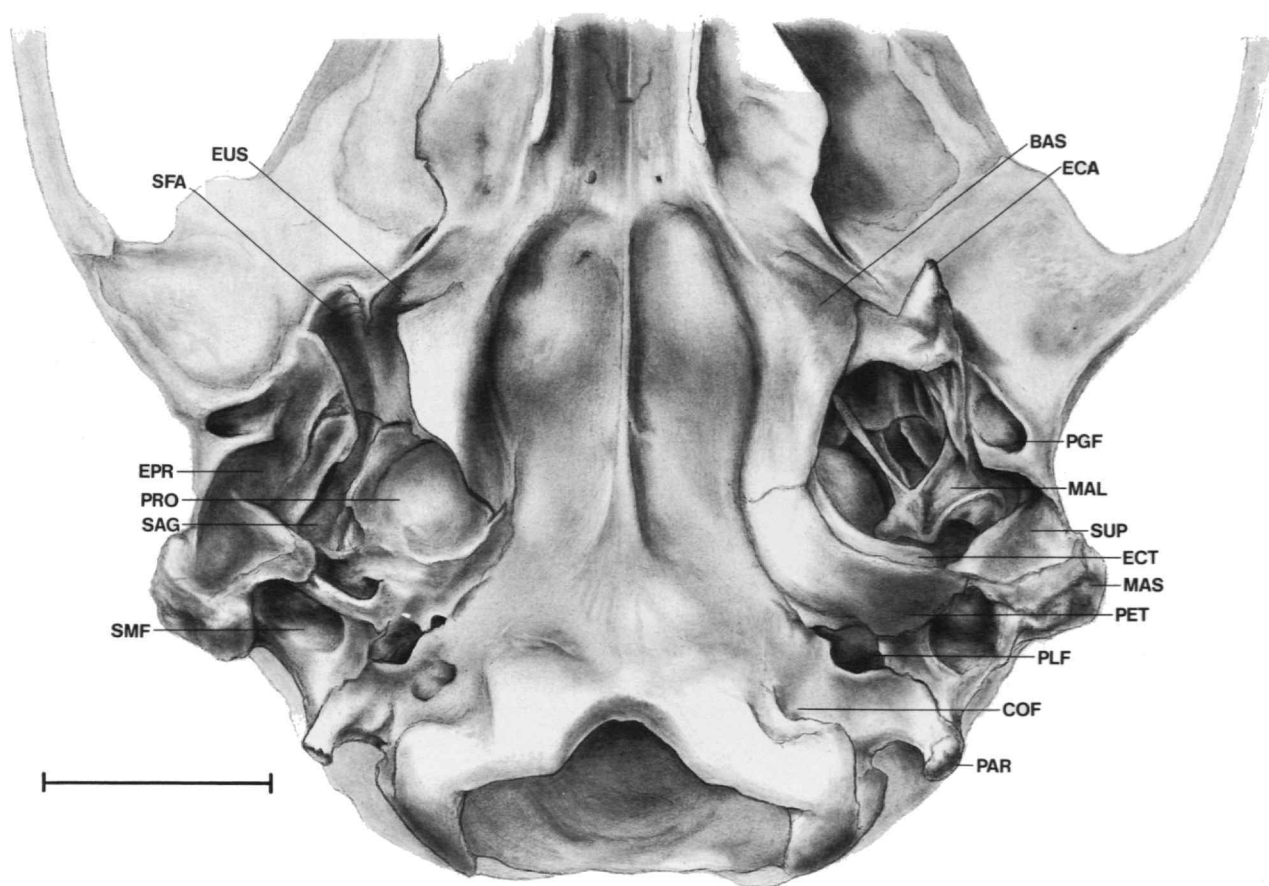


FIGURE 2.—The basicranium of *Podogymnura aureospinula* (ventral view). Left auditory bullae cut away. The reproduction of the ectotympanic ring is taken from *Podogymnura truei*. (Scale = 5 mm; key to abbreviations in Table 2.)

large size reached by *Echinorex*. Its presence and size are perhaps related to the development of the medial pterygoid muscle.

24. Squamosal, zygomatic process (Butler, 1948, 1956): (0) not elevated posteriorly; (1) elevated posteriorly. In the derived condition, the zygomatic process of the squamosal has a distinctive dorsal curve in the lateral view. Even though tenrecoids and soricoids (except for talpids) lack complete zygomatic arches, short zygomatic processes of the squamosal are present in those taxa and this condition therefore can be evaluated.

25. Squamosal, postglenoid foramen: (0) separated from glenoid fossa by entoglenoid process; (1) not separated.

The following three characters concern the shape, composition, and size of the deep pocket dorsal (intra-tympanic) and lateral to the tympanum (see Figures 1, 3). In the erinaceines, the tympanum stretches across two different planes: the ectotympanic is at an acute angle to the horizontal base of the skull and forms the medial attachment; the squamosal/mastoid

pocket rim is on the horizontal plane of the skull and forms the lateral attachment for the tympanum. We are referring to this squamosal/mastoid excavation as the "suprameatal" fossa for purposes of discussion; we are uncertain whether it is homologous to the extratympanic "suprameatal fossa" in †*Leptictis* as described by Novacek (1986) or the fossa referred to by the same name present in some carnivores (both intra- and extratympanic) (Schmidt-Kittler, 1981). The homology of the various fossae and pockets that are associated with the external auditory meatus, whether they be ventrolateral or dorsolateral to the tympanum, is unclear (Wyss, 1987; Wozencraft, 1989). Although these three transformation series are most certainly related, the correlation is not perfect; therefore, they are listed separately.

26. Squamosal, suprameatal fossa, composition: (0) not well defined ("absent") or with mastoid and squamosal contributions nearly equal; (1) squamosal and mastoid contributions subequal to predominately mastoid. We have chosen to include those taxa with poorly developed or no fossa ("absent")

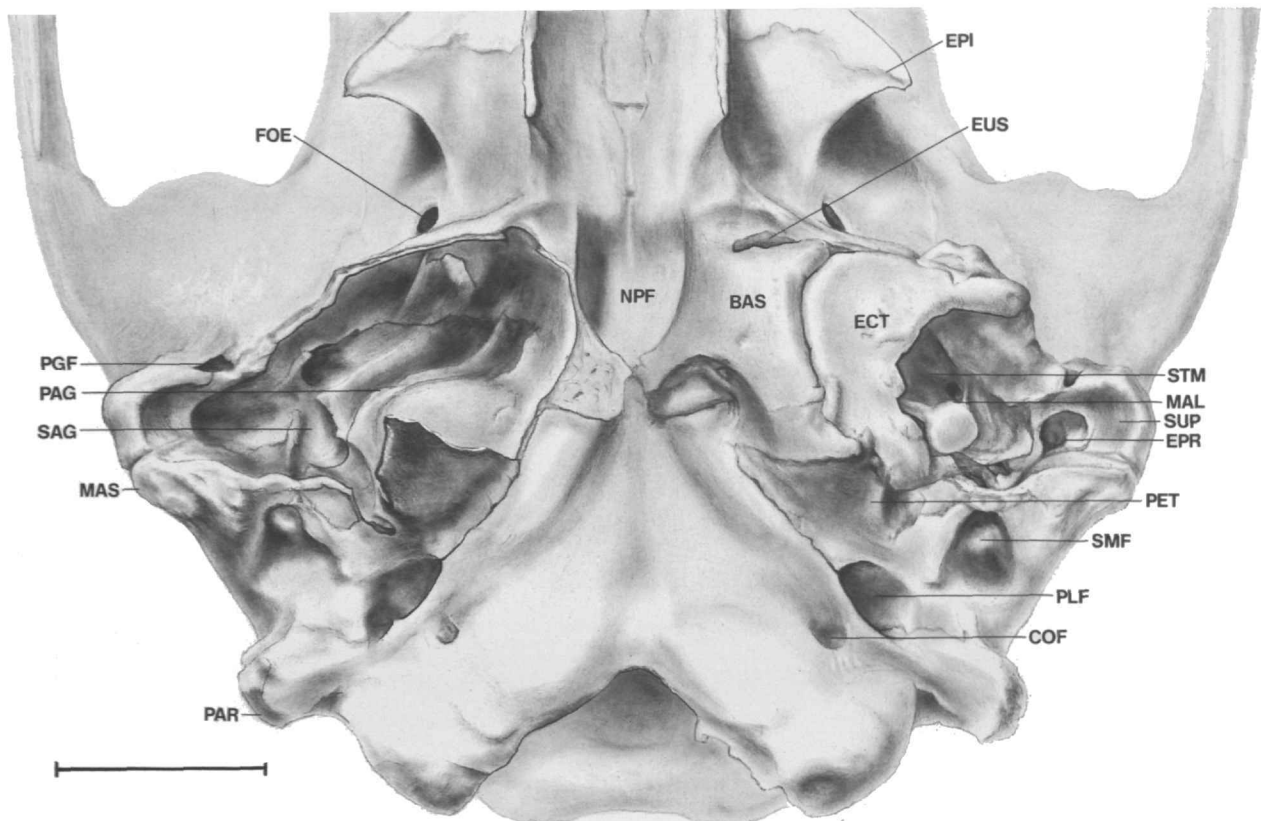


FIGURE 3.—The basicranium of *Hemiechinus dauricus* (ventral view). Left auditory bullae cut away. (Scale = 5 mm; key to abbreviations in Table 2.)

together as the presence or absence of this feature is covered in Transformation Series #27.

27. Squamosal, suprimeatal fossa, depth: (0) absent; (1) shallow; (2) moderately developed; (3) deep; (4) very deep, extends dorsal to glenoid fossa. Corbet (1988) noted the distinction between *H. dauricus* and other *Hemiechinus*, as well as the very inflated nature of *Paraechinus*. Osborn and Helmy (1980) noted the derived nature of *P. aethiopicus* and *P. micropus*. This is a series relating to the increase in volume of the suprimeatal fossa. The description of characters "1" through "3" may sound as though they are somewhat subjective; however, these characters are quite distinctive and not easily confused. Unfortunately, without volumetric measurements, one will have to rely on reference taxa for the relative nature of each character.

28. Squamosal, suprimeatal fossa, shape: (0) "normal," anterior and posterior borders widely separated; (1) "compressed," anterior and posterior borders narrowly separated (e.g., compare Figures 1 and 3).

29. Parietal, relative height of skull (Butler, 1948): (0) parietals relatively higher than frontals; (1) frontals relatively

higher than parietals. Elevation of the frontals in *Erinaceus* and *Atelerix* makes them appear to have more highly inflated frontal sinuses than in *Hemiechinus* and *Paraechinus*. See Transformation Series #15 (frontal inflation).

30. Basisphenoid, nasopharyngeal fossa (= nasopharyngeal pocket of Butler, 1948): (0) absent; (1) present. The occurrence of condition "1" in *Tenrec* does not argue that this feature is a synapomorphy of Tenrecidae + Erinaceinae. *Tenrec* is far removed from the base of tenrec phylogeny (Eisenberg, 1981). In the derived condition, the basisphenoid contribution to the bullae is formed in such a manner that both sides touch medially and are closely appressed to the alisphenoid/pterygoid region. This enclosure, anteromedial to the bullae, is further excavated into a spherical fossa or hollow. In *Paraechinus* and *Hemiechinus* the hollow is slightly more anterior than in *Erinaceus* and *Atelerix*.

31. Basisphenoid, inflation (Corbet, 1988): (0) absent; (1) present. The basisphenoid forms part of the ventral floor and anteromedial wall of the hypotympanic chamber; in the derived condition it is relatively enlarged (Figure 4A). This feature is related to Transformation Series #36, although the correlation

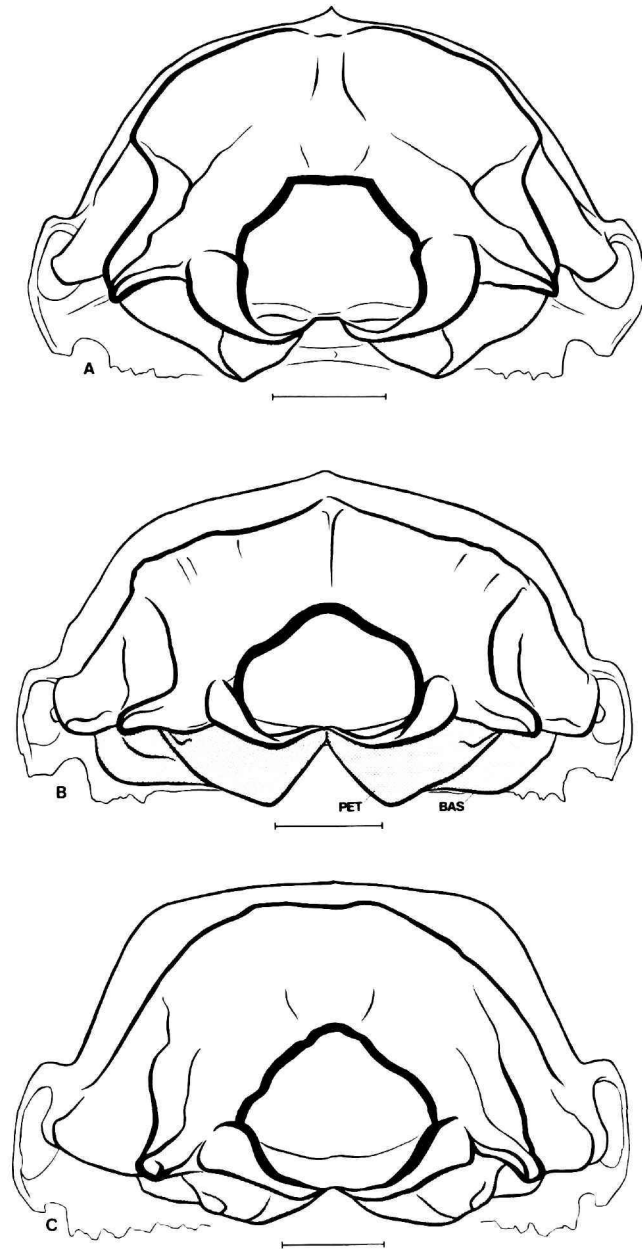


FIGURE 4.—Comparison of the relative inflation of the auditory bullae: A, *Erinaceus amurensis*; B, *Hemiechinus auritus*; and C, *Mesechinus dauuricus*, from the occipital aspect. (Scale = 10 mm.)

is not perfect. It refers to the relative contribution and size of the ventral expansion of the hypotympanic chamber, which is composed of three elements, the relatively slender uninflated ectotympanic and the inflated basisphenoid and petrosal.

32. Ectotympanic (= tympanic of Corbet, 1988) (Butler, 1948): (0) slender, ring-shaped, loosely attached, with a small anterior process; (1) much broader, sometimes engulfing

anterior process, firmly attached. Material of *Podogymnura aureospinula* from which to evaluate this feature was unavailable and is treated as "unknown" in the data matrix. Butler (1948) stated that *Echinosorex* lacks an anterior process on the ectotympanic, otherwise seen in *Hylomys* and *Neotetracus* in material he had at hand. In our material, this process is present in *Echinosorex* as in the other hylomyines; in *Echinosorex* and



*Podogymnura truei* the ectotympanic is partially hidden within the bulla, making observations difficult. Corbet (1988) separated the large hylomyines (*Podogymnura*, *Echinosorex*) from the small ones (*Neotetracus*, *Hylomys*, and *Neohylomys*) on the basis of the small genera having a relatively larger ectotympanic. We could not verify this distinction and believe the major difference is between the erinaceines and the hylomyines. Corbet (1988) also pointed out that *Echinosorex* and *Podogymnura* have weakly attached ectotympanics, easily supported in *Echinosorex* by the difficulty in finding specimens in collections with the bone still attached. However, our examination of *Podogymnura truei* showed an equal proportion of specimens having the ectotympanic present as in other hylomyines.

33. Petrosal: (0) promontorium predominantly confined to bullar roof, squamosal does not participate in bullar roof; (1) promontorium forms posteromedial wall, squamosal is major component of bullar roof (compare the left side of Figures 1 and 2). Depending on how one views the relative topology of this region, one could argue that the distinctiveness of these characters is either attributable to a posterior growth of the squamosal, or a shifting of the petrosal to the posteromedial wall of the bullae.

34. Petrosal, inflation of mastoid process in region between the exoccipital and squamosal (Heaney and Morgan, 1982): (0) absent; (1) present. The occipital face of the mastoid appears slightly inflated in the derived condition (see also Transformation Series #26).

35. Petrosal, mastoid portion of suprameatal fossa (Corbet, 1988): (0) not inflated; (1) inflated. The suprameatal fossa is composed of two bones, the squamosal and the mastoid portion of the petrosal. The relative contribution of these two elements varies (see Transformation Series #26); however, in *Paraechinus*, the fossa is greatly excavated (Figure 1). Corbet (1988) believed that the condition in *P. aethiopicus* is much larger than that found in other erinaceines and that some *Hemiechinus auritus* resemble *Paraechinus*, a conclusion not supported by our specimens. However, there may be a subtle difference in the size of the fossa between *H. auritus* and other erinaceines.

36. Petrosal, expansion of ventral process (Corbet, 1988): (0) not inflated; (1) inflated. Corbet (1988) noted that *Hemiechinus auritus* shares with *Paraechinus* the relative inflation of the petrosal component of the floor of the hypotympanic chamber. Although *H. auritus* does show considerable variation (perhaps greatest in *H. a. megalotis*), in the specimens that we examined, it does not approach the condition found in *Paraechinus* (see also Transformation Series #31).

37. Basioccipital/petrosal suture: (0) narrow slit, exposing the posterior portion of the inferior petrosal sinus; (1) basioccipital/petrosal suture closed; well-defined posterior lacerate foramen.

38. Petrosal, stapedial foramen (for the ramus superior stapedial nerve) (Butler, 1948): (0) posterior to squamosal/alisphenoid suture and posterior to postglenoid foramen; (1)

located on squamosal/alisphenoid suture and close to the postglenoid foramen.

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

40. Paroccipital process (Thomas, 1918): (0) small; (1) robust.

41. Exoccipital: (0) not expanded; (1) expanded. The exoccipital bulges outward, giving an "inflated" appearance in the cleaned skull. This transformation may be implicated in size-related shape changes. We do not have ontogenetic series with which to verify this hypothesis, so we have retained the naive transformational hypothesis. A number of soricoids have expanded exoccipitals, but we do not regard this as the plesiomorphic condition in those taxa.

42. Occipital condyle (Novacek, 1986): (0) condyle emarginated causing the condyle to appear slightly lobed; (1) no condylar emargination.

43. Basioccipital, condylar foramen location (Novacek, 1986): (0) anterior to ventral lip of condyle; (1) on anteroventral lip of condyle.

44. Mandible, coronoid process (Corbet, 1988): (0) narrow, pointed; (1) broad, rounded. Corbet (1988) grouped *Podogymnura aureospinula* with *Hylomys* as having an intermediate condition. We found no difference in the shape of the coronoid process between *Hylomys* and *Neohylomys* on one hand and the species of *Podogymnura* on the other.

#### DENTITION CHARACTERS

We follow the nomenclature of Woodward (1896), Leche (1902), and Butler (1948, 1956).

45. i1 (Leche, 1902; Butler, 1948): (0) present; (1) absent.

46. i1, relative size (Butler, 1948): (0) absent or small; (1) enlarged.

47. i2, relative size (Butler, 1948; Novacek, 1986): (0) nearly equal to other incisors; (1) greatly enlarged.

48. I2, size (Novacek, 1986): (0) greater than I3; (1) less than or equal to I3.

49. I3, number of roots (Butler, 1948; Robbins and Setzer, 1985; Corbet, 1988): (0) one root; (1) two roots, separate; (2) two roots, fused. Concomitant with the change in the number of roots, the I3 becomes larger than the I2. Because it is impossible to tell the polarity between characters "1" and "2," we have treated this transformation as unordered. However, because outgroup comparison allows the inference that the ancestor of Erinaceidae had condition "0" we have thus coded the hypothetical ancestor. See Table 3 for summary of variation in erinaceine taxa.

50. C1, size (Butler, 1948; Corbet, 1988): (0) significantly larger than adjacent post-canine teeth; (1) slightly larger than adjacent post-canine teeth; (2) approximately equal in size to adjacent post-canine teeth. Corbet (1988) used the same transformation series but with polarity reversed.

TABLE 3.—Variation in number of roots of I3 and C1 in *Erinaceus* and *Hemiechinus* (totals <N are due to missing teeth).

Taxon	N	I3 [C1]		
		Separate	Partly fused	Completely fused
<i>Hemiechinus</i> , North Africa				
<i>auritus aegyptius</i>	16	9 [15]	6 [0]	1 [0]
<i>auritus libycus</i>	25	18 [23]	5 [0]	0 [0]
<i>auritus metwallyi</i>	11	7 [11]	2 [0]	2 [0]
<i>Hemiechinus</i> , Middle Asia				
<i>auritus auritus</i>	26	24 [26]	2 [0]	0 [0]
<i>auritus minor</i>	1	1 [1]	0 [0]	0 [0]
<i>auritus megalotis</i>	3	2 [2]	0 [0]	0 [0]
<i>Hemiechinus</i> , Central Asia				
<i>auritus albulus</i>	5	5 [5]	0 [0]	0 [0]
<i>auritus alashanicus</i>	4	4 [4]	0 [0]	0 [0]
<i>Hemiechinus collaris</i>	2	2 [2]	0 [0]	0 [0]
<i>Hemiechinus dauricus</i>	19	16 [16]	2 [0]	0 [3]
<i>Erinaceus amurensis</i>	24	0 [13]	0 [4]	22 [4]
<i>Erinaceus concolor</i>	8	0 [5]	0 [2]	8 [1]
<i>Erinaceus europaeus</i>				
Italy, Spain	6	0 [4]	0 [0]	4 [0]
Switzerland, France	11	0 [6]	1 [3]	10 [1]
Germany	14	0 [10]	0 [2]	13 [2]
Denmark, Sweden	9	0 [1]	0 [5]	7 [3]
British Isles	8	0 [2]	0 [3]	8 [3]

51. C1, number of roots (Butler, 1948; Robbins and Setzer, 1985; Novacek, 1986; Corbet, 1988): (0) two roots; (1) one root or two roots fused. Novacek (1986) noted that two canine roots are primitive for eutherians and this is the condition in early erinaceomorphs. For this reason, we regard the 1-root condition in tenrecoids + soricoids and *Erinaceus* to be non-homologous.

We found this character to be geographically and individually variable (Table 3). However, all species of *Erinaceus* have members that exhibit upper canines with fused (or single) roots. Our hypothesis is that the common ancestor of *Erinaceus* was polymorphic for fusion of canine roots and that this polymorphism is retained in its descendants.

52. c1, relative size (Butler, 1948; Corbet, 1988): (0) approximately equal to, or smaller, than p1; (1) significantly larger than p1. The polarity of the transformation specified by outgroup comparison is surprising. Although enlarged canines is the widespread condition in mammals, local outgroup comparison supports our view that relatively small canines are plesiomorphic in erinaceids. The enlarged lower canines in *Tenrec* we regard as homoplastic. See following transformation series.

53. C1, relative size (Corbet, 1988): (0) equal to, or larger than, I3; (1) subequal to slightly smaller than I3. *Neotetracus* has apparently reduced the size of its canines from the primitive condition.

54. P1: (0) present; (1) absent. Because outgroup comparison is insufficient for polarization, this transformation series was treated as unpolarized in the analysis.

55. p1: (0) present; (1) absent.

56. P2, roots (Corbet, 1988): (0) two roots; (1) one root, or two roots well fused. Corbet (1988) reversed the polarity and considered our derived condition to be two characters; however, in the specimens we have examined, these features (one root and two roots fused) appear to be variable.

57. p3, roots (Butler, 1948; Novacek, 1985, 1986; Corbet, 1988): (0) two roots present, larger in size than p2; (1) one root present, nearly equal in size to p2; (2) absent. Corbet (1988) considered the same transformation series with reversed polarity.

58. P3, lingual lobe (Corbet, 1978, as P2): (0) present, well developed; (1) vestigial or absent. Outgroup comparison is insufficient for polarization, so this transformation was treated as unpolarized even though we think that this feature is related to Transformation Series #60. Butler (1948:461) reported that the P3 lingual lobe was even further enlarged in *Atelexis frontalis* and *A. algirus* (which he distinguished from *A. albiventris* and *A. sclateri*), but we have been unable to verify this observation in our material.

59. P3, size (Butler, 1948; Novacek, 1985; Robbins and Setzer, 1985): (0) normal; (1) reduced. Corbet (1978) referred to this tooth as P2. Butler (1948:461) noted variation in the number of roots across taxa; we have been unable to verify his observations.

60. P3, roots (Corbet, 1988): (0) three roots; (1) fewer than three roots. Corbet (1988) considered finer divisions of this transformation series, with the polarity reversed. Outgroup comparison supports our order; we found his characters (one root, two roots hardly separated, and two roots divergent) to vary interspecifically. This is related to the number of cusps (see Transformation Series #58) although the correlation is not perfect (e.g., in *Podogymnura*).

61. P4, hypocone (Butler, 1948; Novacek, 1985, 1986): (0) triangular, hypocone (if present) vestigial; (1) quadrate, hypocone present. Presumably, this feature is correlated with the size of P3. Novacek (1986) noted that the leptictid P5 (= traditional P4) has a "distinctly developed" hypocone; however, we cannot discern this in his illustrations, or in our material, and Novacek (1985:21, his table 7) indicated that a large, distinct hypocone is present or absent in other erinaceomorphs. Because of this outgroup ambiguity the transformation is treated as unpolarized.

62. P4, lingual roots (Butler, 1948): (0) one lingual root; (1) two unfused roots; (2) two lingual roots, fused. Butler (1948:461) reported the fused roots of erinaceines as a single root. Because outgroup comparison allows the inference that the ancestor of Erinaceidae had condition "0" we have coded the hypothetical ancestor thus, although the overall transformation is unordered.

63. Lower molars, trigonid (Novacek, 1985): (0) high trigonid (significantly higher than talonid), talonid short/vestigial; (1) low trigonid (nearly equal in height to talonid), talonid expanded, large.

64. M1, lingual roots (Butler, 1948): (0) separate; (1) fused for most of their length. Butler (1948:460) referred to the fused condition as a "single lingual root which is flattened bucco-lingually"; he also noted that in *Hylomys* and *Neotetracus* the M1 hypocone had a posterior crest that follows the posterior edge of the crown. In our material we have been unable to see this feature.

65. M3, roots (Butler, 1948): (0) three roots; (1) two roots.

66. M3, hypocone (Butler, 1948; Novacek, 1985, 1986): (0) absent or weak; (1) present, well developed on buccal side. Although Butler (1948:460) used presence of a hypocone as a feature uniting his *Echinosoricinae* (= *Hylomyinae*), he stated the hypocone to be primitively present and lost in erinaceines. Out-group comparison does not support this view and presence was coded as derived. Butler (1948:460) also noted that the degree of the approximation of the M3 metacone and hypocone is less in *Hylomys* than in *Echinosorex*. Although we can see what he was referring to, across all taxa the feature becomes impossible to characterize.

67. M3, metacone (Butler, 1948): (0) present, well developed; (1) present, small; (2) absent.

68. m3, talonid: (0) present; (1) absent.

#### POST-CRANIAL CHARACTERS

We follow the nomenclature of Jayne (1898) and McDowell (1958).

69. Axis, posteroventral keel: (0) absent; (1) present. The axis normally has a convex ventral surface. In the derived condition, there is a posteroventrally projecting flange midway between the transverse processes (Figure 5).

70. Axis, neural spine: (0) low; (1) high. Although this transformation is correlated with the previous transformation, we could not evaluate this condition in †*Leptictis* and have therefore regarded this transformation series as unpolarized. The normal condition is for the neural spine to be horizontally flattened along the dorsal edge with little or no slope to the anterodorsal edge. In the "1" condition (Figure 5) there is a long distinctive projecting spine.

71. Scapula, metacromion process (McDowell, 1958): (0) deltoid, amorphous projection; (1) long, fusiform projection. We have not treated the transformation as polarized in our analysis because we were unable to evaluate the condition in †*Leptictis*. The "0" condition is a rather amorphous projection with a deltoid general shape; the projection is approximately equal to, or only slightly larger than, the acromion process. The metacromion projects at an acute angle to the scapular spine. In the "1" condition (Figure 6) the process is fusiform and much longer than the acromion and at approximately 90 degrees to the scapular spine.

72. Sacral vertebrae, neural spines: (0) not fused into a continuous longitudinal plate; (1) fused into a continuous longitudinal plate. Because we could not evaluate the condition in †*Leptictis* we did not treat this transformation series as

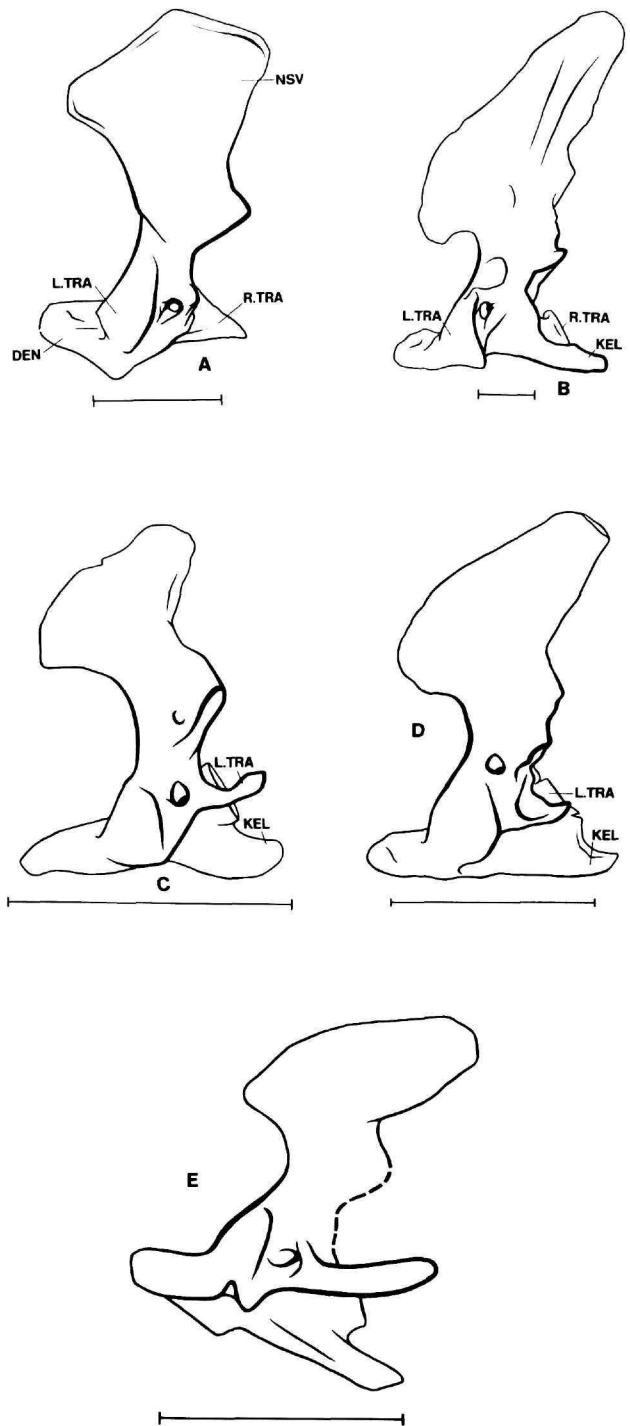


FIGURE 5.—Comparison of the axis vertebrae, lateral aspect, in Hylomyinae and *Erinaceus*. A, *Erinaceus europaeus*; B, *Echinosorex gymnura*; C, *Neotetracus sinensis*; D, *Hylomys suillus*; and E, *Neohylomys hainanensis*. (Scale = 5 mm; key to abbreviations in Table 2.)

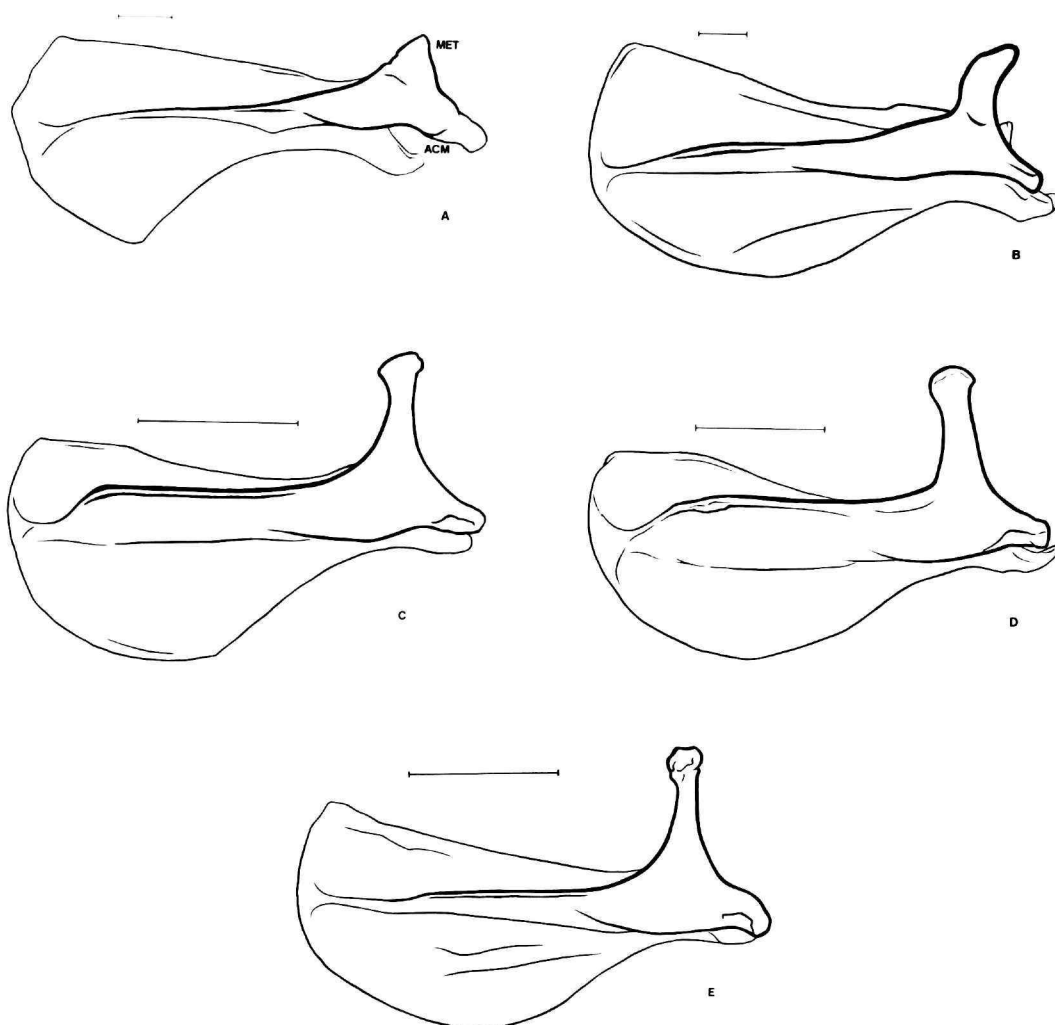


FIGURE 6.—Comparison of the scapula, lateral aspect, in Hylomyinae and *Erinaceus*. A, *Erinaceus europaeus*; B, *Echinorex gymnura*; C, *Neotetracus sinensis*; D, *Hylomys suillus*; and E, *Neohylomys hainanensis*. (Scale = 5 mm; key to abbreviations in Table 2.)

polarized in our analysis. In the “1” condition the neural spines of the sacral vertebrae fuse together to form one long continuous spine (Figure 7).

73. Ischium, posteroventral process (McDowell, 1958): (0) not greatly elongated; (1) greatly elongated. In the primitive condition, there is little, if any, posteroventral process to the ischium, the posteroventral border being rounded. In the derived condition, the posteroventral border (ischiatric tuberosity) is produced into long fusiform processes that projects a considerable distance from the obturator foramen (Figure 7).

74. Tibia, lateral flange: (0) absent or only weakly present; (1) lateral flange on antero-superior margin strongly developed. The tibial crest is produced into a distinctive lateral flange in the derived condition (Figure 8).

#### NON-SKELETAL CHARACTERS

75. External pinnae, length relative to condyloincisive length (Thomas, 1918; Corbet, 1974, 1988; and Robbins and Setzer, 1985, all used this character relative to body length): (0) short (considerably shorter than 65% of condyloincisive length); (1) long, (considerably longer than 65% of condyloincisive length) (Table 4). Even though leptictids cannot be evaluated for this feature, the uniqueness of this feature within lipotyphlan insectivores argues for long ears being apomorphic.

76. Hallux (Thomas, 1918; Robbins and Setzer, 1985; Corbet, 1988): (0) normal; (1) reduced, claw not reaching base of second digit; (2) absent. Because *+Leptictis* cannot be evaluated for this feature, other mammals were used as a

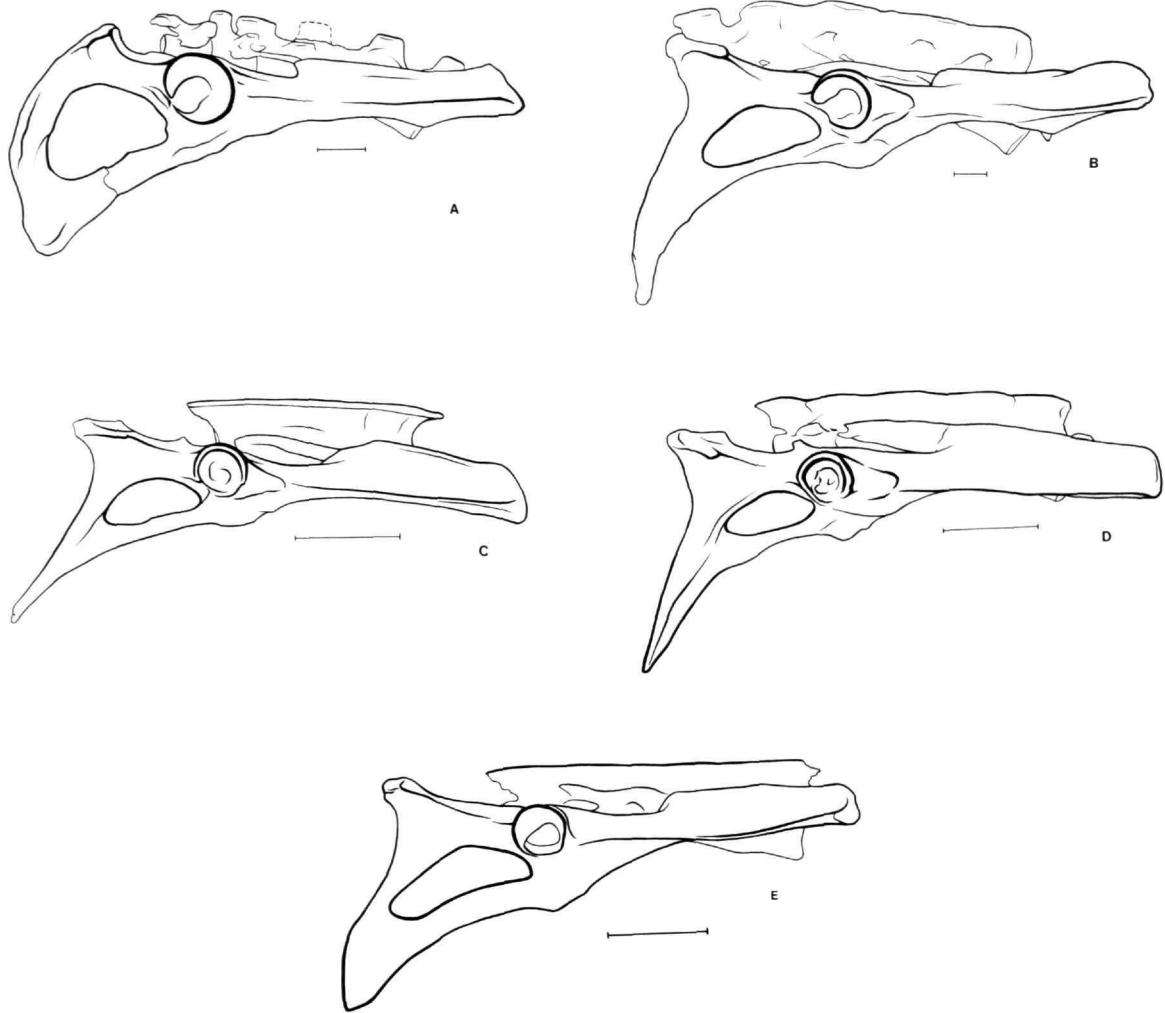


FIGURE 7.—Comparison of the pelvic region, lateral aspect, in Hylomyinae and *Erinaceus*. A, *Erinaceus europaeus*; B, *Echinorex gymnura*; C, *Neotetracus sinensis*; D, *Hylomys sullus*; and E, *Neohylomys hainanensis*. (Scale = 5 mm.)

functional outgroup. We were unable to evaluate this character in our specimen of *Atelerix sclateri* (skull only). However, Corbet (1988) stated that the hallux is present, though small.

77. Pelage, condition (Corbet, 1974, 1988): (0) normal, not spiny; (1) smooth spines; (2) spines papillate, not grooved; (3) spines papillate and grooved. We have relied heavily on Corbet (1988) for the character distribution of this feature. Although a few tenrecids have spiny pelage, the uniqueness of this feature within lipotyphlan insectivores argues for its being apomorphic, and Corbet (1988:131) asserted that the erinaceine spine "is very different from that of the superficially similar spines in the family Tenrecidae." The character "spiny" is restricted to stout heavy spines. *Podogymnura aureospinula* has been

evaluated as having spiny pelage (Heaney and Morgan, 1982); although *P. aureospinula* does have well-developed guard hairs, they are only marginally stouter than those in *Echinorex* and *P. truei* and do not approach the dagger-like development in erinaceines (Poduschka and Poduschka, 1985; Corbet, 1988). For this reason, *P. aureospinula* is coded as "0." Because outgroup comparison is uninformative, this transformation is treated as unordered. Although "spines" is clearly a synapomorphy of erinaceines we have not included it, as such, as a character, for no other reason than "spines present" would be redundant with whatever the basal erinaceine shift from Character 77.0 would be.

78. Pelage, completely white spines among dark spines



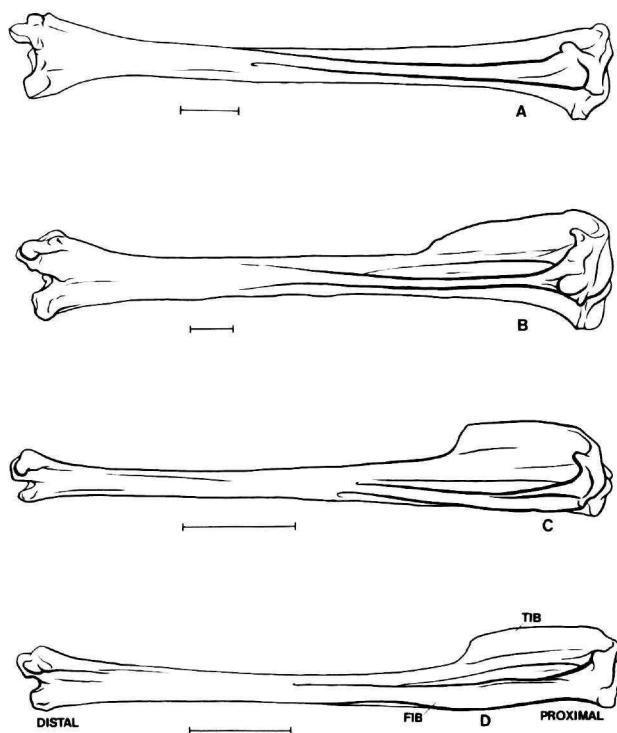


FIGURE 8.—Comparison of the tibia, lateral aspect, in Hylomyiinae and *Erinaceus*. A, *Erinaceus europaeus*; B, *Echinorex gymnura*; C, *Neotetracus sinensis*; and D, *Hylomys suillus*. (Scale = 5 mm.)

TABLE 4.—Measurements of the length of the external pinnae of erinaceins (CIL = condyloincisive length).

Taxon	N	Ear length (EL) mean (range)	EL/CIL
<i>Erinaceus europaeus</i>	7	23.4 (18–29)	0.409
<i>E. concolor</i>	4	30.8 (30–31)	0.520
<i>E. amurensis</i>	11	24.0 (16–30)	0.431
<i>Hemiechinus dauuricus</i>	11	29.5 (24–35)	0.564
<i>H. auritus albulus</i>	6	42.5 (38–50)	0.900
<i>H. a. auritus/megalotis</i>	49	49.1 (39–60)	0.930
<i>H. collaris</i>	6	38.3 (36–41)	0.793
<i>Paraechinus h. hypomelas</i>	12	47.6 (41–55)	0.912
<i>P. h. jerdoni</i>	6	37.0 (35–40)	0.835
<i>P. aethiopicus</i>	6	46.8 (42–55)	0.965
<i>P. micropus</i>	9	30.9 (27–34)	0.719

(Corbet, 1988): (0) absent; (1) present. Corbet (1988) noted that in certain erinaceines, there are distinctive completely white spines irregularly scattered among completely dark or banded spines. We confirmed his observation of the derived condition in *E. amurensis* and *A. frontalis*. Only about one-half of the specimens we examined of *E. europaeus* had the derived condition he indicated; therefore we coded it as “unknown.”

Although Corbet (1988) also listed *A. algirus* as derived, we could not find specimens with this condition.

79. Pelage, medial tract on crown (Corbet, 1988): (0) no spines on top of head; (1) spineless medial crown tract narrow; (2) spineless medial crown tract wide; (3) spineless medial crown tract absent. Thomas (1918), Corbet (1974, 1988), and Robbins and Setzer (1985) recorded crown parting in all spiny genera except *Hemiechinus*, although they noted that it was sometimes inconspicuous. According to Corbet (1988:132), a spineless medial crown tract is present in “new-born *Hemiechinus auritus*,” suggesting that the adult condition is derived, although it could be that the adult condition in the other genera is neotenic; outgroup comparison does not shed light on this transformation. Because outgroup comparison is uninformative for the polarity of this transformation it was included in our analysis as unordered. This feature could not be evaluated in our material of *Atelerix sclateri*, but Corbet (1974, 1988) reported that a spineless crown tract is present.

80. Pelage, condition on ventral side (Corbet, 1974, 1984): (0) soft and densely furred; (1) coarse and relatively sparsely haired.

81. Pelage, body underfur (Corbet, 1988): (0) absent; (1) present. It is difficult in some specimens to determine the difference between underfur and very fine guard hairs. However, the taxa with the derived condition clearly have two types of hair, whereas in others only one is present.

### Characters Not Utilized in Analysis

A number of features have been used in analyses by other authors, but for a number of reasons we have not utilized them here. These features, as well as interesting anatomical novelties that may prove useful to future workers, are discussed.

1. Maxillae, posterior processes: Corbet (1988) united *Erinaceus* on the shortening of the posterior rostral process of the maxilla. In *Erinaceus*, the nasolabialis fossa is only partially composed of the maxilla, with the posteriormost point of the maxilla at or near the level of the lacrimal foramen. We concur with Corbet in recognizing this tendency in *Erinaceus*, which is not found in other erinaceines; however, we found the character too variable within taxa to code.

2. Occipito-parietal suture: The contribution of the parietal bone to the occipital crest, or lack thereof, was used by Corbet (1974) to distinguish among African hedgehogs. We found this character too variable to be useful although, a posteriori, a trend is visible.

3. Nasal-maxilla relationship (Corbet, 1974, 1988): We concur with Leche (1902) and Butler (1948) and find that the contact between the nasal and maxilla exhibited too much intraspecific variation to be useful (Table 5).

TABLE 5.—A comparison of the nasal/maxilla suture length (mm) in the Erinaceinae to the groups of Corbet (1988).

Taxon	N	Mean	Range
CORBET GROUP 1: NO CONTACT BETWEEN MAXILLA AND NASAL			
<i>A. algirus</i>	13	0.67	0-2.69
<i>A. sclateri</i>	1	0	
CORBET GROUP 2: CONTACT AT POINT OR SHORT			
<i>H. auritus</i>	14	1.69	0-3.36
<i>H. collaris</i>	1	3.26	
<i>H. dauuricus</i>	17	1.17	0-4.13
<i>E. europaeus</i>	18	2.00	0-6.38
<i>A. albiventris</i>	13	1.99	0-5.29
<i>P. hypomelas</i>	11	2.50	0-3.61
CORBET GROUP 3: LONG COMMON SUTURE			
<i>E. concolor</i>	6	1.67	0-3.33
<i>E. amurensis</i>	8	3.60	2.4-5.55
<i>A. frontalis</i>	4	5.22	4.29-6.03
<i>P. aethiopicus</i>	12	2.71	0-7.91
<i>P. micropus</i>	1	2.59	

4. p4, metaconid (= lingual cusp of Corbet, 1988): Corbet (1988) used this character to differentiate among erinaceines (*Erinaceus* and *Atelerix* with large cusp; *Paraechinus* and *Hemiechinus* with small cusp; and *Hemiechinus dauuricus* and *Atelerix algirus* with no cusp). We also found no cusp in the series of *H. dauuricus* that we examined. However, we found the variation within species much greater than indicated by Corbet, with all three conditions occurring in most taxa.

5. "Tympanic angle" in posterolateral margin: Corbet (1988) used this character to distinguish *Hemiechinus dauuricus* and *Paraechinus* from other erinaceids. He coded the tympanic angle in the margin as either acute or obtuse. We have not been able to verify this character on our specimens.

6. Mammary (Corbet, 1988): The number of mammary is difficult to evaluate from dry skins and we are skeptical of published values, because much variation is evident (Table 6).

7. Tail length (Corbet, 1988): cursory examination of erinaceids shows considerable variation in tail length, from a very long tail in *Echinosorex* to the very short tail of erinaceines. If these extremes were all there were, we would have no trouble employing tail length as one of our characters. *Podogymnura*, *Hylomys*, *Neohylomys*, and *Neotetracus* are roughly intermediate but difficult to characterize, given the condition of the skins available to us.

8. Pelage, white facial mask: Corbet (1988) distinguished among erinaceines on the presence of a white facial mask. He listed *Atelerix*, *Paraechinus aethiopicus*, and *P. micropus* as having a distinct mask, and *Erinaceus europaeus* and *E. concolor* as having a faint mask. Although we agree that there may be a trend in this direction, we found the presence of a white mask too variable within these species to warrant coding.

9. Pelage, dark sagittal stripe: Corbet (1988) used this character to distinguish between *Hylomys/Neotetracus* with a faint stripe and *Neohylomys* with a prominent stripe. Many of

TABLE 6.—Reported values for numbers of mammae in the Erinaceidae.

Taxon	No. mammae	Citation
<i>Echinosorex</i>	4	Sokolov, 1973
<i>Podogymnura aureospinula</i>	4	Heaney and Morgan, 1982
<i>P. truei</i>	?	
<i>Hylomys suillus</i>	4	Lekagul and McNeeley, 1977; Sokolov, 1973
<i>Neohylomys hainanensis</i>	6	Shaw and Wong, 1959; Sokolov, 1973
<i>Neotetracus sinensis</i>	4 (= 4 pair?)	Sokolov, 1973
	8	Thomas, 1911
<i>Hemiechinus dauuricus</i>	8	R.S. Hoffmann, pers. observ.
<i>Hemiechinus</i>	10	Haltenorth and Diller, 1977
<i>Paraechinus</i>	8	Haltenorth and Diller, 1977
<i>Erinaceus, sensu stricto</i>	10	Cabrera, 1914; Corbet and Southern, 1977; Stroganov, 1957
<i>Atelerix algirus</i>	10 (implied)	Cabrera, 1914
<i>A. frontalis</i>	6	Smithers, 1983
	4-8	Haltenorth and Diller, 1977
<i>Atelerix, sensu stricto</i>	10	Haltenorth and Diller, 1977

the specimens that we have examined of *Hylomys* and *Neotetracus* have no evidence of a stripe, and the type series of *Neohylomys* shows considerable variation in the distinctiveness of the stripe.

10. Pelage, ventral pigmentation: Corbet (1988) coded the variation in pigmentation on the ventral surface in erinaceines. We found the color to vary individually, perhaps being more closely associated with environmental variables.

11. Pre-anal glands: Corbet (1988) used this character to separate *Echinosorex* with pre-anal glands on the anterior margin of the anus from *Hylomys* and *Neotetracus*, where the pre-anal glands are separate from the anal opening. Pre-anal glands appear to be absent in the few erinaceines checked and the condition is unknown in *Podogymnura* or *Neohylomys*. Because of the paucity of information, we have excluded this character.

12. Penis spines: Corbet (1988) pointed out the differences in the arrangement and nature of spines on the penis. We were not able to examine material and therefore did not include this transformation in our analysis. Note, however, that Corbet's (1988) figured distribution of penis spines is more congruent with our tree than his.

13. Penis, glans expanded laterally: Corbet (1988) pointed out that the expansion of the glans penis separated some erinaceines (*A. algirus*, *A. albiventris*, and *A. frontalis*) from the others. We were unable to examine material and therefore did not include his character in our analysis, although it supports our tree.

## Results and Discussion

The least-conflicting global phylogenetic hypothesis (CI = 0.758; 128 steps) is presented in Figure 9. The characters

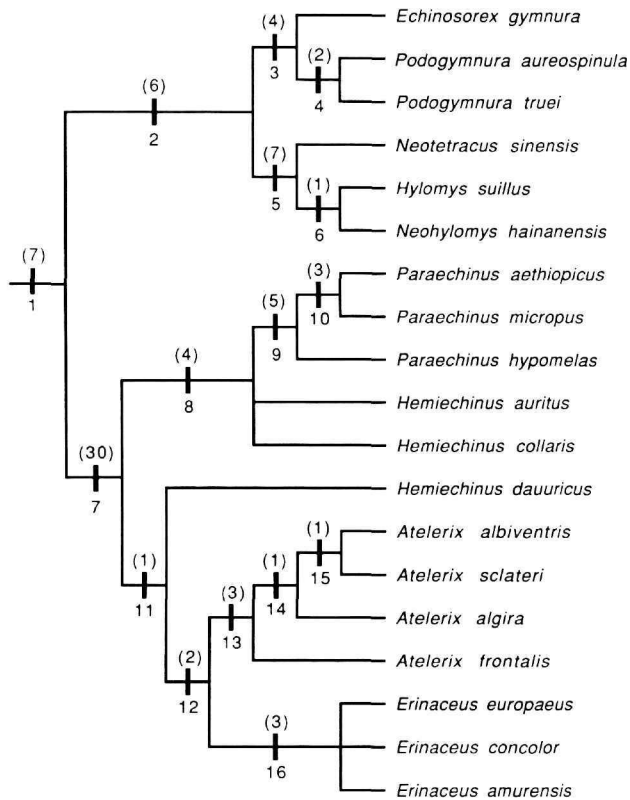


FIGURE 9.—Recovered phylogenetic tree. Lower numbers are the stem numbers (see text), upper numbers are the number of unambiguous apomorphies. Taxonomy used is that of Corbet (1988).

supporting this tree are listed in Appendix 3 (Apomorphy List by Stems) and Appendix 4 (Changes on Stems by Transformation Series). The results of this analysis are as follows:

1. The monophyly of Erinaceidae is highly corroborated by seven unambiguously placed characters (Figure 9, Stem 1; Appendix 3, Stem 1).

2. Hylomyinae (Stem 2) is monophyletic, although without postcranial evidence this would not be clear. Some evidence (i.e., 4.1, 6.1, 50.1, 57.1, and 59.1) suggests that *Hylomys*, *Neotetracus*, and *Neohylomys* are most closely related to erinaceines. Other features, however, both cranial and postcranial (i.e., 8.1, 33.1, 66.1, 69.1, 73.1, and 74.1), support the monophyly of Hylomyinae.

3. The *Hylomys* group (*Neotetracus*, *Neohylomys*, and *Hylomys*) (Stem 5) is well supported by seven unambiguously placed character shifts, of which three features of the orbit are unique and unreversed (i.e., 13.1, 16.1, and 19.1). The relationship between the three species currently placed in the three monotypic genera is only arguably resolved. Although in our preferred cladogram, *Hylomys* and *Neohylomys* are joined by 54.0 (reappearance of the P1), this requires the ancestral

erinaceid to have lost the P1, which then reappeared in *Echinorex* and *Hylomys* + *Neohylomys*. There has been a traditional bias among mammalogists not to support the loss and then later reappearance of a homologous tooth. A one step less parsimonious solution, that of independent loss of the P1 in *Podogymnura*, *Neotetracus*, and erinaceines, remains a viable possibility, and would support the generic distinction of *Neotetracus* from *Hylomys*.

4. *Podogymnura* (Stem 4) is arguably monophyletic, supported by two unambiguously placed characters, 22.1 and 48.1. Although two cranial characters (34.1 and 41.1) argue that *P. truei* is more closely related to the *Hylomys* group than to *P. aureospinula*, for these to be homologues would require the unique unreversed apomorphies of Stem 4 and Stem 3 to be homoplasies. Also there is some evidence that the relative size of these features may be allometric.

5. A sister-taxon relationship of *Echinorex* and *Podogymnura* (Stem 3) is supported by four unambiguously placed apomorphies (5.1, 44.1, 52.1, and 81.1). Additionally, the tendency for the ectotympanic to be somewhat hidden within the bulla supports this conclusion.

6. Erinaceinae (Stem 7) is highly corroborated with 30 unambiguously placed synapomorphies. Within this group, two groups can be recognized: (1) a well-supported clade composed of *Hemiechinus* (excluding *H. dauuricus*) and *Paraechinus* (Stem 8); (2) a weakly supported clade composed of *Hemiechinus dauuricus*, *Erinaceus*, and *Atelerix* (Stem 11).

7. The monophyly of the *Hemiechinus* (excluding *H. dauuricus*)-*Paraechinus* clade (Stem 8) appears strong (although disputed by Corbet, 1988), supported by three cranial and one external pelage character (3.1, 27.2, 31.1, and 75.1).

8. *Paraechinus* (Stem 9) is also a well-supported monophyletic group, supported by unreversed basicranial characters (11.2, 27.3, 35.1, and 36.1), as well as one unordered feature (79.2).

9. Within *Paraechinus* it is clear that *Paraechinus hypomelas* is the sister taxon of *P. micropus* + *P. aethiopicus* (Stem 10). *Paraechinus hypomelas* does not exhibit any discovered apomorphies with respect to Stem 10 and could therefore be considered to approach the diagnosis of the ancestor of living *Paraechinus*. Likewise, *P. micropus* lacks any apomorphies with respect to *P. aethiopicus*.

10. *Hemiechinus* is not monophyletic, because *H. dauuricus* demonstrates a possible special relationship with the *Erinaceus*-*Atelerix* clade (Stem 12). It may be argued that the degree of difference between *Paraechinus* (Stem 9; see point 8 above) and *Hemiechinus* (*H. auritus* and *H. collaris*, excluding *H. dauuricus*) warrants generic distinction. However, we have no evidence to support the monophyly of the remaining *Hemiechinus* and it remains possible that, regardless of overall similarity, *Hemiechinus* (sensu stricto) is paraphyletic with respect to *Paraechinus*.

11. The monophyly of the clade composed of *Hemiechinus dauuricus*, *Erinaceus*, and *Atelerix* (Stem 11) is weakly

supported by Character 80.1 (coarse ventral pelage). Single characters make poor flagpoles, however, and we are not overly confident of this conclusion, because at least one other Transformation Series, #77 (spine condition), if considered an ordered series, would argue for the monophyly of *H. dauuricus* + (other *Hemiechinus* + *Paraechinus*). *Hemiechinus dauuricus* is best considered to be in a polytomy with the *Hemiechinus-Paraechinus* clade (Stem 8) and the *Erinaceus-Atelerix* clade (Stem 12).

12. The *Erinaceus-Atelerix* clade (Stem 12) is supported by two characters of the skull and pelage (29.1 and 79.1) the second of which is part of an unordered series.

13. *Erinaceus* (Stem 16) has its monophyly supported by two unique unreversed features of the teeth (49.2 and 51.1) and a reversal (76.0). In trees of one extra step in Transformation Series #80, Character 76.0 succeeds, in some topologies, in placing *Erinaceus* as the sister taxon of the remaining erinaceines. No resolution between the species of *Erinaceus* was obtained.

14. The *Atelerix* clade (Stem 13) is supported by three unambiguously placed characters of the skull and teeth (22.1, 26.1, and 56.0).

15. *Aethechinus* (sensu Robbins and Setzer, 1985; i.e., *Atelerix algirus* and *A. frontalis*) does not have any apomorphies to support an hypothesis of monophyly. Conversely, however, Character 60.1 (P3 with two roots) supports paraphyly of *Aethechinus* (Stem 14). Additionally, even though we could not use the shape of the parieto-occipital suture (Corbet, 1974) because of individual variation, the "trend" suggests the same results: that *Aethechinus* is, in fact, paraphyletic, with *A. algirus* being closer to *Atelerix* than is *Aethechinus frontalis*.

16. *Atelerix albiventris* plus *A. sclateri* (Stem 15) is monophyletic, supported by one feature on P3 (58.1).

### Recommended Taxonomy

Although any number of taxonomies are consistent with our preferred tree (Figure 10), we have designed a taxonomy that attempts to maintain usage without distorting phylogenetic information. Our adopted taxonomy is listed below. Salient features are as follows:

1. Following Van Valen (1967) and Nowak and Paradiso (1983), the monotypic genera *Neohylomys* and *Neotetracus* are synonymized with *Hylomys*. We could continue to recognize three monotypic genera (as did Corbet, 1988), but that arrangement would carry no phylogenetic information and would leave the highly corroborated stem subtending these taxa without a name.

2. *Hemiechinus dauuricus* (and tentatively, *H. hughii*) is placed in *Mesechinus*, which we regard as in a polytomy with the *Hemiechinus-Paraechinus* clade and the *Erinaceus-Atelerix* clade.

3. *Paraechinus* is placed as a subgenus within an expanded *Hemiechinus*. Although we have no evidence bearing on the monophyly of a subgenus *Hemiechinus*, it appears that *Hemiechinus collaris* may be a peripheral isolate of *H. auritus* and, therefore, would form a monophyletic taxon. Further data are needed.

4. Following earlier authors (Table 7), species formerly in *Erinaceus*, *Aethechinus*, and *Atelerix* are placed in two genera, *Erinaceus* and *Atelerix* (including former *Aethechinus*). Although a phylogenetically more symmetrical taxonomy would have *Atelerix* and *Erinaceus* as sister subgenera, the evidence linking these two taxa is only one unambiguously placed character. Because trees of one step longer allow *Erinaceus* to form the sister taxon of the remaining genera, we maintain the two genera. Regardless, our taxonomy is logically consistent with our recovered phylogeny.

Where the species listed differ from those discussed previously, see the relevant taxonomic accounts. Comparison of our taxonomy with those used by other authors is shown in Table 7. The taxonomy we propose follows.

#### Family ERINACEIDAE

##### Subfamily HYLOMYINAE

*Hylomys*  
*H. hainanensis*  
*H. sinensis*  
*H. suillus*  
*Echinosorex gymnura*  
*Podogymnura*  
*P. aureospinula*  
*P. truei*

##### Subfamily ERINACEINAE

*Hemiechinus*  
*H. auritus*  
*H. collaris*  
*H. (Paraechinus)*  
*H. (P.) aethiopicus*  
*H. (P.) hypomelas*  
*H. (P.) micropus*  
*H. (P.) nudiventris*

*Mesechinus*  
*M. dauuricus*  
*M. hughii*

*Erinaceus*  
*E. amurensis*  
*E. concolor*  
*E. europaeus*

*Atelerix*  
*A. algirus*  
*A. frontalis*  
*A. albiventris*  
*A. sclateri*

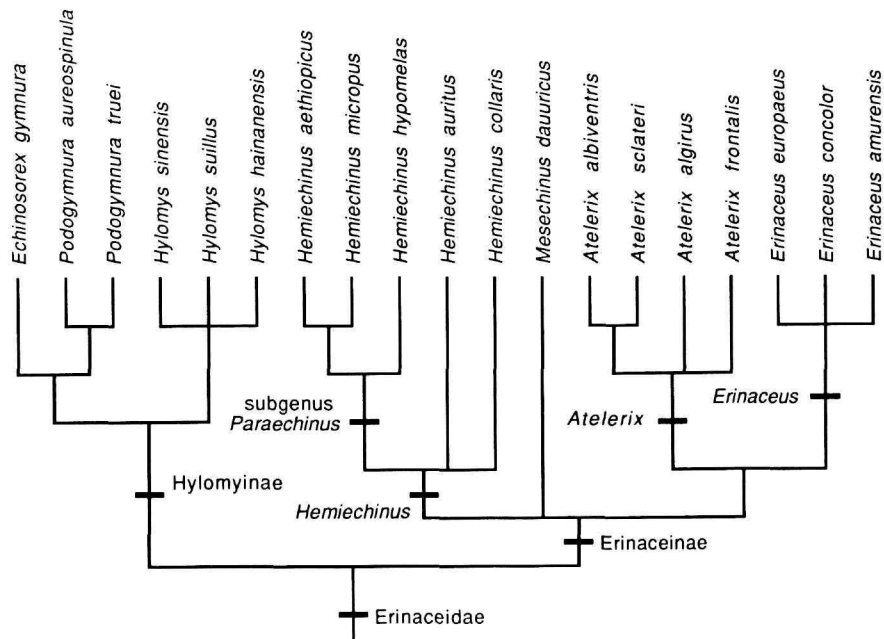


FIGURE 10.—Taxonomic tree reflecting our proposed nomenclature.

TABLE 7.—A comparison of classifications of Recent Erinaceidae.

Honacki et al., 1982	Corbet, 1988	This paper
<i>Echinorex gymnurus</i>	<i>Echinorex gymnurus</i>	<i>Echinorex gymnura</i>
<i>Podogymnura aureospinula</i>	<i>Podogymnura aureospinula</i>	<i>Podogymnura aureospinula</i>
<i>Podogymnura truei</i>	<i>Podogymnura truei</i>	<i>Podogymnura truei</i>
<i>Hylomys suillus</i>	<i>Hylomys suillus</i>	<i>Hylomys suillus</i>
<i>Neohylomys hainanensis</i>	<i>Neohylomys hainanensis</i>	<i>Hylomys hainanensis</i>
<i>Neotetracus sinensis</i>	<i>Neotetracus sinensis</i>	<i>Hylomys sinensis</i>
<i>Erinaecus amurensis</i>	<i>Erinaecus amurensis</i>	<i>Erinaecus amurensis</i>
<i>Erinaecus concolor</i>	<i>Erinaecus concolor</i>	<i>Erinaecus concolor</i>
<i>Erinaecus europaeus</i>	<i>Erinaecus europaeus</i>	<i>Erinaecus europaeus</i>
<i>Erinaecus albiventris</i>	<i>Atelerix albiventris</i>	<i>Atelerix albiventris</i>
<i>Erinaecus frontalis</i>	<i>Atelerix frontalis</i>	<i>Atelerix frontalis</i>
<i>Erinaecus algirus</i>	<i>Atelerix algirus</i>	<i>Atelerix algirus</i>
<i>Erinaecus sclateri</i>	<i>Atelerix sclateri</i>	<i>Atelerix sclateri</i>
<i>Hemiechinus auritus</i>	<i>Hemiechinus auritus</i>	<i>Hemiechinus auritus</i>
<i>Hemiechinus collaris</i>	<i>Hemiechinus collaris</i>	<i>Hemiechinus collaris</i>
<i>Hemiechinus dauuricus</i>	<i>Hemiechinus dauuricus</i>	<i>Mesechinus dauuricus</i>
<i>Hemiechinus hughii</i>	<i>Hemiechinus hughii</i>	<i>Mesechinus hughii</i>
<i>Hemiechinus sylvaticus</i>	( <i>Hemiechinus hughii</i> )	( <i>Mesechinus hughii</i> )
<i>Paraechinus aethiopicus</i>	<i>Paraechinus aethiopicus</i>	<i>Hemiechinus aethiopicus</i>
<i>Paraechinus hypomelas</i>	<i>Paraechinus hypomelas</i>	<i>Hemiechinus hypomelas</i>
<i>Paraechinus micropus</i>	<i>Paraechinus micropus</i>	<i>Hemiechinus micropus</i>



### Comparisons with Previous Hypotheses of Relationships

Other than Leche (1902), most authors (e.g., Butler, 1948; Novacek, 1985, 1986) have accepted the monophyly of Hylomyinae (as Galericinae or Echinisoricinae), albeit without much supporting data. Leche (1902) supported the view that *Hylomys* had a special relationship with the erinaceines; without postcranial data this view would be as parsimonious as one supporting monophyly of the hylomyines.

Heaney and Morgan (1982) and Corbet (1988) considered *Podogymnura* to be a monophyletic taxon, most closely related to *Echinorex*. The former presented no evidence to support this conjecture, other than a subjective evaluation of general similarity, but Corbet (1988) presented a number of features that were used in our analysis. Butler (1948) also regarded *Podogymnura* to be most closely related to *Echinorex* (together in a tribe, Echinoricini), based on overall similarity.

Although the monophyly of Erinaceinae has been universally accepted, the number of erinaceine genera has been the source of some controversy. Dobson (1882) considered all erinaceines to be in *Erinaceus*. Corbet (1974, 1978) accepted three genera, *Erinaceus* (including *Atelerix*), *Hemiechinus*, and *Paraechinus*. Elleman and Morrison-Scott (1951) and Nowak and Paradiso (1983) recognized the same three genera, but recognized two subgenera, *Erinaceus* and *Atelerix*, within the genus *Erinaceus*. Corbet (1988) later separated *Atelerix* from *Erinaceus*. With some disagreement on the assignment of some species, Thomas (1918), Cabrera (1925), Allen (1939), and Robbins and Setzer (1985) accepted five genera: *Atelerix*, *Aethechinus*, *Erinaceus*, *Hemiechinus*, and *Paraechinus*. With the exception of the one-genus arrangement of Dobson (1882), which does not improve on the information implicit in the group name Erinaceinae, none of these arrangements is consistent (Hull, 1964; Wiley, 1981) with our inferred phylogeny of the group. That is, they recognize at least one paraphyletic genus, *Hemiechinus*.

Most of these authors based their genera only on some subjective measure of similarity rather than relationship. Only Robbins and Setzer (1985) supplied a comprehensive rationale for their arrangement, but they had conflicting goals (e.g., recognize monophyletic taxa, group phenetically similar species, and identify "adaptive zones"). Their scheme of relationship is almost completely in disagreement with ours. In their dendrogram *Aethechinus* and *Erinaceus* are allied, apparently solely on the basis of size, as there were no synapomorphies suggested, nor have we found any support for this hypothesis. We also know of no support for the monophyly of their group containing *Atelerix* (in the more restricted sense), *Hemiechinus* (in the sense of including *dauuricus*), and *Paraechinus*. Our only point of agreement is the close relationship of *Paraechinus* and *Hemiechinus* (excluding

*dauuricus*). We, however, do not regard their *Hemiechinus* as demonstrably monophyletic. Our differences from the evolutionary model presented by Robbins and Setzer (1985) appear to be due to the fact that phenetic techniques, because of their underlying assumptions, are inappropriately applied to historical questions (Sokal, 1986).

Most recently, Corbet (1988) has addressed the systematics of Erinaceidae using techniques superficially similar to ours and has come to a number of different conclusions. The reason for these differences stems from his use of subjective weighting. Although we do not categorically state that his approach renders his conclusions untestable, we do think that subjective weighting does not allow for objective comparisons with our results. Corbet (1988) regarded *Hylomys suillus* as the sister taxon of *Neohylomys* (our *Hylomys hainanensis*) and *Neotetracus* (our *H. sinensis*) on the basis of their shared loss of the P1. However, the presence of this tooth is variable in the type series (Shaw and Wong, 1959). One more parsimonious solution is that the P1 reappeared in *Hylomys hainanensis* + *H. suillus*. Although Corbet (1988) retained the monotypic genera *Neohylomys* and *Neotetracus* as separate from *Hylomys*, this difference has nothing to do with data analysis, but rather with a difference of opinion as to the importance of phenotypic similarity. We see no value in recognizing monotypic genera when to do so does not improve perception of cladistic relationships.

In the erinaceines, Corbet (1988) regarded *Hemiechinus* (including *dauuricus*) as the sister taxon of the remaining erinaceines on the basis of not having a spineless tract on the scalp. Regardless of the attractiveness of this notion, it requires at least five convergences between *Paraechinus* and *Hemiechinus*, excluding *dauuricus* (i.e., 3.1 (incisors closely approximating medially), 27.2 (moderately developed suprarectal fossa), 31.1 (basisphenoid inflation), and 75.1 (enlarged ears)), and also requires the coarse ventral fur (Character 80.1) to be convergent in former *Hemiechinus dauuricus* and the *Erinaceus-Atelerix* group. We believe it inappropriate to base the tree on a single transformation (presence/absence of a spineless crown tract), particularly when this transformation cannot be polarized.

Another relationship suggested by Corbet (1988) was the alliance of *Paraechinus* with *Atelerix*, rather than with *Hemiechinus* (excluding *dauuricus*), a result inconsistent with our tree. When compared with our data, each of his proposals necessitates considerably more homoplasy. As a general observation, when our data are cast on Corbet's tree, the obtained consistency index is 0.703 (compared with 0.758 for our tree). Although these numbers appear similar, bear in mind that 25% of all character shifts in our analysis appear on the Erinaceinae stem. What these numbers do reflect is a lack of parsimony in Corbet's tree. We concur, however, with his species limits.

**Key to the Skulls of the Erinaceidae**

1. Pterygoid with epipterygoid process; zygomatic arch complete; quadrate M1 and M2; basioccipital-petrosal suture closed forming distinct foramen (ERINACEIDAE) . . . . . 2  
     Pterygoid without epipterygoid processes; zygomatic arch incomplete; triangular M1 and M2; basioccipital-petrosal suture open, not forming distinct foramen . . . . . (other, including TENRECIDAE)
2. Rostrum long (>42% of skull length); paroccipital process small; basisphenoid flat without distinctive hollow; postglenoid foramen posterior to glenoid fossa; orbital wing of alisphenoid without anterior process; occipital condyle emarginated; p3 and i1 present; 10 teeth in lower jaw (HYLOMYINAE) . . . . . 3  
     Rostrum short (<35% of skull length); paroccipital process robust; basisphenoid with distinctive fossa or hollow; postglenoid foramen confluent with glenoid fossa; orbital wing of alisphenoid with anterior process (developed most in old adults); occipital condyle not emarginated; p3 and i1 absent; eight teeth in lower jaw (ERINACEINAE) . . . . . 8
3. C1 significantly larger than adjacent teeth; p3 with two roots and larger than p2; infraorbital canal dorsal or posterodorsal to the P4-M1 area; anterior palatine foramina anterior to the maxilla/palatine suture; supraorbital processes of the frontal absent or weak . . . . . 4  
     C1 only slightly larger than adjacent teeth; p3 with one root and near equal in size to p2; infraorbital canal dorsal to the P3-P4 region; anterior palatine foramina posterior to or at the maxilla/palatine suture; supraorbital processes of the frontal prominent and sharp . . . . . 6
4. Palatine with lateral fossa posterodorsal to the postpalatal torus; I2 greater in size than I3; zygoma with prominent posteroventral process . . . . .  
     . . . . . *Echinosorex gymnura*  
     [Plate 1]  
     Palatine without lateral fossa posterodorsal to the postpalatal torus; I2 less than or equal to I3; zygoma posteroventral process if present, weakly defined . . . . . 5
5. Frontals not inflated; mastoid occipital face inflated; exoccipital inflated; P3 two or three rooted without lingual cusp; condylobasal length <45 mm . . . . .  
     . . . . . *Podogymnura truei*  
     [Plate 3]  
     Frontals inflated; mastoid occipital face not inflated; exoccipital not inflated; P3 three rooted with lingual cusp; condylobasal length >45 mm . . . . .  
     . . . . . *Podogymnura aureospinula*  
     [Plate 2]
6. P1 absent; c1 subequal to slightly smaller than i3; C1 approximately equal in size to adjacent teeth; i1 enlarged; posteriormost portion of nasals extends medial or posterior to the level of the antorbital rim . . . . . *Hylomys sinensis*  
     [Plate 5]  
     P1 present; equal to or larger than i3; C1 slightly larger than adjacent teeth; i1 absent or small; posteriormost portion of nasals anterior to the level of the antorbital rim . . . . . 7
7. p1 present . . . . . *Hylomys suillus*  
     [Plate 6]  
     p1 absent . . . . . *Hylomys hainanensis*  
     [Plate 4]
8. Basisphenoid inflated; suprameatal fossa moderately deep to very deep; rostrum narrow, anterior upper incisors closely approximating . . . . . 9  
     Basisphenoid not inflated; suprameatal fossa shallow; rostrum wide, anterior incisors widely separate . . . . . 13

9. Alisphenoid inflated; ventral process of petrosal inflated; zygoma posteroventral process prominent; mastoid portion of suprameatal fossa well inflated . . . . 10  
 Alisphenoid not inflated; ventral process of petrosal not well inflated; zygoma posteroventral process small; mastoid portion of suprameatal fossa not well inflated . . . . . 12
10. P3 with three distinct roots and with lingual lobe; suprameatal fossa does not extend dorsal to glenoid fossa . . . . . *Hemiechinus hypomelas*  
 [Plate 17]  
 P3 with one or two roots and without or with vestigial lingual lobe; suprameatal fossa extends dorsal to glenoid fossa . . . . . 11
11. Epipterygoid processes inflated . . . . . *Hemiechinus aethiopicus*  
 [Plate 14]  
 Epipterygoid processes not inflated . . . . . *Hemiechinus micropus*  
 [Plate 18]
12. P2 with two roots . . . . . *Hemiechinus auritus*  
 [Plate 15]  
 P2 with one root . . . . . *Hemiechinus collaris*  
 [Plate 16]
13. Lacrimal/maxilla suture unfused and/or distinct in adults; suprameatal fossa compressed anteroposteriorly; frontals lower than parietals . . . . .  
 . . . . . *Mesechinus dauuricus*  
 [Plate 19]  
 Lacrimal/maxilla suture fused and indistinct in adults; suprameatal fossa not compressed anteroposteriorly; frontals higher than parietals . . . . . 14
14. Posterior palatal shelf without posteriorly directed spine; suprameatal fossa composed of predominately mastoid and only some squamosal; P2 and C1 with two distinct roots (*Atelerix*) . . . . . 15  
 Posterior palatal shelf with posteriorly directed spine; suprameatal fossa composed of near equal portions of mastoid and squamosal; P2 and C1 with one root or two roots unfused (*Erinaceus*) . . . . . 18
15. P3 lingual lobe vestigial or absent . . . . . 16  
 P3 lingual lobe present, well developed . . . . . 17
16. Maxilla does not share common suture with nasals . . . . . *Atelerix sclateri*  
 [Plate 10]  
 Maxilla shares common suture with nasals . . . . . *Atelerix albiventris*  
 [Plate 7]
17. P2 with one or two roots . . . . . *Atelerix algirus*  
 [Plate 8]  
 P2 with three roots . . . . . *Atelerix frontalis*  
 [Plate 9]
18. Basisphenoid fossa V-shaped and not continuous on posterior margin; incomplete inferior stapedial foramen . . . . . *Erinaceus amurensis*  
 [Plate 11]  
 Basisphenoid fossa U-shaped with continuous posterior margin; complete inferior stapedial foramen . . . . . 19
19. Postero-dorsal processes of maxilla long, extending posterior to lacrimal foramen . . . . . *Erinaceus concolor*  
 [Plate 12]  
 Postero-dorsal processes of maxilla short, not extending posterior to lacrimal foramen . . . . . *Erinaceus europaeus*  
 [Plate 13]

### Taxonomic Accounts, Diagnoses, and Comments on Species Relationships

All characters supporting the tree in Figure 9 are supplied in Appendices 3 (list of character changes by stem) and 4 (list of changes by transformation series). For this reason, with the exception of Erinaceidae, the diagnoses supplied with the accounts are not lists of apomorphies. Instead they are comparable lists of attributes that will serve to allow easy comparison. Numbers in brackets indicate character transformation series. Synonymies include names based on fossils only when those names affect the stability of current nomenclature (e.g., Galericipini). Type localities are listed with each species. When possible, we have recorded the corresponding longitude and latitude of the type locality as listed in the U.S. Board of Geographic Names Gazetteers. This information follows the type locality description.

#### Family ERINACEIDAE Fischer, 1817

ERINACEIDAE Fischer, 1817:372. [Type genus: *Erinaceus* Linnaeus, 1758.]

DIAGNOSIS.—Erinaceidae is apomorphic with respect to soricoids, tenrecoids, and †Leptictidae in having (1) an epipterygoid process of the pterygoid [11.1]; (2) a lacrimal-maxilla suture fused in young adults (reversed in *Mesechinus dauuricus*) [12.1]; (3) the basioccipital/petrosal suture closed [37.1]; (4) 2 lingual roots of the P4, either fused or not [62]; (5) low trigonids on the lower molars and having the talonid expanded [63.1]; (6) M3 metacone reduced or absent [67.1]. Corbet (1988:119) also listed as derived “the quadrate, low-cusped form of M1 and M2 (with P4 and M3 tending toward that form), the labial styles being reduced to a cingulum; and the subrectangular form of m1 and m2.”

#### Subfamily HYLOMYINAE Anderson, 1879

GALERICES Pomel, 1848:249. [Type genus: *Galerix* Pomel, 1848 (fossil). See nomenclatural comment.]

GYMNURINAE Gill, 1872:19. [Type genus: *Gymnura* Lesson, 1827 (not *Gymnura* Kuhl, 1823).]

HYLOMIDAE Anderson, 1879:138. [Type genus: *Hylomys* Müller, 1839.]

ECHINOSORICINAE Cabrera, 1925:57. [Type genus: *Echinorex* de Blainville, 1838.]

GALERICIPINI Butler, 1948:262. [Type genus: *Galerix* Pomel, 1848. See comment.]

DIAGNOSIS.—(1) rostrum long, greater than 42% of skull length [2.0]; (2) anterior palatine foramina do not include middle palatine foramina [4.0–1]; (3) lacrimal foramen hidden in lateral view by well-developed antorbital flange [8.1]; (4) jugal does not reach posteroventral process of zygoma [10.2]; (5) anterior process of alisphenoid absent [17.0]; (6) suboptic foramen anterior to sphenorbital fissure [20.2]; (7) sphenopalatine foramen anterodorsal or slightly posterodorsal to the

palatine transverse torus [21.0]; (8) zygomatic process of squamosal not elevated posteriorly [24.0]; (9) postglenoid foramen posterior to glenoid fossa [25.0]; (10) suprameatal fossa absent [27.0]; (11) nasopharyngeal pocket of basisphenoid absent [30.0]; (12) ectotympanic slender and ring-shaped [32.0]; (13) stapedial foramen posterior to squamosal/alisphenoid suture and posterior to postglenoid foramen [38.0]; (14) epitympanic recess formed by squamosal [39.0]; (15) paroccipital process small [40.0]; (16) occipital condyle emarginated, giving it a slightly lobed appearance [42.0]; (17) condylar foramen of basioccipital anterior to ventral lip of condyle [43.0]; (18) i1 present [45.0]; (19) i2 subequal to other incisors [47.0]; (20) I2 greater than I3 [48.0]; (21) p3 present [57.0]; (22) M3 hypocone and metacone well developed [66.1, 67.1]; (23) posteroventral keel present on axis [70.1]; (24) metacromion process of scapula elongated, fusiform [71.1]; (25) sacral vertebral not fused into a longitudinal plate [72.1]; (26) greatly elongated posteroventral process of pubis [73.1]; (27) strongly developed lateral flange on anterosuperior margin of tibia [74.1]; (28) pelage not composed of stout spines [77.0].

CONTENT.—*Echinorex* de Blainville, 1838; *Podogymnura* Mearns, 1905; *Hylomys* Müller, 1839.

DISTRIBUTION.—From northeastern Burma and southern China (Yunnan, Sichuan, Guizhou, Hainan Island) south through Indochina, Indonesia (Sumatra, Borneo, and Java), and the Philippine Islands (Dinagat and Mindanao).

NOMENCLATURE COMMENT.—The use of the name Galericipini for this taxon is incorrect. Pomel (1848:249) first used the French collective Galerices based on *Galerix* Pomel, 1848. Unlike other names proposed in the same work, a Latin equivalent was not supplied. According to the *International Code of Zoological Nomenclature* (1985, Art. 11(f)iii), “A family group name published before 1900 ..., but in itself not fully latinized, is available with its original author and date, provided that it has been latinized by later authors and that it has been generally accepted as valid by authors interested in the group concerned and as dating from that first publication as a vernacular name.” However, Galericipini does not meet these requirements and, in fact, the name was not formally proposed before Butler (1948) as Galericipini. Prior to Van Valen (1967), who employed the name Galericipini, the subfamilial name of universal use was Echinoricinae Cabrera, 1925 (e.g., Simpson, 1945; Findley, 1967; Butler, 1948, 1956), even though this is not the family-group name of priority. Although some workers have followed Van Valen (1967) (e.g., Novacek, 1985, 1986; Corbet, 1988), others (Yates, 1984) have continued to employ Echinoricinae. Also “galericipini” has not been employed as a vernacular name “from that first publication.” Therefore Galericipini is not the family-group name of priority. Surprisingly, when erecting Echinoricinae for this group, Cabrera (1925) mentioned the family-group name Hylomidae (sic) of Anderson (1879), which is the family-group name of priority.

### Genus *Echinosorex* de Blainville, 1838

*Gymnura* Lesson, 1827:171 [not *Gymnura* Kuhl, 1823]. [Type species: *Gymnura rafflesii* Lesson, 1827 (= *Viverra gymnura* Raffles, 1822).]

*Echinosorex* de Blainville, 1838:742. [Type species: *Viverra gymnura* Raffles, 1822.]

DIAGNOSIS.—(1) palatine foramina small [4.0] and anterior to the maxilla/palatine suture [5.1]; (2) infraorbital canal dorsal or posterodorsal to the P4-M2 region [6.0]; (3) antorbital fossa not present (except weakly in some old adults) [7.1]; (4) posteroventral process of maxillary part of zygoma present, prominent [9.2]; (5) supraorbital processes absent or poorly defined [13.0], bases not formed by anterior processes of parietal [16.0]; (6) ophthalmic foramen joined with or closely adjacent to ethmoid foramen [19.0]; (7) lateral fossa present in palatine anterodorsal to the postpalatal torus [23.1]; (8) coronoid process of dentary broad and rounded [44.1]; (9) I2 larger than I3 [48.0]; (10) C1 significantly larger than adjacent teeth [50.0]; (11) c1 significantly larger than p1 [52.1]; (12) P3 lingual lobe well developed [58.0], P3 normal sized [59.0]; (13) underfur present [81.1].

CONTENT.—*Echinosorex gymnura* (Raffles, 1822:272) (note: the widespread spelling of the epithet as *gymnurus* is incorrect; *gymnura* is a noun in apposition, meaning “naked-tail” and does not change its form to match the gender of the generic name); type locality not given, “Sumatra” implied.

DISTRIBUTION.—Tropical forests of southern Burma and Thailand, Malaya, Sumatra, and Borneo.

DISCUSSION.—The moonrat (or greater gymnure) retains a primitive suite of morphological characters, reminiscent of the common opossums (*Didelphis*) of the New World. We have been able to identify only a few autapomorphies among the characters that we have analyzed. The lateral fossa of the palatine, which serves for the insertion of the medial pterygoid muscle, is one of the most easily recognized apomorphies of a basically primitive *Echinosorex*. Butler (1956) pointed out the distinctive eye muscle depression above the optic foramen; however, our examination of other hylomyines reveals this to be a size-related feature. A few dubious qualitative characters might also be considered derived: large body size, *Echinosorex* being the largest species of insectivore; long tail; possibly aposematic, black-and-white to mostly white pelage (Corbet, 1988); and pre-anal glands that emit a strong ammonia-like scent (Gould, 1978).

In contrast to other insectivores, female *Echinosorex* are somewhat larger than males (Ralls, 1976). Geographic variation in size has been reported from Thailand, more northerly populations being larger than those adjacent to the equator (Lekagul and McNeeley, 1977).

### Genus *Podogymnura* Mearns, 1905

*Podogymnura* Mearns, 1905:436. [Type species: *Podogymnura truei* Mearns, 1905.]

DIAGNOSIS.—(1) anterior palatine foramina small [4.0] and

anterior to the maxilla/palatine suture [5.1]; (2) infraorbital canal dorsal or posterodorsal to the P4-M1 region [6.0]; (3) antorbital fossa present [7.0]; (4) posteroventral process of maxillary part of zygoma present, small (*P. truei*) to prominent (*P. aureospinula*) [9.1-2]; (5) supraorbital processes of frontal absent [13.0], not formed by anterior processes of parietal [16.0]; (6) ophthalmic foramen joined with or closely adjacent to the ethmoid foramen [19.0]; (7) lateral fossa absent from palatine anterodorsal to the postpalatal torus [23.0]; (8) coronoid process of dentary broad and rounded [44.1]; (9) I2 larger than I3 [48.0]; (10) C1 significantly larger than adjacent teeth [50.0]; (11) c1 significantly larger than p1 [52.1]; (12) P3 lingual lobe vestigial or absent [58.1], P3 normal sized [59.0]; (13) underfur present [81.1].

CONTENT.—*Podogymnura aureospinula* Heany and Morgan, 1982:14; type locality: “Plaridel, Albor Municipality, Dinagat Island, Surigao del Norte Province, Republic of the Philippines” [Dinagat Island is at 10°12'N, 125°35'E]. *Podogymnura truei* Mearns, 1905:437; type locality: “Mount Apo at 6,000 feet altitude, southern Mindanao, Philippine Islands” [= 6°59'N, 125°16'E].

DISTRIBUTION.—Dinagat and Mindanao islands, Philippines.

### Genus *Hylomys* Müller, 1839

*Hylomys* Müller, 1839:50. [Type species: *Hylomys suillus* Müller, 1839:50.]

*Neotetracus* Trouessart, 1909:389. [Type species: *Neotetracus sinensis* Trouessart, 1909:389.]

*Neohylomys* Shaw and Wong, 1959:422. [Type species: *Neohylomys hainanensis* Shaw and Wong, 1959:422.]

DIAGNOSIS.—(1) anterior palatine foramina elongated posteriorly [4.1] and at the palatine/maxilla suture [5.0]; (2) infraorbital foramen dorsal to the P3-P4 region [6.1]; (3) antorbital fossa present [7.0]; (4) posteroventral process of maxillary part of zygoma absent [9.0]; (5) supraorbital processes of frontal sharp, readily identifiable [13.1], bases formed by long anterior processes of parietals that extend along the supraorbital rim [16.1]; (6) ophthalmic foramen widely separated from the ethmoid foramen [19.1]; (7) lateral fossa absent from palatine anterodorsal to the postpalatal torus [23.1]; (8) coronoid process of dentary narrow and pointed [44.0]; (9) I2 smaller than or subequal to I3 [48.1]; (10) C1 slightly larger than or subequal to adjacent teeth [50.1-2]; (11) c1 approximately equal to, or smaller than, p1 [52.0]; (12) P3 lingual lobe vestigial or absent [58.1], P3 reduced [59.1]; (13) underfur not present [81.0].

CONTENT.—*Hylomys hainanensis* (Shaw and Wong, 1959:422); type locality: English translation, page 426: “Pai-sa Hsian, Hainan Island” [= Baisha Xian, which is an administrative unit at 19°13'N, 109°26'E]. *Hylomys sinensis* (Trouessart, 1909:389); type locality: “Ta-tsen-lou, province of Se-tchouen (China Occidental) at an altitude of 2454 meters” [= Kangding, Sichuan Sheng, 30°07'N, 102°02'E]. *Hylomys suillus* Müller, 1839:50; type locality: “Java.”



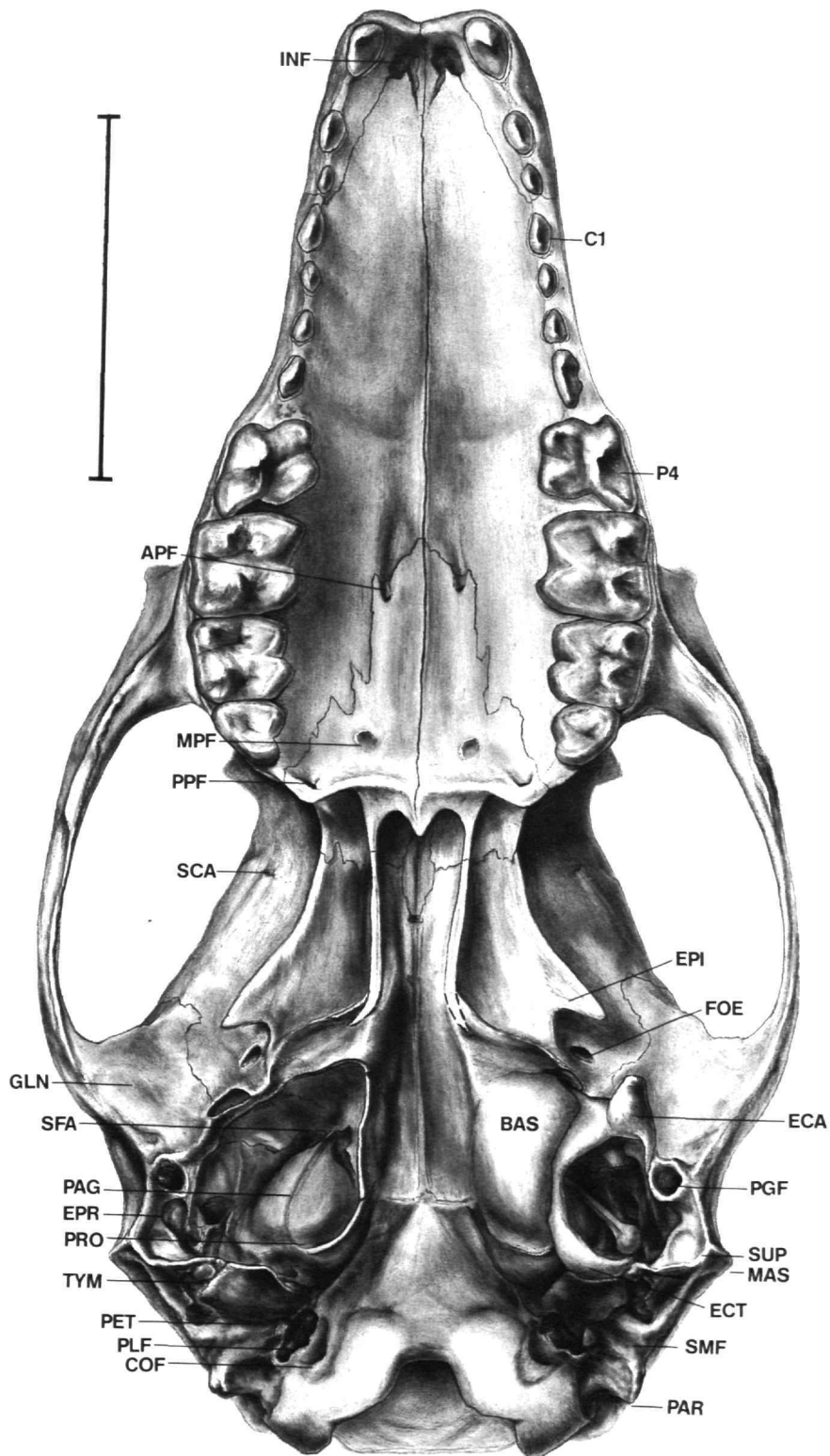


FIGURE 11.—Detailed ventral view of skull of *Hylomys hainanensis*. (Scale = 10 mm; key to abbreviations in Table 2.)

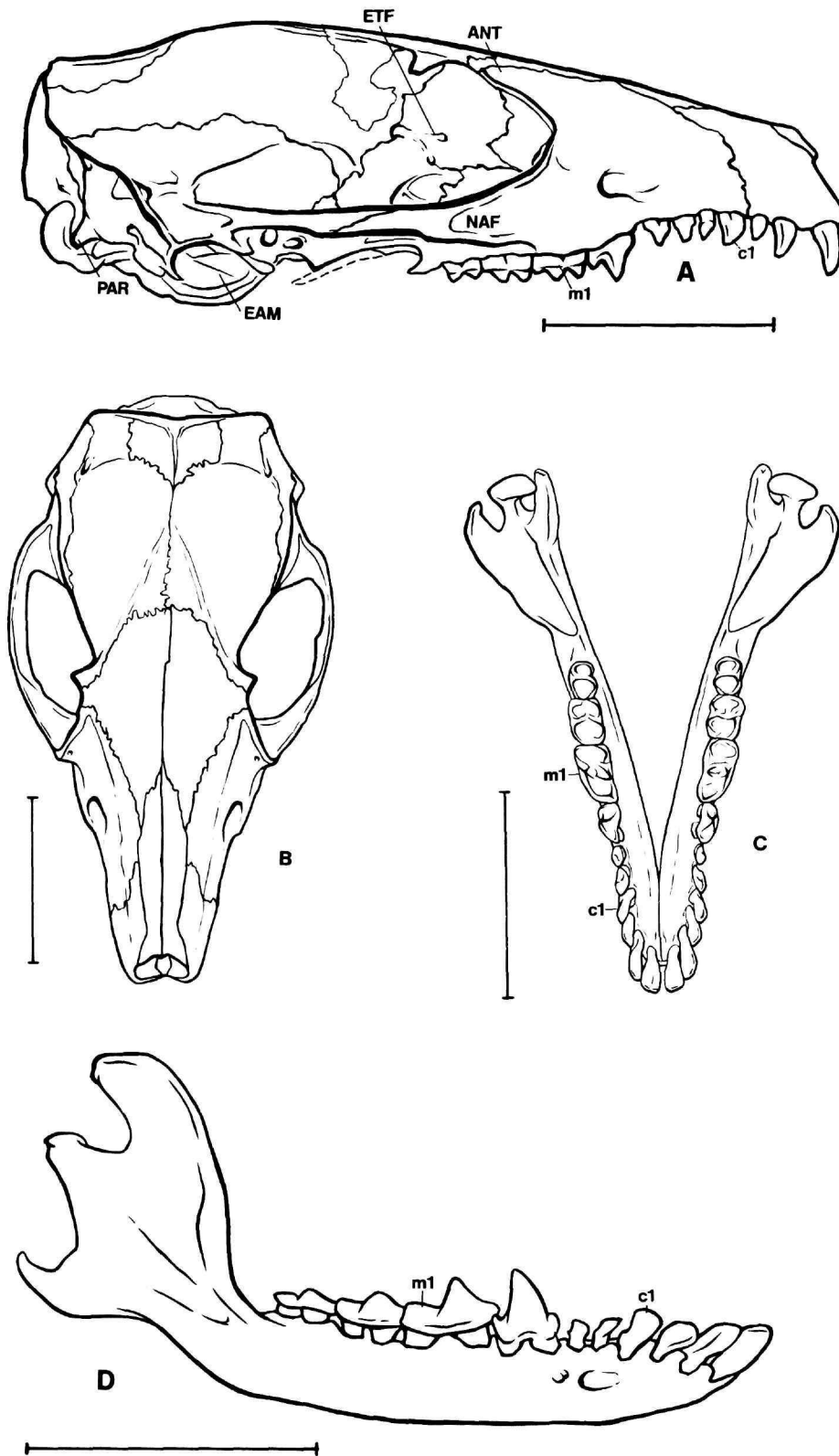


FIGURE 12.—*Hylomys hainanensis*, A, lateral, B, dorsal, C, occlusal view of lower mandible; D, lateral view of lower mandible. (Scale = 10 mm; key to abbreviations in Table 2).

DISTRIBUTION.—From northeastern Burma, northern Vietnam, and China (Yunnan, Sichuan, Guizhou) (*H. sinensis*); south through eastern Burma, Thailand, Laos, Vietnam, Malaya, Sumatra, Borneo, and Java (*H. suillus*); and Hainan Island (*H. hainanensis*).

COMMENTS.—*Hylomys suillus* is parapatric with the more northerly *H. sinensis*; they may have a zone of contact in eastern Burma and northern Thailand (Lekagul and McNeely, 1977) and perhaps Yunnan, although no area of sympatry is yet known.

### Subfamily ERINACEINAE Fischer, 1817

ERINACEINAE Fischer, 1817:372. [Type genus: *Erinaceus* Linnaeus, 1758.]

DIAGNOSIS.—(1) rostrum short, less than 35% of skull length [2.1]; (2) anterior palatine foramina elongated to include middle palatine foramina [4.2]; (3) lacrimal foramen not hidden in lateral view, antorbital flange poorly developed [8.0]; (4) jugal vestigial, not reaching posteroventral process of zygoma [10.1]; (5) anterior process of alisphenoid present [17.1]; (6) suboptic foramen in medial wall of sphenorbital transverse torus [20.1]; (7) sphenopalatine foramen decidedly posterodorsal to palatine transverse torus [21.1]; (8) zygomatic process of squamosal elevated posteriorly [24.1]; (9) postglenoid foramen confluent with glenoid fossa [25.1]; (10) suprameatal fossa moderately to extremely deep [27.1–4]; (11) nasopharyngeal fossa of basisphenoid deep [30.1]; (12) ectotympanic broad [32.1]; (13) stapedia foramen located on squamosal/alisphenoid suture and adjacent to postglenoid foramen [38.1]; (14) epitympanic recess formed by mastoid [39.1]; (15) paroccipital processes robust [40.1]; (16) no emargination of occipital condyle [42.1]; (17) condylar foramen of basioccipital on anteroventral lip of condyle [43.1]; (18) i1 absent [45.1]; (19) i2 greatly enlarged over other incisors [47.1]; (20) i2 less than or equal to i3 [48.1]; (21) p3 absent [57.2]; (22) M3 hypocone and metacone absent [66.0, 67.0]; (23) posteroventral keel absent from axis [70.0]; (24) metacromion process of scapula deltoid [71.0]; (25) sacral vertebrae fused into a longitudinal plate [72.1]; (26) no greatly elongated posteroventral process of ischium [73.0]; (24) no strongly developed lateral flange on anterosuperior margin of tibia [74.0]; (25) pelage composed of stout spines [77.1–3].

CONTENT.—*Atelerix* Pomel, 1848; *Erinaceus* Linnaeus, 1758; *Hemiechinus* Fitzinger, 1866; *Mesechinus* Ognev, 1951.

DISTRIBUTION.—Europe, northern Asia south through the Arabian and Indian peninsulas, and into central China; Africa, except for the tropical forest zone.

### Genus *Hemiechinus* Fitzinger, 1866

*Ericius* Sundevall, 1842:223 [not *Ericius* Tilesius von Tilenau, 1813]. [Type species: *Erinaceus auritus* Gmelin, 1770 (= *Hemiechinus auritus*).]

*Hemiechinus* Fitzinger, 1866:565. [Type species: *Erinaceus platyotis* Sundevall, 1842:232 (= *Hemiechinus auritus*).]

*Paraechinus* Trouessart, 1879:242. [Type species: *Erinaceus micropus* Blyth in Hutton, 1846:170.]

*Macroechinus* Satunin, 1907:189. [Type species: *Erinaceus hypomelas* Brandt, 1836:32.]

*Erinaceolus* Ognev, 1928:132. [Type species: *Hemiechinus microtis* Laptev, 1925. Nomen inquirenda, see discussion.]

DIAGNOSIS.—(1) rostrum narrow, anterior incisors closely approximated [3.1]; (2) lacrimal/maxilla suture fused and indistinct in young adults [12.1]; (3) posterior palatal shelf with a well-developed spine [22.0]; (4) suprameatal fossa entirely in squamosal [26.0]; (5) suprameatal fossa moderately to extremely well developed [27.2–4]; (6) anterior and posterior borders of suprameatal fossa widely separated [28.0]; (7) parietals relatively higher than frontals [29.0]; (8) basisphenoid inflated [31.1]; (9) squamosal does not participate in bullar roof [33.0]; (10) i3 with two separate roots [49.1]; (11) P2 with 1 root or 2 roots fused [56.1]; (12) long ears [75.1]; (13) hallux reduced [76.1]; (14) pelage spines papillate and grooved [77.3]; (15) ventral pelage soft and densely furred [80.0].

CONTENT.—*Hemiechinus auritus* (Gmelin, 1770:519); type locality: “in regione Astrachanensi” [Astrakhan’skaya Oblast’, U.S.S.R., 46°21’N, 48°03’E]. *Hemiechinus collaris* (Gray, 1830–1834, plate 8); type locality: “Doab.” Restricted by Wroughton (1910:81) to “between Jumna and Ganges Rivers.” [India]. Subgenus *Paraechinus* Trouessart, 1879 (see separate account under *Paraechinus*).

DISTRIBUTION.—Northern Africa eastward through Arabia and the Near and Middle East to India, Soviet Middle Asia, Mongolia, and western China.

DISCUSSION.—Species in the subgenus *Paraechinus* are treated in a separate account. *Hemiechinus auritus* and *H. collaris*, the species not included in the *Paraechinus* monophyletic group, are treated in this comment. Excluding the subgenus *Paraechinus*, *Hemiechinus* species have a distribution on Cyprus, and from coastal Libya eastward through the Near and Middle East to northwestern India, and through Soviet Middle Asia to Mongolia and western China.

Corbet (1984, 1988) recognized three species within his *Hemiechinus* (which he regarded as a distinct genus not including *Paraechinus*), two quite restricted geographically. The most widely distributed species, *H. auritus*, occurs from eastern North Africa through the Near and Middle East to Mongolia and western China (Xinjiang), with a southern extension into Pakistan and northwestern India. Populations of eastern Iran, Afghanistan, and Pakistan have been considered by some to be a distinct species, *H. megalotis* (Lay, 1967; Roberts, 1977). However, Gropp et al. (1969), Hassinger (1973), and Niethamer (1969) provided evidence that the smaller, lighter *H. auritus* intergrades with larger, darker populations of *H. megalotis* in central Iran, and our observations support this. There is, however, an abrupt break in this clinal trend in geographic variation evident along the western side of the Indus River valley. The small, very dark *Hemiechinus* of the Indus Valley and adjacent northern India

TABLE 8.—Cranial measurements of *Hemiechinus* in Afghanistan and Pakistan.

Taxon	Locality	Mean ± SE	Range	N
CONDYLO-INCISIVE LENGTH				
<i>Hemiechinus auritus megalotis</i>	Afghanistan	55.03±0.56	49.6–58.9	19
<i>Hemiechinus auritus megalotis</i>	Pakistan	54.24±0.38	52.4–56.5	10
<i>Hemiechinus collaris</i>	Pakistan	48.36±0.42	46.3–51.1	10
<i>Hemiechinus hypomelas hypomelas</i>	Pakistan	50.70±1.87	46.5–55.6	4
<i>Hemiechinus hypomelas jerdoni</i>	Pakistan	44.29±0.54	42.5–46.7	7
<i>Hemiechinus micropus</i>	Pakistan	42.93±0.53	40.7–45.1	9
MASTOID WIDTH				
<i>Hemiechinus auritus megalotis</i>	Afghanistan	25.82±0.18	24.1–26.9	19
<i>Hemiechinus auritus megalotis</i>	Pakistan	25.71±0.27	24.5–26.7	11
<i>Hemiechinus collaris</i>	Pakistan	23.05±0.17	22.2–23.8	11
<i>Hemiechinus hypomelas hypomelas</i>	Pakistan	25.08±0.68	23.5–26.8	4
<i>Hemiechinus hypomelas jerdoni</i>	Pakistan	22.51±0.30	21.3–23.3	7
<i>Hemiechinus micropus</i>	Pakistan	23.78±0.24	22.9–24.9	9
ZYGOMATIC WIDTH				
<i>Hemiechinus auritus megalotis</i>	Afghanistan	31.12±0.40	28.0–33.9	18
<i>Hemiechinus auritus megalotis</i>	Pakistan	30.45±0.37	28.1–32.4	11
<i>Hemiechinus collaris</i>	Pakistan	27.83±0.30	25.9–29.2	11
<i>Hemiechinus hypomelas hypomelas</i>	Pakistan	28.90±1.05	26.5–31.6	4
<i>Hemiechinus hypomelas jerdoni</i>	Pakistan	25.76±0.41	23.9–27.1	7
<i>Hemiechinus micropus</i>	Pakistan	27.01±0.86	25.8–28.2	9
WIDTH OF M2-M2, BUCCAL MARGINS				
<i>Hemiechinus auritus megalotis</i>	Afghanistan	20.24±0.19	19.1–22.0	19
<i>Hemiechinus auritus megalotis</i>	Pakistan	19.48±0.22	18.6–20.7	11
<i>Hemiechinus collaris</i>	Pakistan	18.16±0.14	17.3–18.9	11
<i>Hemiechinus hypomelas hypomelas</i>	Pakistan	18.30±0.49	17.6–19.7	4
<i>Hemiechinus hypomelas jerdoni</i>	Pakistan	16.64±0.26	15.6–17.5	7
<i>Hemiechinus micropus</i>	Pakistan	16.63±0.14	16.0–17.3	9
UPPER TOOTH ROW LENGTH				
<i>Hemiechinus auritus megalotis</i>	Afghanistan	26.81±0.24	25.0–28.7	19
<i>Hemiechinus auritus megalotis</i>	Pakistan	26.35±0.22	25.5–27.8	11
<i>Hemiechinus collaris</i>	Pakistan	24.04±0.18	23.2–25.1	11
<i>Hemiechinus hypomelas hypomelas</i>	Pakistan	23.95±0.97	22.0–26.6	4
<i>Hemiechinus hypomelas jerdoni</i>	Pakistan	21.57±0.26	20.6–22.8	7
<i>Hemiechinus micropus</i>	Pakistan	21.00±0.17	19.9–21.5	9

also have been considered a subspecies, *H. auritus collaris*, but no zone of potential contact between the large *H. a. megalotis* of montane Pakistan and the smaller *H. a. collaris* in the Indus Valley has been identified (Roberts, 1977), although one may exist. The taxa exhibit virtually no overlap in size (Table 8), and also differ in relative ear length (Table 4), length and color pattern of spines, and pelage color of face and throat (Roberts, 1977). No intermediates are known, and given the marked differences between the taxa, they should be retained as separate species, as did Corbet (1988), pending evidence of present or former intergradation. Should this evidence be found, that will constitute evidence of monophyly of *Hemiechinus auritus* + *H. collaris*.

The taxon *micropus* is an enigmatic one, originally described

by Laptev (1925) as a new species belonging to the genus *Hemiechinus*. The species is based on only two specimens, both captured alive in "Tashkent city gardens" in Uzbekistan, U.S.S.R. Laptev (1925) based his generic assignment on the absence of a medial spineless tract on the crown, a characteristic of *Hemiechinus*, but a suite of unusual cranial characters subsequently led Ognev (1928) to erect a monotypic genus, *Erinaceolus*, to accommodate the species. Bobrinskii et al. (1944:39) next opined that the taxon was based on aberrant individuals because "all the distinctive features... are connected with an anomalous under-development of the hearing apparatus," and most now regard the name as a synonym of *H. auritus*.

### Subgenus *Paraechinus* Trouessart, 1879

*Paraechinus* Trouessart, 1879:242. [Type species: *Erinaceus micropus* Blyth in Hutton, 1846:170.]

*Macroechinus* Satunin, 1907:189. [Type species: *Erinaceus hypomelas* Brandt, 1836.]

DIAGNOSIS.—(1) alisphenoid inflated [11.2] (not so in other *Hemiechinus*); (2) suprameatal fossa very deep [27.3] (less so in other *Hemiechinus*); (3) ventral process of petrosal inflated [36.1]; (4) spineless tract on crown wide [79.2] (tract absent in other *Hemiechinus*).

CONTENT.—*Hemiechinus aethiopicus* (Ehrenberg, 1833, Dec 2, leaf k recto (footnote)); type locality: "In desertis dongolanis habitat." [approximately at 19°22'N, 30°45'E]. *Hemiechinus hypomelas* (Brandt, 1836:32); type locality: "pays des Turcomans" [the "country of the Turkmens" is roughly equivalent to the Turkmen, Uzbek, Kazak, and Karakalpak regions of the U.S.S.R.]. *Hemiechinus micropus* (Blyth in Hutton, 1846:170); type locality: "Bahawalpur" [= Bahawalpur, Pakistan, 29°23'N, 71°39'E]. *Hemiechinus nudiventris* (Horsfield, 1851:136); type locality: "Madras" ["Madras" could refer to the city at 13°05'N, 80°17'E or the older name for the Tamil Nadu province].

DISTRIBUTION.—Northern Africa, south to Mauritania and northern Somalia, and east throughout the Arabian Peninsula and Middle Asia to western and southern India.

DISCUSSION.—The subgenus *Paraechinus* shows considerably more size variation when compared to other *Hemiechinus* (Table 8). All species have a well-defined basisphenoid fossa and a greatly enlarged hypotympanic sinus. This sinus is extended into the alisphenoid and pterygoids such that they form a significant part of the anterior part of the sinus. Some characters that have been used to separate species (i.e., maxilla-nasal contact, palatine transverse torus straight or curved) we found too variable within taxa to be of diagnostic use. This subgenus also shows the greatest development of the auditory region of any insectivore. The hypotympanic chamber has expanded laterally, dorsally, and anteriorly to form an extremely large sinus. Within this group, *H. aethiopicus* and *H. micropus* show the most extreme development.

*Hemiechinus (Paraechinus) aethiopicus* (sensu lato) ranges throughout North Africa and eastward through Sinai and Arabia to Iraq, but only as far as the Tigris-Euphrates region. It is usually light in color, with light-tipped spines, a robust skull with broad maxilla, a relatively high, more dome-shaped braincase, very inflated auditory region, and large teeth (Table 6), but P3 is reduced to a single cusp, or absent. Osborn and Helmy (1980), following Setzer (1957), recognized within the former *H. (P.) aethiopicus* three species (*H. (P.) aethiopicus*, *H. (P.) deserti*, and *H. (P.) dorsalis*). These three putative species are mutually allopatric. In the absence of critical data from zones of potential contact between these taxa, and in the light of the considerable variation evident in some of the characters evinced by these taxa, we consider the three as subspecies of *H.*

*aethiopicus*.

*Hemiechinus a. deserti* is widespread in North Africa, from Mauritania and Morocco in the west to the Nile in the east. Osborn and Helmy (1980) distinguished it from others on the basis of its pale spine tips, lesser parapterygoid inflation, a small medial cusp on p4, straight postpalatal bridge, and the maxillae not contacting the nasals. While this diagnosis holds true of specimens from Egypt that we have examined, those from farther west in Libya (Hufnagel, 1972), Morocco, Niger, and Mauritania are more variable in color. A series of 22 from the western end of the taxon's distribution included 17 that were typically pale, but five possessed dark spines, including the tips. Moreover, the relationship of maxillae to nasals (Table 5), degree of parapterygoid inflation, and size of medial cusp on p4 are also individually variable in these western populations.

*Hemiechinus a. aethiopicus* occurs east of the Nile and south of the delta region in the Eastern Desert of Egypt, extending southward to northern Ethiopia and Somalia. Its westward extension in Sudan, and possible contact with *P. a. deserti*, which is known from Niger, is unknown. Osborn and Helmy (1980) believed it distinctive on the basis of its dark spine tips, relatively greater parapterygoid inflation, the absence of a medial cusp on p4, straight postpalatal bridge, and the maxillae contacting the nasals. In the specimens that we examined (Appendix 1), these characters seem to hold, except for the degree of inflation of the parapterygoids, which was variable, and not much different from the condition seen in *H. a. deserti*.

*Hemiechinus a. dorsalis* occurs from the Sinai on the west throughout the Arabian Peninsula, and north and eastward to the Tigris-Euphrates region of Iraq. Contact with *H. a. aethiopicus* is presumed to have been in the Suez region. Osborn and Helmy (1980) described it as the darkest of the three taxa, with dorsal spines entirely dark, relatively moderate parapterygoid inflation, the medial cusp on p4 vestigial, the maxillae contacting the nasals, and a slightly V-shaped postpalatal bridge. However, coloration is again quite variable, with some specimens being considerably lighter than usual (e.g., USNM 321572). We found the variation in the pterygoid inflation to be large (to be sure, correlated with the great amount of variation typical of this subgenus) and very subtle among the allopatric populations. There was considerable variation in the shape of the postpalatal bridge and nasal-maxilla contact (Table 5).

*Hemiechinus (Paraechinus) micropus* is found in the lower Indus Valley of Pakistan (Roberts, 1977) and adjacent India south to Gujarat. It is a small, pale-colored hedgehog with relatively short ears (Table 2), short light-tipped spines, and the "same mask pattern [that] occurs in *P. aethiopicus* ... and may be conspecific" (Roberts, 1977:20). The skull resembles that of *H. aethiopicus* in being robust with a relatively short rostrum, with broad maxillae, broad high braincase, and relatively large teeth (Table 6), but a reduced P3. Corbet (1988) distinguishes between *H. aethiopicus* and *H. micropus* on the relative inflation of the mastoid. We could discern no difference in the



relative inflation of the mastoid per se; however, the suprêmeatal fossa (with mastoid and squamosal components) is greatly inflated in these taxa, with *H. hypomelas* with the smallest and *H. aethiopicus* with the greatest. In *H. micropus* and *H. aethiopicus*, this cavity is further enlarged to extend posterodorsal to the glenoid fossa. *Hemiechinus (P.) micropus* probably represents a peripheral isolate of *H. (P.) aethiopicus*, whose ranges are now separated by a gap occupied by *H. (P.) hypomelas* and *H. auritus*.

Biswas and Ghose (1970) proposed that specimens from Rajasthan, Madhya Pradesh, and Gujarat represent a second species, *H. intermedius*, which is, in part, sympatric with *H. micropus*. They distinguished *H. intermedius* on the basis of smaller size and different color pattern, especially on the face. However, facial pattern is variable (Roberts, 1977) and the sample of cranial measurements is small (N=4); we have not examined this form, and provisionally consider it a synonym of *H. micropus*, as did Corbet (1988).

Neither have we examined specimens of *H. (P.) nudiventris*, which Biswas and Ghose (1970) also considered a distinct species (but which Corbet, 1978, 1988, considered to be a subspecies of *H. (P.) micropus*). It is an isolated population, restricted to the states of Madras (= Tamil Nadu) and Travancore (= Kerala) in southeastern India. This taxon differs from *H. (P.) micropus* in possessing a narrower cranium, incomplete zygomatic arch, and vestigial P3 (which Biswas and Ghose referred to as P2) in the two skulls that they examined. It also differs in size and shape of ear, tail length, and sole of the forefoot. The vestigial P3 is clearly a derived condition. As described by Biswas and Ghose (1970) the incomplete zygomatic arch is the result of the absence of the "malar" (= jugal) bone, and separation of the zygomatic processes of the maxilla and squamosal. This condition, if not an artifact of preparation, is unique to the family, and clearly an autapomorphy; *H. (P.) nudiventris* is therefore provisionally considered a distinct species, possibly derived from or allied with *H. (P.) micropus*.

*Hemiechinus (Paraechinus) hypomelas* is found from the Transcaspian and Aral regions southward through Iran and eastward to the Indus River in Pakistan. It is also reported from the Punjab in northwestern India (Roberts, 1977; Corbet, 1978). It is the only species of hedgehog that exhibits color dimorphism. Most populations are dark with dark-tipped spines, but populations containing nearly white individuals occur in the northern and central part of its range. The skull is relatively light, with narrow maxilla and a flat braincase, and small teeth, but the P3 has three distinct cusps. In Pakistan, two populations of dark-colored *H. (P.) hypomelas* occur that differ greatly in size. *Hemiechinus h. hypomelas* is large and found in the foothills of western Pakistan, whereas *H. h. blanfordi* (= *jerdoni*, see below) is small with relatively small ears (Tables 4 and 8), and short spines (Roberts, 1977), and is found in the Indus Valley. The ranges of size overlap only slightly (Table 8). Thus, these taxa parallel in size and distribution *Hemiechinus*

*auritus megalotis* and *H. collaris* occurring in the same geographic area (see above). As in that case, no zone of potential contact is known.

G.B. Corbet (in litt.) has informed us that *H. h. blanfordi* Anderson (1878) "is a *Hemiechinus collaris* as is clear from the original description and as pointed out by Agrawal (1973)..." Thus, the name *jerdoni* Anderson (1878) must be employed instead for the small dark subspecies of *H. (P.) hypomelas* that inhabits the Indus Valley. Externally, *H. (P.) hypomelas jerdoni* and *H. collaris* are very similar, and in the zone of sympatry may be difficult to distinguish. Nevertheless, *H. (P.) hypomelas* possesses a well-defined medial spineless tract on the crown, rugose rather than smooth spines, and a reduced hallux, all characters that are not present in *H. collaris*.

### Genus *Mesechinus* Ognev, 1951

*Mesechinus* Ognev, 1951:8. [Type species: *Erinaceus dauuricus* Sundevall, 1842:237.]

DIAGNOSIS.—(1) rostrum broad, anterior incisors not closely approximating [3.0]; (2) lacrimal/maxilla suture not fused in young adults [12.0]; (3) posterior palatal shelf with a well-developed spine [22.0]; (4) suprêmeatal fossa entirely in squamosal [26.0]; (5) suprêmeatal fossa shallow [27.1]; (6) anterior and posterior borders of suprêmeatal fossa narrowly separated [28.1]; (7) parietals relatively higher than frontals [29.0]; (8) basisphenoid not inflated [31.0]; (9) squamosal forming a major part of bullar roof [33.1]; (10) I3 with 2 separate roots [49.1]; (11) P2 with 1 or 2 roots fused [56.1]; (12) ears short [75.0]; (13) hallux reduced [76.1]; (14) pelage spines papillate, not grooved [77.2]; (15) ventral pelage coarse [80.1].

CONTENT.—*Mesechinus dauuricus* (Sundevall, 1842:237); type locality: "Dauuria" [U.S.S.R., Transbaikalia, Dauria, 49°57'N, 116°55'E]. *Mesechinus hughi* (Thomas, 1909:966); type locality: "Paochi, Shen-si" [= Baoji, Shaanxi Sheng, China, 34°23'N, 107°09'E].

DISTRIBUTION.—Northeastern and central Mongolia and limited adjacent areas in China and the U.S.S.R. (*M. dauuricus*); in Shanxi and Shaanxi of north central China (*M. hughi*).

DISCUSSION.—Bobrinskii et al. (1965) considered *M. dauuricus* to be a subspecies of *Erinaceus europaeus*, although most authors had placed it in the genus *Hemiechinus* (Stroganov, 1957; Corbet, 1978). Subsequently, Zaitsev (1982) and Pavlinov and Rossolimo (1987) employed the subgenus *Mesechinus* Ognev, 1951, within *Erinaceus*, for this species.

South and west of the range of *M. dauuricus*, in central China (Shanxi and Shaanxi), another hedgehog occurs, originally named *Erinaceus hughi* (Thomas, 1909). Corbet (1978) reallocated it to *Hemiechinus*, and later (1984) elevated it to full species status and also included *Hemiechinus sylvaticus* (Ma, 1964) as a junior synonym. The holotype of *hughi* is a skin only, and the taxon is apparently known from only two

localities. We have examined the holotypes of both named forms, and concur with Corbet (1978) that *hughi* (including *sylvaticus*) probably represents a distinct species. It shares with *M. dauuricus* absence of a median spineless tract, a possible synapomorphy with *Hemiechinus* (not including *Paraechinus*), or (following Corbet, 1988) a character plesiomorphic for erinaceines.

The form *miodon* of northern Shaanxi has been assigned in the past to *M. dauuricus* but is separated from Mongolian populations of *M. dauuricus* by nearly 1600 km of apparently unsuitable semidesert and desert. It is much closer geographically to *M. hughi*, and its relationships should be re-examined.

*Mesechinus* is distinctive in many features, most notably the unique shape of the suprimeatal fossa. Whereas in most erinaceines, the lateral borders of this fossa are somewhat C-shaped, in *Mesechinus*, the anterior and posterior rim are nearly parallel, giving the fossa a more angular or U-shaped appearance. The basisphenoid inflation is intermediate between the condition more typical of *Hemiechinus* and that found in *Aterix* and *Erinaceus* (Figure 4). The development of the lingual lobe on P3 was individually variable among the specimens we examined.

#### Genus *Erinaceus* Linnaeus, 1758

*Erinaceus* Linnaeus, 1758:52. [Type species: *Erinaceus europaeus* Linnaeus, 1758.]

DIAGNOSIS.—(1) rostrum broad, anterior incisors not closely approximating [3.0]; (2) lacrimal/maxilla suture fused and indistinct in young adults [12.1]; (3) posterior palatal shelf with a well-developed spine [22.0]; (4) suprimeatal fossa entirely in squamosal [26.0]; (5) suprimeatal fossa shallow [27.1]; (6) anterior and posterior borders of suprimeatal fossa widely separated [28.0]; (7) frontals relatively higher than parietals [29.1]; (8) basisphenoid not inflated [31.0]; (9) squamosal not participating in bullar roof [33.0]; (10) I2 with 2 roots fused [49.2]; (11) P2 with 1 root or 2 roots fused [56.1]; (12) ears short [75.0]; (13) hallux normal [76.0]; (14) pelage spines smooth [77.1]; (15) ventral pelage coarse [80.0].

CONTENT.—*Erinaceus europaeus* Linnaeus, 1758:52; type locality: "Europa." *Erinaceus concolor* Martin, 1838:103; type locality: "apud Trebizond" [= Trabzon, Turkey, 40°00'N, 39°43'E]. *Erinaceus amurensis* Schrenk, 1859:100; type locality: "In der Nähe der Stadt Aigun, im mandshurischen Dorfe Gulssoja am Amur . . ."

DISTRIBUTION.—Throughout the western Palearctic, from Ireland and Spain to Turkey, the western shore of the Caspian Sea, and central Siberia (80° E long.) (*E. europaeus*, *E. concolor*). A separate area is occupied by *E. amurensis* in the Korean peninsula and adjacent Manchuria, and from the vicinity of Beijing south to the Yangtze River valley, and westward to the vicinity of western Hubei province. The status of specimens reported from farther west is unclear (see Corbet, 1988).

DISCUSSION.—Most authors now agree that two sibling species of hedgehogs occur in Europe, the western and northern *E. europaeus* and the eastern and southern *E. concolor* (Corbet, 1984, 1988). Their distribution is parapatric to narrowly sympatric in Poland, Czechoslovakia, and Austria (Ruprecht, 1973; Kratochvil, 1975; Puček and Raczynski, 1983; Corbet, 1988) and perhaps elsewhere, where they are distinguishable on the basis of ventral coloration, and maxillary and mandibular structure (Puček, 1981; Zaitsev, 1984; Corbet, 1988). Corbet (1988) separated *E. concolor* and *E. europaeus* on two features of the rostrum, both involving the posterior extension of the maxilla. Although there appears to be a general trend to support *E. concolor* having a longer naso/maxilla suture than *E. europaeus*, we found this feature variable (Table 5). However, we found no exceptions to Corbet's notice of the maxilla extending farther posterior in *E. concolor* than in *E. europaeus*.

In the Far East, other populations of *Erinaceus* exist widely disjunct from the two European species, ranging from the Amur River drainage of southern Siberia on the north, south throughout the Korean Peninsula and Manchuria, to the northeastern provinces of China. These were allocated to *E. europaeus* in the past, before *E. concolor* was recognized as distinct. More recently, Far Eastern hedgehogs have been elevated to specific status as *E. amurensis* (Corbet, 1984; Zaitsev, 1984), including the possibly allopatric southern populations (*E. dealbatus*). In *E. amurensis* and *E. concolor* the maxilla/premaxilla suture is nearly perpendicular to the nasals, whereas in *E. europaeus*, the sutures meet at an acute angle. Additionally, *E. amurensis* shares with *E. concolor* the tendency for the posterior extension of the maxilla beyond the lacrimal foramen (Puček, 1981; Zaitsev, 1984). Whether these features are due to synapomorphy or homoplasy, we do not know, although Corbet (1988) interpreted these as synapomorphies. The Far Eastern species also differs from the two European taxa in having a shorter ear, both absolutely and relatively (Table 4), a V-shaped basisphenoid fossa (Corbet, 1988), and a consistently light venter, and the face is also usually light, though these last two characters show some variation. All three species possess a dark snout.

#### Genus *Aterix* Pomel, 1848

*Aterix* Pomel, 1848:251. [Type species: *Erinaceus albiventris* Wagner, 1841, by subsequent designation of Thomas (1918).]

*Peroechinus* Fitzinger, 1866:565. [Type species: *Erinaceus pruneri* Wagner, 1841 (= *Aterix albiventris*).]

*Aethechinus* Thomas, 1918:194. [Type species: *Erinaceus algirus* Lereboullet in Duvernoy and Lereboullet, 1842.]

DIAGNOSIS.—(1) rostrum broad, anterior incisors not closely approximating [3.0]; (2) lacrimal/maxilla suture fused and indistinct in young adults [12.1]; (3) posterior palatal shelf without a well-developed spine [22.1]; (4) suprimeatal fossa with mastoid contribution greater than or subequal to squamo-

sal contribution [26.1]; (5) suprameatal fossa shallow [27.1]; (6) anterior and posterior borders of suprimeatal fossa widely separated [28.0]; (7) frontals relatively higher than parietals [29.1]; (8) basisphenoid not inflated [31.0]; (9) squamosal not participating in bullar roof [33.0]; (10) I3 with 2 roots separate [49.1]; (11) P2 with 2 roots [56.0]; (12) ears short [75.0]; (13) hallux reduced or absent [76.1]; (14) pelage spines smooth [77.1]; (15) ventral pelage coarse [80.1].

CONTENT.—*Atelerix albiventris* (Wagner, 1841:22); type locality: unknown; Wagner stated that the holotype arrived with a shipment of specimens from India. Anderson and de Winton (1902) believed it to be from "Senegambia." *Atelerix algirus* (Lereboullet in Duvernoy and Lereboullet, 1842:4); type locality: "provient d'Oran" [Algeria, currently the province Wilaya d'Oran]. *Atelerix frontalis* (Smith, 1831); type locality: "Cape" [Province, South Africa]. *Atelerix sclateri* (Anderson, 1895:415); type locality: "Taf in Central Somaliland."

DISTRIBUTION.—Northwestern Africa to eastern Libya; Senegal to Somalia; southern Angola and Zimbabwe south to South Africa; in East Africa south to Malawi. Also on Canary and certain Mediterranean islands and Mediterranean coast of Spain and France, where probably introduced.

DISCUSSION.—*Aethechinus* has usually been considered a synonym of *Erinaceus* (Corbet, 1978, 1984; Smithers, 1983), but recently Robbins and Setzer (1985) advanced arguments supporting its distinctness and included two species: *Aethechinus algirus* from northern Morocco to Libya and (probably introduced) southern Spain and France as well as the Balearic and Canary Islands and Malta; and *A. frontalis*, from southern Africa. Robbins and Setzer (1985) concluded, on the basis of a morphometric analysis, that *A. frontalis* and *A. algirus* were closest to *Erinaceus*, while *Atelerix albiventris* was closest to *Paraechinus* and *Hemiechinus*; they recommended that *Aethechinus* and *Atelerix* be recognized as separate genera. As previously noted, our phylogenetic analysis did not produce results concordant with their phenetic analysis. The phenetic similarity exhibited by *Erinaceus* and *Aethechinus* (sensu Robbins and Setzer) appears to be due to similarity in size; as they noted, *Erinaceus* spp., *Aethechinus frontalis*, and *Aethechinus algirus* are larger, while *Atelerix albiventris* is the smallest species of spiny hedgehog. Corbet (1988) supplied a third alternative, placing *A. algirus* and *A. frontalis* within *Atelerix*, along with *A. albiventris* and *A. sclateri*.

Gropp and Natarajan (1972:267) found that *A. algirus* shared with *Erinaceus* the presence of "sizable blocks of distally located heterochromatin," two in the former and three in the latter, which are not present in *Hemiechinus* (species not noted). They interpreted this as indicating close relationship between *A. algirus* and *Erinaceus*. Unfortunately, they did not study *A. albiventris*.

The widespread African hedgehog *Atelerix albiventris* occurs south of the Sahara and north of the forest zone from Senegal eastward to Somalia, and southward in East Africa to Tanzania (Corbet, 1974), Malawi, and to the Zambezi River (central Mozambique) (Corbet, 1988). Its distribution is allopatric with the other species of African hedgehogs, except for a narrow zone of potential contact in Sudan and perhaps Ethiopia. However, the poorly known taxon *A. sclateri* occurs in northern Somalia, and may be parapatric or sympatric with *A. albiventris*. In this study, we were only able to examine one young adult male and, therefore, could not take into account interspecific variation. The characters of *A. sclateri* include the primitive well-developed (though small) hallux (Corbet, 1974, 1988) (also in *A. algirus* and *A. frontalis*) and the derived reduced P3 (also in *A. albiventris*). The shape of the parietal/occipital suture (Corbet, 1974) is too variable in other taxa to be of diagnostic use. The relationship of nasal to maxilla (Corbet, 1974) was individually variable in most specimens of erinaceines examined (Table 5); however, as pointed out by Corbet (1988), our specimen of *A. sclateri* did not have a maxilla-nasal contact. Our specimen of *A. sclateri* differed from other *Atelerix* in other features as well. P3 in *A. sclateri* is an extremely small, peg-like tooth, and is considerably less than one-half the size of P2. In *A. frontalis*, although P3 is reduced, it is closer in size to P2. *Atelerix sclateri* also has a uniquely shaped nasal. As a reflection of the posterior growth of the rostral process of the premaxilla, the nasals are widest posteriorly at the point that the premaxilla and frontals meet. In other *Atelerix* the nasals are nearly parallel sided.

Ventral coloration is dark in *A. frontalis*, light in *A. albiventris*, and variable in *A. algirus* and *A. sclateri*; dark ventral pelage is probably primitive, because it is found widely in other hedgehog genera. The few available specimens of *A. sclateri* (Corbet, 1974, 1988; Kingdon, 1974) suggest that it is the sister taxon of *A. albiventris*, which retains a few plesiomorphies. Additional specimens may show, however, that it intergrades with typical *A. albiventris* in southern Somalia and northern Kenya.

As in the *A. albiventris*-*A. sclateri* clade, *A. frontalis* can be separated from *A. algirus* on the relative sizes of P2 and P3 and the morphology of m3. P2 in *A. frontalis* is a robust tooth, being larger than either adjacent tooth, whereas in *A. algirus*, P2 is somewhat smaller and similar in morphology to C1. Although P3 is reduced, in both species there is a well-developed lingual lobe.

Corbet (1988) distinguished among *Atelerix* on the basis of the naso/maxilla suture. We found the individual variation to mask his implied morphological gaps (Table 5). However, we found no exceptions to his characterization of *A. frontalis* as having a long common suture and *A. sclateri* with no common suture.

# Appendix 1

## List of Specimens Examined

AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences of Philadelphia; BEIJ = Beijing, Institute of Zoology; BMNH = British Museum (Natural History); DMNH = Delaware Museum of Natural History; FMNH = Field Museum of Natural History; HMCZ = Harvard University, Museum of Comparative Zoology; KU = University of Kansas, Museum of Natural History; MGU = Moscow State University, Zoological Museum; UPLB = University of the Philippines at Los Baños, Museum of Natural History; USNM = former collections of the United States National Museum, now deposited at the National Museum of Natural History, Smithsonian Institution. Arranged alphabetically by taxon and locality, and grouped by sex within each locality.

### *Atelerix albiventris*

USNM	421118	?	Benin: Borgou Region
USNM	421120	?	Benin: Borgou Region
USNM	421136	♀	Benin: Borgou Region
USNM	421138	♀	Benin: Borgou Region
USNM	421127	♂	Benin: Borgou Region
USNM	421132	♂	Benin: Borgou Region
USNM	439833	♂	Ghana: Eastern Region
USNM	424630	♀	Ghana: Northern Region
USNM	439834	♀	Ghana: Northern Region
USNM	424631	♂	Ghana: Northern Region
USNM	a470571	♂	Ghana: Northern Region
USNM	161699	♂	Kenya: Kapita Plains
USNM	181442	♀	Kenya: Lime Springs
KU	41112	?	Kenya: Nairobi Area
USNM	164022	♂	Kenya: Ulucania Hills
USNM	402202	♀	Nigeria: Northern Region
USNM	402203	♀	Nigeria: Northern Region
USNM	483167	♂	Nigeria

### *Atelerix algirus*

USNM	302065	♀	Libya: Bin Jawwad, Baladiyat
USNM	476060	♂	Morocco: Agadir, Province d'
USNM	476058	♂	Morocco: Agadir, Province d'
USNM	476055	♂	Morocco: Fes, Province de
USNM	476052	♀	Morocco: Ksar-es-souk, Province de
USNM	476053	♀	Morocco: Ksar-es-souk, Province de
USNM	470573	♂	Morocco: Ouarzazate, Province d'
USNM	470572	♀	Morocco: Ouarzazate, Province d'
USNM	470574	♂	Morocco: Ouarzazate, Province d'
USNM	470575	♂	Morocco: Ouarzazate, Province d'
USNM	b470571	♀	Morocco: Ouarzazate, Province d'
USNM	476050	♀	Morocco: Oujda, Province d'
USNM	476057	♂	Morocco: Oujda, Province d'
USNM	476062	♀	Morocco: Tetouan, Province de

### *Atelerix frontalis*

USNM	260742	♂	Botswana: Gaborones
USNM	380487	♂	South Africa: Orange Free State
USNM	468211	♀	South Africa: Transvaal
USNM	267653	♂	South Africa: Transvaal

### *Atelerix sclateri*

USNM	63220	♂	Somalia: Woqooyi Galbeed, Gobolka
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### *Echinosorex gymnura*

USNM	145585	?	Indonesia: Kalimantan
KU	92668	?	Malaysia: Sabah
KU	92669	♂	Malaysia: Sabah
USNM	145584	♂	Malaysia: Sabah
USNM	487887	?	Malaysia: West
USNM	357885	♀	Malaysia: West
USNM	357887	♀	Malaysia: West
USNM	487886	♀	Malaysia: West
USNM	487889	♀	Malaysia: West
USNM	487892	♀	Malaysia: West
USNM	487898	♀	Malaysia: West
USNM	487899	♀	Malaysia: West
USNM	487900	♀	Malaysia: West
USNM	487902	♀	Malaysia: West
USNM	487903	♀	Malaysia: West
USNM	487894	♂	Malaysia: West
USNM	487897	♂	Malaysia: West
USNM	487901	♂	Malaysia: West
USNM	83499	?	Thailand: Trang, Changwat
USNM	86785	?	Thailand: Trang, Changwat

### *Erinaceus amurensis*

AMNH	57219	♂	China: Anhui Sheng
BEIJ	60000	♀	China: Beijing Shi
BMNH	61.6.2.5	?	China: Beijing Shi
BEIJ	15856	♀	China: Jilin Sheng Dixing

BEIJ	12741	♀	China: Jilin Sheng Dixing (?)	<i>Erinaceus concolor</i>		
BEIJ	09341	♂	China: Jilin Sheng Dixing	FMNH	96338	♀ Iran: Azarbaijan-e Gharbi, Ostan-e
AMNH	56095	♂	China: Hebei Sheng	FMNH	96339	♀ Iran: Azarbaijan-e Gharbi, Ostan-e
USNM	176251	♂	China: Hebei Sheng	FMNH	96340	♀ Iran: Azarbaijan-e Gharbi, Ostan-e
USNM	199681	♂	China: Hebei Sheng	FMNH	96341	♀ Iran: Azarbaijan-e Gharbi, Ostan-e
BEIJ	13305	♀	China: Heilongjiang Sheng Dixing	FMNH	96344	♀ Iran: Azarbaijan-e Gharbi, Ostan-e
USNM	270542	♀	China: Heilongjiang Sheng Dixing	FMNH	96345	♀ Iran: Azarbaijan-e Gharbi, Ostan-e
BEIJ	15854	♂	China: Henan Sheng Dixing	FMNH	110955	♂ Iran: Azarbaijan-e Gharbi, Ostan-e
HMCZ	7132	♂	China: Hubei Sheng	FMNH	92893	♂ Iran: Kerman, Ostan-e
AMNH	57218	♀	China: Hunan Sheng	FMNH	92894	♂ Iran: Kerman, Ostan-e
USNM	239591	♀	China: Hunan Sheng	USNM	369533	♂ Iran: Khuzestan, Ostan-e
USNM	239592	♀	China: Hunan Sheng	FMNH	84448	♂ Iraq
USNM	239590	♂	China: Hunan Sheng	USNM	37464	? Lebanon
ANSP	20447	♀	China: Jiangsu Sheng	FMNH	94242	♂ Lebanon
ANSP	20446	♂	China: Jiangsu Sheng	FMNH	94244	♂ Lebanon
USNM	174605	?	China: Jiangsu Sheng	HMCZ	8593	? Palestine
USNM	240325	?	China: Jiangsu Sheng	HMCZ	12436	? Palestine
USNM	252158	?	China: Jiangsu Sheng	HMCZ	12602	? Palestine
BMNH	10.5.1.2	♀	China: Jilin Sheng	HMCZ	12603	? Palestine
USNM	197779	♀	China: Jilin Sheng	HMCZ	17333	? Palestine
USNM	270541	♂	China: Liaoning Sheng	HMCZ	17331	? Palestine
ANSP	16684	♀	China: Shandong Sheng	HMCZ	17332	? Palestine
BMNH	8.2.8.2	♀	China: Shandong Sheng	HMCZ	17334	? Palestine
BEIJ	05120	♀	China: Shandong Sheng	FMNH	74343	♀ Turkey: Ankara
BEIJ	05122	♀	China: Shandong Sheng	FMNH	83350	♀ Turkey: Ankara
BEIJ	05123	♀	China: Shandong Sheng	FMNH	82113	♀ Turkey: Bitlis
BEIJ	05124	♀	China: Shandong Sheng	FMNH	82121	♀ Turkey: Bitlis
ANSP	16679	♂	China: Shandong Sheng	FMNH	82122	♂ Turkey: Bitlis
ANSP	16680	♂	China: Shandong Sheng	FMNH	82124	♂ Turkey: Bitlis
ANSP	16681	♂	China: Shandong Sheng	FMNH	82127	♂ Turkey: Bitlis
ANSP	16682	♂	China: Shandong Sheng	FMNH	82110	♀ Turkey: Elazig Ili
BMNH	8.2.8.1	♂	China: Shandong Sheng	FMNH	82109	♂ Turkey: Elazig Ili
BEIJ	05121	♂	China: Shandong Sheng	FMNH	82111	♂ Turkey: Elazig Ili
BEIJ	05125	♂	China: Shandong Sheng	FMNH	82112	♂ Turkey: Elazig Ili
ANSP	16683	?	China: Shandong Sheng	HMCZ	51529	♂ Turkey: Elazig Ili
BMNH	74.1.24.23	?	China: Shandong Sheng	FMNH	74338	♀ Turkey: Hatay Ili
HMCZ	25884	?	China: Shandong Sheng	FMNH	74341	♀ Turkey: Hatay Ili
HMCZ	25885	?	China: Shandong Sheng	FMNH	74340	♂ Turkey: Hatay Ili
BEIJ	0001	♀	China: Shanghai Shi	FMNH	74342	♂ Turkey: Hatay Ili
BEIJ	356	♀	China: Shanghai Shi	FMNH	82115	♂ Turkey: Hatay Ili
BEIJ	0002	♂	China: Shanghai Shi	USNM	327188	♂ Turkey: Icel
BEIJ	354	♂	China: Shanghai Shi	USNM	327187	♀ Turkey: Istanbul, Ili
USNM	239770	?	China: Zhejiang Sheng	USNM	327190	♂ Turkey: Istanbul, Ili
BMNH	22.10.6.2	?	Korea	USNM	327189	♀ Turkey: Kayseri
HMCZ	37692	?	Korea	FMNH	82126	♂ Turkey: Urfa
USNM	302902	?	Korea			
USNM	302903	?	Korea			
FMNH	48372	♀	Korea	<i>Erinaceus europaeus</i>		
HMCZ	37691	♀	Korea	USNM	174830	♂ Denmark
BMNH	22.10.6.1	♂	Korea	USNM	174831	♂ Denmark
FMNH	48371	♂	Korea	USNM	251763	? Germany
HMCZ	37690	♂	Korea	USNM	112336	♀ Germany
AMNH	18355	♀	U.S.S.R.: R.S.F.S.R., Primorsk. krai	USNM	112338	♂ Germany
BMNH	1938.3.30.6	♀	U.S.S.R.: R.S.F.S.R., Primorsk. krai	USNM	153413	♂ Italy: Roma, Provincia di
HMCZ	24731	♂	U.S.S.R.: R.S.F.S.R., Primorsk. krai	USNM	154161	? Spain: Burgos, Provincia de
				USNM	154162	♀ Spain: Burgos, Provincia de



USNM	153417	♂	Spain: Burgos, Provincia de
KU	11420	?	Spain: Madrid, Provincia de
USNM	153414	♀	Spain: Oviedo, Provincia de
USNM	153415	♂	Spain: Oviedo, Provincia de
USNM	186554	♀	Sweden: "Uppsala"
USNM	186555	♀	Sweden: "Uppsala"
USNM	85086	♀	Sweden: "Uppsala"
USNM	85090	♀	Sweden: "Uppsala"
USNM	85092	♂	Sweden: "Uppsala"
USNM	847740	♂	Switzerland: Appenfell, Canton
USNM	115198	♀	Switzerland: Saint Gallen, Canton
USNM	105881	?	Switzerland: Saint Gallen, Canton
USNM	84739	?	Switzerland: Saint Gallen, Canton
USNM	115196	?	Switzerland: Saint Gallen, Canton
USNM	115197	?	Switzerland: Saint Gallen, Canton
USNM	115199	♀	Switzerland: Tessin (Ticino), Canton
USNM	795	?	United Kingdom: England
USNM	153410	♂	United Kingdom: England
USNM	174660	♂	United Kingdom: England
USNM	153409	♂	United Kingdom: Wales
USNM	251643	?	Unknown
HMCZ	51529	♂	Turkey

*Hemiechinus aethiopicus*

USNM	311732	♂	Egypt
USNM	311737	?	Egypt: Sahra' al Gharbiyah, Muhafazat
USNM	311738	?	Egypt: Sahra' al Gharbiyah, Muhafazat
USNM	311731	♂	Egypt: Sharqiyah, as Sahra' ash
USNM	325906	♀	Egypt: Sina, Muhafazat
USNM	325908	♀	Egypt: Sina, Muhafazat
USNM	311739	♀	Egypt: Sina, Muhafazat
USNM	325907	♂	Egypt: Sina, Muhafazat
USNM	311740	♂	Egypt: Sina, Muhafazat
FMNH	123048	♂	Egypt: Sina, Muhafazat
BMNH	21.12.3.1	♀	Iran: Tanb Island
USNM	384832	♂	Mauritania: Adrar, Cercle de l'
USNM	410873	?	Mauritania: Assaba, Cercle de l'
USNM	410873	♀	Mauritania: Assaba, Cercle de l'
USNM	410872	♂	Mauritania: Assaba, Cercle de l'
USNM	470569	♀	Morocco: Ouarzazate, Province de
USNM	470566	♂	Morocco: Ouarzazate, Province de
USNM	470567	♂	Morocco: Ouarzazate, Province de
USNM	470568	♂	Morocco: Ouarzazate, Province de
USNM	482512	♂	Niger
BMNH	52.1468	♀	Oman
AMNH	166942	?	Saudi Arabia
BMNH	1934.8.4.4	?	Saudi Arabia
BMNH	48.378	♀	Saudi Arabia: Jawf, Mintaqat al
BMNH	10.6.30.3	?	Yemen (Aden)
BMNH	10.6.30.4	♀	Yemen (Aden)
BMNH	10.6.30.5	♀	Yemen (Aden)
USNM	321572	♀	Yemen (Aden)
BMNH	54.1020	♂	Yemen (Aden)
BMNH	10.6.30.1	♂	Yemen (Aden)
BMNH	10.6.30.2	♂	Yemen (Aden)

*Hemiechinus auritus*

BMNH	86.10.15.6	♀	Afghanistan: Badghis, Velayat-e
FMNH	102001	♀	Afghanistan: Baghlan, Velayat-e
FMNH	102008	♀	Afghanistan: Baghlan, Velayat-e
FMNH	102011	♀	Afghanistan: Baghlan, Velayat-e
FMNH	102012	♀	Afghanistan: Baghlan, Velayat-e
FMNH	102013	♀	Afghanistan: Baghlan, Velayat-e
FMNH	48483	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102003	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102004	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102005	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102007	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102009	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102014	♂	Afghanistan: Baghlan, Velayat-e
FMNH	102015	♀	Afghanistan: Faryab, Velayat-e
FMNH	102016	♂	Afghanistan: Faryab, Velayat-e
FMNH	102017	♀	Afghanistan: Herat, Velayat-e
FMNH	102021	♀	Afghanistan: Herat, Velayat-e
FMNH	102020	♂	Afghanistan: Herat, Velayat-e
BMNH	47.360	♀	Afghanistan: Kabul, Velayat-e
FMNH	102022	♀	Afghanistan: Kabul, Velayat-e
FMNH	102026	♀	Afghanistan: Kabul, Velayat-e
FMNH	102027	♀	Afghanistan: Kabul, Velayat-e
FMNH	102029	♀	Afghanistan: Kabul, Velayat-e
BMNH	47.359	♂	Afghanistan: Kabul, Velayat-e
FMNH	102023	♂	Afghanistan: Kabul, Velayat-e
FMNH	102024	♂	Afghanistan: Kabul, Velayat-e
FMNH	102025	♂	Afghanistan: Kabul, Velayat-e
FMNH	102028	♂	Afghanistan: Kabul, Velayat-e
BMNH	81.8.16.2	?	Afghanistan: Qandahar, Velayat-e
BMNH	79.11.21.515	?	Afghanistan: Qandahar, Velayat-e
BMNH	79.11.21.516	?	Afghanistan: Qandahar, Velayat-e
FMNH	102030	♀	Afghanistan: Qandahar, Velayat-e
FMNH	102036	♀	Afghanistan: Qandahar, Velayat-e
FMNH	102037	♀	Afghanistan: Qandahar, Velayat-e
FMNH	102031	♂	Afghanistan: Qandahar, Velayat-e
FMNH	102032	♂	Afghanistan: Qandahar, Velayat-e
FMNH	102033	♂	Afghanistan: Qandahar, Velayat-e
FMNH	102034	♂	Afghanistan: Qandahar, Velayat-e
FMNH	102035	♂	Afghanistan: Qandahar, Velayat-e
BMNH	69.8.24.2	♀	Afghanistan: "Beloschittan"
USNM	240761	♀	China: Gansu Sheng
USNM	240758	♂	China: Gansu Sheng
USNM	240759	♂	China: Gansu Sheng
USNM	240760	♂	China: Gansu Sheng
BEIJ	24796	♀	China: Nei Monggol Zizhiqu Dixing
BEIJ	18327	♂	China: Nei Monggol Zizhiqu Dixing
BEIJ	18332	♂	China: Nei Monggol Zizhiqu Dixing
BEIJ	21918	♂	China: Nei Monggol Zizhiqu Dixing
BMNH	75.3.30.5	♀	China: Xinjiang Uygur Zizhiqu Dixing
USNM	62181	♀	China: Xinjiang Uygur Zizhiqu Dixing
USNM	62184	♀	China: Xinjiang Uygur Zizhiqu Dixing
BEIJ	24795	♀	China: Xinjiang Uygur Zizhiqu Dixing
BEIJ	10659	♀	China: Xinjiang Uygur Zizhiqu Dixing

BEIJ	10662	♀	China: Xinjiang Uygur Zizhiq Dixing	USNM	326693	♀	Iran: Khorasan, Ostan-e
BEIJ	13610	♀	China: Xinjiang Uygur Zizhiq Dixing	USNM	326694	♀	Iran: Khorasan, Ostan-e
BEIJ	13611	♀	China: Xinjiang Uygur Zizhiq Dixing	USNM	326703	♀	Iran: Khorasan, Ostan-e
BEIJ	13612	♀	China: Xinjiang Uygur Zizhiq Dixing	USNM	326705	♀	Iran: Khorasan, Ostan-e
BEIJ	21236	♀	China: Xinjiang Uygur Zizhiq Dixing	USNM	327911	♀	Iran: Khorasan, Ostan-e
BEIJ	13608	♂	China: Xinjiang Uygur Zizhiq Dixing	FMNH	96348	♂	Iran: Khorasan, Ostan-e
BEIJ	24794	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326675	♂	Iran: Khorasan, Ostan-e
BEIJ	23269	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326676	♂	Iran: Khorasan, Ostan-e
BEIJ	13604	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326677	♂	Iran: Khorasan, Ostan-e
BEIJ	19275	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326678	♂	Iran: Khorasan, Ostan-e
BEIJ	21237	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326679	♂	Iran: Khorasan, Ostan-e
BEIJ	21753	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326680	♂	Iran: Khorasan, Ostan-e
BEIJ	13295	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326681	♂	Iran: Khorasan, Ostan-e
BEIJ	13603	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326682	♂	Iran: Khorasan, Ostan-e
BEIJ	13607	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326688	♂	Iran: Khorasan, Ostan-e
BEIJ	21238	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	326692	♂	Iran: Khorasan, Ostan-e
BMNH	89.6.8.1	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	327912	♂	Iran: Khorasan, Ostan-e
USNM	62182	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	350115	♀	Iran: Khuzestan
USNM	62183	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	340934	♀	Iran: Mazanderan, Ostan-e
USNM	62185	♂	China: Xinjiang Uygur Zizhiq Dixing	USNM	340936	♂	Iran: Mazanderan, Ostan-e
BEIJ	25722	?	China: Xinjiang Uygur Zizhiq Dixing	USNM	340938	♂	Iran: Mazanderan, Ostan-e
BEIJ	25721	?	China: Xinjiang Uygur Zizhiq Dixing	USNM	340933	♂	Iran: Mazanderan, Ostan-e
AMNH	31246	?	China: Xinjiang Uygur Zizhiq Dixing	USNM	340933	♂	Iran: Mazanderan, Ostan-e
BMNH	66.675	?	China: Xinjiang Uygur Zizhiq Dixing	AMNH	184605	?	Israel
BMNH	75.3.30.4	?	China: Xinjiang Uygur Zizhiq Dixing	AMNH	57221	♀	Mongolia: Hovd Aymag
USNM	311692	♂	Egypt: Jizah, Mudiriyat al	AMNH	57216	♂	Mongolia: Hovd Aymag
USNM	311730	♀	Egypt: Kaf ash Shaykh, Mudiriyat	AMNH	57217	♂	Mongolia: Hovd Aymag
USNM	311706	♀	Egypt: Sahra al Gharbiyah, Muhafazat	AMNH	57222	♂	Mongolia: Hovd Aymag
USNM	311710	♂	Egypt: Sahra al Gharbiyah, Muhafazat	HMCZ	20683	♂	Mongolia: Hovd Aymag
USNM	311729	♀	Egypt: Sharqiyah, Mudiriyat ash	AMNH	34001	♂	Mongolia: Ovorhangay Aymag
FMNH	96350	♀	Iran: Kerman, Ostan-e	AMNH	217232	?	Pakistan: Baluchistan Province
FMNH	96353	♀	Iran: Kerman, Ostan-e	AMNH	217233	?	Pakistan: Baluchistan Province
FMNH	96354	♀	Iran: Kerman, Ostan-e	AMNH	217234	?	Pakistan: Baluchistan Province
FMNH	96357	♀	Iran: Kerman, Ostan-e	AMNH	217235	?	Pakistan: Baluchistan Province
FMNH	96347	♂	Iran: Kerman, Ostan-e	AMNH	244377	?	Pakistan: Baluchistan Province
FMNH	96349	♂	Iran: Kerman, Ostan-e	AMNH	244378	?	Pakistan: Baluchistan Province
FMNH	96352	♂	Iran: Kerman, Ostan-e	AMNH	244379	?	Pakistan: Baluchistan Province
FMNH	96355	♂	Iran: Kerman, Ostan-e	AMNH	244380	?	Pakistan: Baluchistan Province
FMNH	96356	♂	Iran: Kerman, Ostan-e	AMNH	244381	?	Pakistan: Baluchistan Province
FMNH	96358	♂	Iran: Kerman, Ostan-e	AMNH	244382	?	Pakistan: Baluchistan Province
FMNH	96359	♂	Iran: Kerman, Ostan-e	AMNH	244383	?	Pakistan: Baluchistan Province
FMNH	96360	♂	Iran: Kerman, Ostan-e	BMNH	82.883	?	Pakistan: Baluchistan Province
FMNH	96361	♂	Iran: Kerman, Ostan-e	BMNH	82.884	?	Pakistan: Baluchistan Province
FMNH	96362	♂	Iran: Kerman, Ostan-e	AMNH	170230	♀	Pakistan: Baluchistan Province
FMNH	96363	♂	Iran: Kerman, Ostan-e	BMNH	19.11.8.6	♀	Pakistan: Baluchistan Province
FMNH	96346	♀	Iran: Khorasan, Ostan-e	BMNH	19.11.7.18	♀	Pakistan: Baluchistan Province
USNM	326683	♀	Iran: Khorasan, Ostan-e	FMNH	82613	♀	Pakistan: Baluchistan Province
USNM	326684	♀	Iran: Khorasan, Ostan-e	USNM	368929	♀	Pakistan: Baluchistan Province
USNM	326685	♀	Iran: Khorasan, Ostan-e	AMNH	170226	♂	Pakistan: Baluchistan Province
USNM	326686	♀	Iran: Khorasan, Ostan-e	AMNH	170227	♂	Pakistan: Baluchistan Province
USNM	326687	♀	Iran: Khorasan, Ostan-e	AMNH	170228	♂	Pakistan: Baluchistan Province
USNM	326689	♀	Iran: Khorasan, Ostan-e	AMNH	170229	♂	Pakistan: Baluchistan Province
USNM	326690	♀	Iran: Khorasan, Ostan-e	AMNH	244384	♂	Pakistan: Baluchistan Province
USNM	326691	♀	Iran: Khorasan, Ostan-e	BMNH	19.11.8.4	♂	Pakistan: Baluchistan Province
USNM	326691	♀	Iran: Khorasan, Ostan-e	BMNH	19.11.8.5	♂	Pakistan: Baluchistan Province

FMNH	82612	♂	Pakistan: Baluchistan Province	FMNH	102039	♂	Afghanistan: Nangarhar, Velayat-e
USNM	200318	♂	Pakistan: Baluchistan Province	BMNH	81.8.16.3	?	Afghanistan: Qandahar, Velayat-e
USNM	410930	♂	Pakistan: Baluchistan Province	BMNH	85.11.5.5	♂	Afghanistan: Qandahar, Velayat-e
USNM	413464	♂	Pakistan: Baluchistan Province	USNM	327914	♀	Iran: Dasht-e-lut
AMNH	31248	?	Palestine: Sarepta (= as Sarafand, Lebanon?)	USNM	327915	♀	Iran: Dasht-e-lut
BMNH	7.1.1.8	?	U.S.S.R.: "Volga"	USNM	327913	♂	Iran: Dasht-e-lut
BMNH	7.1.1.129	?	U.S.S.R.: "Volga"	FMNH	110959	?	Iran: Fars, Ostan-e
AMNH	85309	♂	U.S.S.R.: Kazakh.S.S.R., Kzyl-Ordinsk.	FMNH	57974	?	Iran: Fars, Ostan-e
AMNH	85308	♂	U.S.S.R.: Kazakh.S.S.R., Kzyl-Ordinsk.	FMNH	96365	?	Iran: Fars, Ostan-e
USNM	258739	?	U.S.S.R.: Kazakh.S.S.R., Akmolinsk.	FMNH	110960	♂	Iran: Fars, Ostan-e
BMNH	11.12.14.5	♀	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	FMNH	110961	?	Iran: Fars, Ostan-e
BMNH	14.5.10.31	♀	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	FMNH	110962	?	Iran: Fars, Ostan-e
BMNH	14.5.10.32	♀	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	FMNH	110063	?	Iran: Ilam, Ostan-e
BMNH	11.12.14.3	♂	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	USNM	326701	♀	Iran: Khorasan, Ostan-e
BMNH	11.12.14.1	♂	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	USNM	326697	♀	Iran: Khorasan, Ostan-e
BMNH	11.12.14.2	♂	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	USNM	326695	♀	Iran: Khorasan, Ostan-e
BMNH	11.12.14.4	♂	U.S.S.R.: Kazakh.S.S.R., Taldy-Kurgansk.	USNM	326699	♀	Iran: Khorasan, Ostan-e
USNM	251642	?	U.S.S.R.: R.S.F.S.R., Altaisk. krai	USNM	326696	♀	Iran: Khorasan, Ostan-e
HMCZ	23298	?	U.S.S.R.: R.S.F.S.R., Altaisk. krai	USNM	326698	♂	Iran: Khorasan, Ostan-e
HMCZ	23299	?	U.S.S.R.: R.S.F.S.R., Altaisk. krai	USNM	326700	♂	Iran: Khorasan, Ostan-e
BMNH	20.7.4.1	?	U.S.S.R.: Turkmen.S.S.R., Krasnovodsk.	BMNH	21.12.3.2	♂	Iran: Tanb Island
FMNH	106648	♀	U.S.S.R.: Turkmen.S.S.R., Krasnovodsk.	BMNH	88.6.18.3	?	Oman: Muscat
KU	117036	?	U.S.S.R.: Turkmen.S.S.R., Maryisk.	BMNH	85.11.5.5	♂	Oman: Muscat
AMNH	176282	♀	U.S.S.R.: Turkmen.S.S.R., Maryisk.	USNM	352951	♂	Pakistan: Baluchistan Province
AMNH	87085	?	U.S.S.R.: Uzbek.S.S.R., Fergansk.	USNM	368930	♂	Pakistan: Baluchistan Province
<i>Hemiechinus collaris</i>				FMNH	82609	?	Pakistan: Punjab Province
HMCZ	5187	?	India	FMNH	82608	♀	Pakistan: Punjab Province
AMNH	214190	♀	India	USNM	368933	♀	Pakistan: Punjab Province
FMNH	-	?	Pakistan: Punjab Province	USNM	368937	♀	Pakistan: Punjab Province
FMNH	-	♂	Pakistan: Punjab Province	USNM	368931	♂	Pakistan: Punjab Province
USNM	326277	?	Pakistan: Punjab Province	USNM	368932	♂	Pakistan: Punjab Province
USNM	326278	♂	Pakistan: Punjab Province	USNM	368934	♂	Pakistan: Punjab Province
AMNH	185103	?	Pakistan: Sind Province	USNM	368935	♂	Pakistan: Punjab Province
BMNH	75.06	♀	Pakistan: Sind Province	USNM	368936	♂	Pakistan: Punjab Province
BMNH	75.09	♀	Pakistan: Sind Province	USNM	410929	♂	Pakistan: Punjab Province
BMNH	75.1399	♀	Pakistan: Sind Province	BMNH	87.4.2.2	♀	Pakistan: Sind Province
BMNH	75.1400	♀	Pakistan: Sind Province	BMNH	2.11.22.2	♂	Yemen (Aden)
BMNH	75.05	♂	Pakistan: Sind Province	<i>Hemiechinus micropus</i>			
BMNH	75.08	♂	Pakistan: Sind Province	FMNH	82604	♀	India
BMNH	80.12.15.11	♂	Pakistan: Sind Province	FMNH	82605	♀	India
<i>Hemiechinus hypomelas</i>				FMNH	82607	♀	India
FMNH	102038	♂	Afghanistan: Nangarhar, Velayat-e	FMNH	82606	♀	India
				USNM	369316	♀	Pakistan: Punjab Province
				KU	125480	?	Pakistan: Sind Province
				BMNH	75.1413	♀	Pakistan: Sind Province
				BMNH	75.1418	♀	Pakistan: Sind Province
				BMNH	75.1414	♂	Pakistan: Sind Province
				BMNH	75.1415	♂	Pakistan: Sind Province
				BMNH	75.1416	♂	Pakistan: Sind Province
				BMNH	75.1417	♂	Pakistan: Sind Province
				<i>Hylomys hainanensis</i>			
				BEIJ	70875	♂	China: Hainan Dao
				BEIJ	70891	♂	China: Hainan Dao



FMNH	38890	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38891	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38892	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38893	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38894	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38895	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38896	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38897	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	38898	♂	Vietnam: Hoang Lien Son, Tinh
FMNH	41296	♂	Vietnam: Hoang Lien Son, Tinh
HMCZ	38252	♂	Vietnam: Hoang Lien Son, Tinh
HMCZ	38261	♂	Vietnam: Hoang Lien Son, Tinh

*Hylomys suillus*

USNM	481285	♀	Indonesia: Java
HMCZ	20687	♀	Burma: Kachin State
AMNH	44113	♀	China: Yunnan Sheng
AMNH	44272	♀	China: Yunnan Sheng
AMNH	44112	♂	China: Yunnan Sheng
AMNH	44275	♂	China: Yunnan Sheng
FMNH	32309	♂	China: Yunnan Sheng
USNM	481289	♀	Indonesia: Java
USNM	521660	♂	Indonesia: Java
USNM	521661	♂	Indonesia: Java
USNM	481286	♀	Indonesia: Java
AMNH	87313	♀	Laos: Bolovens, Plateau des
FMNH	32308	♂	Laos: Phong Saly, Khoueng
BMNH	26.10.4.42	♀	Laos: Xien Quang Koo
USNM	292338	?	Malaysia: Sabah
USNM	292339	?	Malaysia: Sabah
USNM	292340	?	Malaysia: Sabah
USNM	292356	♀	Malaysia: Sabah
USNM	292357	♀	Malaysia: Sabah
USNM	292348	♂	Malaysia: Sabah
USNM	292354	♂	Malaysia: Sabah
USNM	300816	♂	Malaysia: Sabah
USNM	487911	♀	Malaysia: West
USNM	307548	♂	Malaysia: West
USNM	487920	♂	Malaysia: West
BMNH	20.7.3.12	♀	Thailand
HMCZ	35452	♀	Thailand: Chiang Mai Changwat
HMCZ	35453	♀	Thailand: Chiang Mai Changwat
USNM	320486	♂	Vietnam
USNM	320492	♀	Vietnam
BMNH	26.10.4.40	♀	Vietnam: Gia Lai-Kon Tum, Tinh
BMNH	26.10.4.41	♀	Vietnam: Gia Lai-Kon Tum, Tinh
BMNH	26.10.4.36	♂	Vietnam: Gia Lai-Kon Tum, Tinh
BMNH	26.10.4.37	♂	Vietnam: Gia Lai-Kon Tum, Tinh
BMNH	26.10.4.38	♂	Vietnam: Gia Lai-Kon Tum, Tinh
BMNH	26.10.4.39	♂	Vietnam: Gia Lai-Kon Tum, Tinh
FMNH	46631	♀	Vietnam: Lam Dong, Tinh
FMNH	46632	♂	Vietnam: Lam Dong, Tinh
FMNH	46633	♂	Vietnam: Lam Dong, Tinh
FMNH	46634	♂	Vietnam: Lam Dong, Tinh

FMNH	46636	♂	Vietnam: Lam Dong, Tinh
FMNH	46637	♂	Vietnam: Lam Dong, Tinh
FMNH	46638	♂	Vietnam: Lam Dong, Tinh

*Mesechinus dauuricus*

BEIJ	01826	♀	China: Jilin Sheng Dixing
BEIJ	01827	♀	China: Jilin Sheng Dixing
BEIJ	01828	♀	China: Jilin Sheng Dixing
MGU	83740	♀	China: Liaoning Sheng
USNM	270540	♀	China: Liaoning Sheng
USNM	270539	♂	China: Liaoning Sheng
BEIJ	21295	♀	China: Nei Monggol Zizhiqu Dixing
BEIJ	24276	♀	China: Nei Monggol Zizhiqu Dixing
BEIJ	10666	♀	China: Nei Monggol Zizhiqu Dixing
BEIJ	15855	♀	China: Nei Monggol Zizhiqu Dixing
BEIJ	20565	♀	China: Nei Monggol Zizhiqu Dixing
BEIJ	24277	♂	China: Nei Monggol Zizhiqu Dixing
BEIJ	25210	♂	China: Nei Monggol Zizhiqu Dixing
BEIJ	10667	♂	China: Nei Monggol Zizhiqu Dixing
BEIJ	10665	♂	China: Nei Monggol Zizhiqu Dixing
BEIJ	20842	♂	China: Nei Monggol Zizhiqu Dixing
BMNH	9.1.1.2	♂	China: Shaanxi Sheng
BMNH	9.1.1.3	♂	China: Shaanxi Sheng
BMNH	9.1.1.4	♂	China: Shaanxi Sheng
BMNH	9.1.1.5	♂	China: Shaanxi Sheng
BMNH	9.1.1.6	♂	China: Shaanxi Sheng
BMNH	9.1.1.7	♂	China: Shaanxi Sheng
BMNH	9.1.1.8	♂	China: Shaanxi Sheng
BMNH	9.1.1.9	♂	China: Shaanxi Sheng
BMNH	9.1.1.10	♂	China: Shaanxi Sheng
MGU	107219	♀	Mongolia: Ch'er-Khangai Aymag
MGU	130413	?	Mongolia: Khentei Aymag
MGU	113799	?	Mongolia: Vostochnyi Aymag
MGU	100455	♀	U.S.S.R.: Buryat-A.S.S.R.
MGU	42341	♂	U.S.S.R.: Buryat-A.S.S.R.
MGU	100456	♂	U.S.S.R.: Buryat-A.S.S.R.
MGU	42340	?	U.S.S.R.: R.S.F.S.R. Chitinsk.
MGU	83733	♀	U.S.S.R.: R.S.F.S.R. Chitinsk.
MGU	83738	♀	U.S.S.R.: R.S.F.S.R. Chitinsk.
MGU	43833	♂	U.S.S.R.: R.S.F.S.R. Chitinsk.
MGU	83732	♂	U.S.S.R.: R.S.F.S.R. Chitinsk.
MGU	83735	♂	U.S.S.R.: R.S.F.S.R. Chitinsk.
MGU	83737	♂	U.S.S.R.: R.S.F.S.R. Chitinsk.

*Mesechinus hughii*

BMNH	0.6.27.2	♀	China: Shaanxi Sheng
BEIJ	19434	♀	China: Shaanxi Sheng
MGU	83744	♀	China: Shaanxi Sheng
MGU	83745	♂	China: Shaanxi Sheng
BEIJ	19433	♂	China: Shaanxi Sheng

*Microgale talazaci*

USNM	341696	♀	Madagascar
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*Podogymnura aureospinula*

UPLB 3753 ♂ Philippine Islands: Dinagat Island

*Podogymnura truei*

DMNH 5948 ? Philippine Islands: Mindanao Island

DMNH 5949 ♀ Philippine Islands: Mindanao Island

DMNH 5950 ♀ Philippine Islands: Mindanao Island

DMNH 5951 ♀ Philippine Islands: Mindanao Island

DMNH 5952 ♂ Philippine Islands: Mindanao Island

DMNH 5953 ♂ Philippine Islands: Mindanao Island

KU 98141 ♂ Philippine Islands: Mindanao Island

*Setifer setosus*

USNM 122489 ? Madagascar

USNM 254983 ? Madagascar

*Solenodon cubanus*

USNM 2230/1395 ? Cuba

*Solenodon paradoxus*

USNM 290520 ♂ Zoo Specimen

USNM 364952 ♂ Zoo Specimen

*Tenrec ecaudatus*

USNM 294495 ? Madagascar

USNM 63313 ♂ Madagascar

*Uropsilus andersoni*

ANSP 16594 ♂ China: Sichuan Sheng

*Uropsilus soricipes*

USNM 256119 ? China: Sichuan Sheng

USNM 260743 ? China: Sichuan Sheng

USNM 260751 ♀ China: Sichuan Sheng

## Appendix 2

### Data Matrix

Abbreviations are as follows:

ANCE = Hypothetical ancestor

ECHG = *Echinosorex gymnura*

PODA = *Podogymnura aureospinula*

PODT = *Podogymnura truei*

HYLS = *Hylomys sinensis*

HYLU = *Hylomys suillus*

HYLH = *Hylomys hainanensis*

HEME = *Hemiechinus aethiopicus*

HEMH = *Hemiechinus hypomelas*

HEMM = *Hemiechinus micropus*

HEMA = *Hemiechinus auritus*

HEMC = *Hemiechinus collaris*

MESD = *Mesechinus dauuricus*

ERIA = *Erinaceus amurensis*

ERIC = *Erinaceus concolor*

ERIE = *Erinaceus europaeus*

ATXF = *Atelerix frontalis*

ATXG = *Atelerix algirus*

ATXA = *Atelerix albiventris*

ATXS = *Atelerix sclateri*

TENR = Tenrecoids

SORI = Soricoids

LEPT = †Leptictidae

Unordered characters are 10, 20, 49, 62, 77, 79.

Unpolarized characters are 14, 54, 58, 61, 70, 71, 72.

	Character																														
	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	
ANCE	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
ECHG	0	0	0	0	1	0	1	1	2	2	1	1	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0
PODA	0	0	0	0	1	0	0	1	2	2	1	1	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	0
PODT	0	0	0	0	1	0	0	1	1	2	1	1	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0
HYLS	1	0	0	1	0	1	0	1	0	2	1	1	1	0	0	1	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0
HYLU	0	0	0	1	0	1	0	1	0	2	1	1	1	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
HYLH	0	0	0	1	0	1	0	1	0	2	1	1	1	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
HEME	1	1	1	2	0	1	1	0	2	1	3	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	4	0	0	1	
HEMH	1	1	1	2	0	1	1	0	2	1	2	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	3	0	0	1	
HEMM	1	1	1	2	0	1	1	0	2	1	2	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	4	0	0	1	
HEMA	1	1	1	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	2	0	0	1	
HEMC	1	1	1	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	2	0	0	1	
MESD	1	1	0	2	0	1	1	0	2	1	1	0	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	1	0	1	
ERIA	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	1	0	1	1
ERIC	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	1	0	1	1
ERIE	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	1	0	1	1
ATXF	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1
ATXG	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1
ATXA	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1
ATXS	1	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1
TENR	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SORI	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
LEPT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0



## Appendix 3

### Apomorphy List by Stems

Abbreviations are explained in Appendix 2. Double daggers (§) denote characters of analytically ambiguous placement.

Unordered characters are 10, 20, 49, 62, 77, 79.

Unpolarized characters are 14, 54, 58, 61, 70, 71, 72.

Stem	Transformation Series	Ancestral Character	Derived Character	Stem	Transformation Series	Ancestral Character	Derived Character	
ECHG	7	0	1	13	22	0	1	
	23	0	1		26	0	1	
	54	1	0		56	1	0	
	55	1	0	12	29	0	1	
	‡58	1	0		‡77	2	1	
PODA	15	0	1	79	3	1		
	29	0	1	11	‡77	3	2	
PODT	9	2	1	80	0	1		
	34	0	1	10	27	3	4	
	41	0	1		58	0	1	
HYLS	1	0	1		60	0	1	
	22	0	1	9	11	1	2	
	46	0	1		27	2	3	
	‡50	1	2		35	0	1	
	53	0	1		36	0	1	
55	1	0	79		3	2		
HYLU				8	3	0	1	
HYLH					27	1	2	
HEME	11	2	3		31	0	1	
HEMH				7	75	0	1	
HEMM					1	0	1	
HEMA					2	0	1	
HEMC					4	1	2	
MESD	12	1	0		7	0	1	
	28	0	1	‡10	15	0	1	
	33	0	1		17	0	1	
ERIA	78	0	1		18	0	1	
ERIC					‡20	2	1	
ERIE					21	0	1	
ATXF	78	0	1	24	0	1		
ATXG				25	25	0	1	
ATXA	76	1	2		27	0	1	
ATXS					30	0	1	
16	49	1	2		32	0	1	
	51	0	1		38	38	0	1
	76	1	0	39		39	0	1
15	58	0	1					
14	60	0	1					

Stem	Transformation Series	Ancestral Character	Derived Character
7	40	0	1
	42	0	1
	43	0	1
	45	0	1
	47	0	1
	48	0	1
	49	0	1
	50	1	2
	‡57	1	2
	‡58	1	0
	64	0	1
	65	0	1
	67	1	2
	68	0	1
	‡70	1	0
	‡71	1	0
	‡72	1	0
	76	0	1
	‡77	0	3
	79	0	3
6	54	1	0
5	‡9	2	0
	13	0	1
	14	1	0
	16	0	1
	19	0	1
	34	0	1
	41	0	1
	60	0	1
4	22	0	1
	48	0	1

Stem	Transformation Series	Ancestral Character	Derived Character
3	‡4	1	0
	5	0	1
	‡6	1	0
	44	0	1
	‡50	1	0
	52	0	1
	‡57	1	0
	‡59	1	0
	81	0	1
2	8	0	1
	33	0	1
	‡62	2	1
	66	0	1
	69	0	1
	73	0	1
	74	0	1
1	‡4	0	1
	‡6	0	1
	‡9	0	2
	11	0	1
	12	0	1
	37	0	1
	‡50	0	1
	55	0	1
	56	0	1
	‡57	0	1
	‡59	0	1
	‡61	0	1
	‡62	0	2
	63	0	1
	67	0	1



## Appendix 4

### Changes on Stems by Transformation Series

Unordered or unpolarized transformations are noted with a "U." Characters of ambiguous placement are noted by a double dagger (‡).

Transformation Series	Changed		Along Branch	Consistency	Transformation Series	Changed		Along Branch	Consistency
	From	To				From	To		
1	0	1	7		25	0	1	7	1.000
	0	1	HYLS	0.500	26	0	1	13	1.000
2	0	1	7	1.000		3	4	10	1.000
3	0	1	8	1.000	28	0	1	MESD	1.000
4	‡0	1	1		29	0	1	12	
	1	2	7			0	1	PODA	0.500
	‡1	0	3	0.667	30	0	1	7	1.000
5	0	1	3	1.000	31	0	1	8	1.000
6	‡0	1	1		32	0	1	7	1.000
	‡1	0	3	0.500		0	1	MESD	0.500
7	0	1	7		34	0	1	5	
	0	1	ECHG	0.500		0	1	PODT	0.500
8	0	1	2	1.000	35	0	1	9	1.000
9	‡0	2	1		36	0	1	9	1.000
	‡2	0	5		37	0	1	1	1.000
	2	1	PODT	0.400	38	0	1	7	1.000
U 10	‡2	1	7	1.000	39	0	1	7	1.000
11	0	1	1		40	0	1	7	1.000
	1	2	9		41	0	1	5	
	2	3	HEME	1.000		0	1	PODT	0.500
12	0	1	1		42	0	1	7	1.000
	1	0	MESD	0.500	43	0	1	7	1.000
13	0	1	5	1.000	44	0	1	3	1.000
U 14	1	0	5	1.000	45	0	1	7	1.000
15	0	1	7		46	0	1	HYLS	1.000
	0	1	PODA	0.500	47	0	1	7	1.000
16	0	1	5	1.000		0	1	4	0.500
17	0	1	7	1.000		1	2	16	1.000
18	0	1	7	1.000	50	‡0	1	1	
19	0	1	5	1.000		‡1	0	3	
U 20	‡2	1	7	1.000		1	2	HYLS	0.500
21	0	1	7	1.000	51	0	1	16	1.000
22	0	1	13		52	0	1	3	1.000
	0	1	4		53	0	1	HYLS	1.000
	0	1	HYLS	0.333	U 54	1	0	6	
23	0	1	ECHG	1.000		1	0	ECHG	0.500
24	0	1	7	1.000	55	0	1	1	

Transformation Series	Changed		Along Branch	Consistency
	From	To		
55	1	0	HYLU	
	1	0	ECHG	0.333
56	0	1	1	
	1	0	13	0.500
57	‡0	1	1	
	‡1	0	3	0.667
	0	1	15	
	0	1	10	
	‡1	0	ECHG	0.250
59	‡0	1	1	
	‡1	0	3	0.500
60	0	1	14	
	0	1	10	
	0	1	5	0.333
U 61	‡0	1	1	1.000
U 62	‡0	2	1	
	‡2	1	2	1.000
63	0	1	1	1.000
64	0	1	7	1.000
65	0	1	7	1.000
66	0	1	2	1.000

Transformation Series	Changed		Along Branch	Consistency
	From	To		
67	0	1	1	
	1	2	7	1.000
68	0	1	7	1.000
69	0	1	2	1.000
U 70	‡1	0	7	1.000
U 71	‡1	0	7	1.000
U 72	‡1	0	7	1.000
73	0	1	2	1.000
74	0	1	2	1.000
75	0	1	8	1.000
	1	0	16	
	1	2	ATXA	0.667
	‡3	2	11	
	‡2	1	12	1.000
78	0	1	ATXF	
	0	1	ERIA	0.500
	3	1	12	
	3	2	9	1.000
80	0	1	11	1.000
81	0	1	3	1.000

## Literature Cited

- Agrawal, V.C.  
1973. A Note on the Taxonomic Status of *Erinaceus blanfordi* Anderson and *Erinaceus jerdoni* Anderson (Mammalia: Insectivora). *Journal of the Zoological Society of India*, 25(1/2):158-159.
- Allen, G.M.  
1939. *The Mammals of China and Mongolia*. Volume 1, 620 pages. New York: American Museum of Natural History.
- Anderson, J.  
1878. On the Indian Species of the Genus *Erinaceus*. *Journal of the Asiatic Society of Bengal*, 47(4):195-211.  
1879 ("1878"). *Anatomical and Zoological Researches: Comprising an Account of the Zoological Results of Two Expeditions to Western Yunnan in 1868 and 1875, and a Monograph of the Two Cetacean Genera Platanista and Orcella*. Volume 1, 998 pages; volume 2, plates. London: Quaritch.  
1895. On a New Species of the Genus *Erinaceus* from Somaliland. *Proceedings of the Zoological Society of London*, 1895:414-421.
- Anderson, J., and W.E. de Winton  
1902. *Zoology of Egypt: Mammalia (by the Late John Anderson, Revised and Completed by W.E. de Winton)*. 374 pages. London: Hugh Rees.
- Biswas, B., and R.K. Ghose  
1970. Taxonomic Notes on the Indian Pale Hedgehogs of the Genus *Paraechinus*. *Mammalia*, 34:467-477.
- Blainville, H.M.D. de  
1838. Recherches sur l'ancienneté des Mammifères insectivores à la surface de la terre; précédées de l'histoire de la science à ce sujet, des principes de leur classification et de leur distribution géographique actuelle. *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences*, 6:738-744.
- Bobrinskii, N.A., B.A. Kuznetov, and A.P. Kuzyakin  
1944. *Opredelitel' mlekopitayushchikh v SSSR* [Guide to the Mammals of the USSR]. 383 pages. Moscow: Sovetskaya Nauka.  
1965. *Opredelitel' mlekopitayushchikh v SSSR* [Guide to the Mammals of the USSR]. Edition 2, 382 + 96 pages. Moscow: "Proveshchenie."
- Brandt, J.F.  
1836. [Miscellaneous note in "Mélances"]. *Bulletin Scientifique l'Académie Impériale des Sciences de Saint Pétersbourg*, 1(4):32.
- Butler, P.M.  
1948. On the Evolution of the Skull and Teeth in the Erinaceidae, with Special Reference to Fossil Material in the British Museum. *Proceedings of the Zoological Society of London*, 118:446-500.  
1956. The Skull of *Ictops* and the Classification of the Insectivora. *Proceedings of the Zoological Society of London*, 126:453-481.  
1972. The Problem of Insectivore Classification. In K.A. Joysey and T.S. Kemp, editors, *Studies in Vertebrate Evolution*, pages 253-265. New York: Winchester Press.  
1988. Phylogeny of the Insectivores. In M.J. Benton, editor, *The Phylogeny and Classification of the Tetrapods*, 2(Mammals):117-141. Oxford: Clarendon Press.
- Cabrera, A.  
1914. *Fauna Iberica: Mammiferos*. xviii + 441 pages. Madrid: Museo Nacional de Ciencias Naturales.  
1925. *Genera Mammalium, Insectivora Galeopithecica*. 232 pages. Madrid: Museo Nacional de Ciencias Naturales.
- Corbet, G.B.  
1974 ("1971"). Family Erinaceidae. In J. Meester and H.W. Setzer, editors, *The Mammals of Africa: An Identification Manual*, Part 1.4. Washington, D.C.: Smithsonian Institution Press.
1978. *The Mammals of the Palearctic Region: A Taxonomic Review*. 314 pages. London and Ithaca: British Museum (Natural History) and Cornell University Press.
1984. *The Mammals of the Palearctic Region: A Taxonomic Review*. Supplement, 45 pages. London: British Museum (Natural History).  
1988. The Family Erinaceidae: A Synthesis of Its Taxonomy, Phylogeny, Ecology and Zoogeography. *Mammalian Review*, 18:117-172.
- Corbet, G.B., and H.N. Southern, editors  
1977. *The Handbook of British Mammals*. 2nd edition, xxxii + 520 pages. Oxford: Blackwell Scientific Publishers.
- de Blainville, H.M.D. See Blainville, H.M.D. de
- Dobson, G.E.  
1882. *A Monograph of the Insectivora, Systematic and Anatomical, Part I: Including the Families Erinaceidae, Centetidae, and Solenodontidae*. iv + 96 pages. London: John Van Voort.
- Duvernoy, G.L., and A. Lereboullet  
1840-1846 ("1842"). Notes et renseignements sur les animaux vertébrés de l'Algérie qui font partie du musée de Strasbourg. *Mémoires de la Société du Muséum d'Histoire Naturelle de Strasbourg*, 3(2):4.
- Ehrenberg, C.G.  
1833. Mammalia. In P.C. Hemprich and C.G. Ehrenberg, *Symbolae physicae, seu icones et descriptiones corporum naturalium novorum aut minus cognitorum quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam*. 4 volumes. Berlin.
- Eisenberg, J.F.  
1981. *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*. 610 pages. Chicago: The University of Chicago Press.
- Ellerman, J.R., and T.C.S. Morrison-Scott  
1951. *Checklist of Palaearctic and Indian Mammals 1758 to 1946*. 810 pages. London: British Museum (Natural History).
- Findley, J.S.  
1967. Insectivores and Dermoptera. In S. Anderson and J.K. Jones, Jr., editors, *Recent Mammals of the World: A Synopsis of Families*, pages 87-108. New York: Ronald Press.
- Fischer, G.  
1817. *Adversarium zoologorum fasciculus primus*, 2: De systemate mammalium; 3: De mammalium generibus. *Mémoires de la Société Impériale des Naturalistes de Moscou*, 5:356-446.
- Fitzinger, L.J.  
1866. Systematische Übersicht der Säugethiere Nordost-Afrika's mit Einschluss der arabischen Küste, des rothen Meeres, der Somali- und der Nilquellen-Länder, südwärts bis zum vierten Grade nördlicher Breite. *Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematische-Naturwissenschaftliche Klasse*, 54(6-10):537-611.
- Gill, T.  
1872. Arrangement of the Families of Mammals with Analytical Tables. *Smithsonian Miscellaneous Collections*, 11:1-98.
- Gmelin, S.G.  
1770. De Capra saiga et Erinaceo aurito. *Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae*, 14:512-524.
- Gould, E.  
1978. The Behavior of the Moonrat, *Echinorex gymnurus* (Erinaceidae) and the Pentail Shrew, *Ptilocercus lowii* (Tupaiaidae), with Com-

- ments on the Behavior of Other Insectivora. *Zeitschrift für Tierpsychologie*, 48:1-27.
- Gray, J.E.  
1830-1834. *Illustrations of Indian Zoology: Chiefly Selected from the Collection of Major-General Hardwicke*. London: Treuttel, Wurtz, Treuttel, Jun. and Richter.
- Gropp, A., P. Citoler, and M. Geisler  
1969. Karyotypenvariation und Heterochromatinstreifenmuster bei Igel (Erinaceus und Hemiechinus). *Chromosoma* (Berlin), 27:288-307.
- Gropp, A., and A.T. Natarajan  
1972. Karyotype and Heterochromatin Pattern of the Algerian Hedgehogs. *Cytogenetics*, 11:259-269.
- Haltenorth, T., and H. Diller  
1977. *Säugetiere Afrikas und Madagaskars*. 403 pages. Munich: BVL Bestimmungsbuch.
- Hassinger, J.D.  
1973. A Survey of the Mammals of Afghanistan. *Fieldiana: Zoology*, 60:1-195.
- Heaney, L.R., and G.S. Morgan  
1982. A New Species of Gymnure, *Podogymnura*, (Mammalia: Erinaceidae) from Dinagat Island, Philippines. *Proceedings of the Biological Society of Washington*, 95(1):13-26.
- Honacki, J.H., K.E. Kinman, and J.W. Koeppl, editors  
1982. *Mammal Species of the World: A Taxonomic and Geographic Reference*. ix + 690 pages. Lawrence: Association of Systematics Collections and Allen Press, Inc.
- Horsfield, T.  
1851. *A Catalogue of the Mammalia in the Museum of the Hon. East-India Company*. 205 pages. London: W.H. Allen & Co.
- Hufnagel, E.  
1972. *Libyan Mammals*. 85 pages. New York: Oleander Press.
- Hull, D.L.  
1964. Consistency and Monophyly. *Systematic Zoology*, 13:1-11.
- Hutton, T.  
1845-1846. Rough Notes on the Zoology of Candahar and the Neighbouring Districts: With Notes by Ed. Blyth. *Journal of the Asiatic Society of Bengal*, 14:340-354; 15:135-170.
- International Commission of Zoological Nomenclature (ICZN)  
1985. *International Code of Zoological Nomenclature*. Third edition, xx + 328 pages. London: International Trust for Zoological Nomenclature.
- Jayne, H.  
1898. *Mammalian Anatomy: A Preparation for Human and Comparative Anatomy, Part I: The Skeleton of the Cat: Its Muscular Attachments, Growth, and Variations Compared with the Skeleton of Man*. 816 pages. Philadelphia: J.B. Lippincott Co.
- Kingdon, J.  
1974. *East African Mammals: An Atlas of Evolution in Africa*. Volume 2 (Part A, Insectivores and Bats), 341 pages. New York: Academic Press.
- Kluge, A.G., and J.S. Farris  
1969. Quantitative Phyletics and the Evolution of Anurans. *Systematic Zoology*, 18:1-32.
- Kratochvil, J.  
1975. Zur Kenntnis der Igel der Gattung *Erinaceus* in der CSSR (Insectivora, Mamm.). *Zoologické Listy*, 24:297-312.
- Kuhl, W.  
1823. [Gymnura.] *Algemeene konst en Letterbode*, page 316. Haarlem.
- Laptev, M.K.  
1925. Novyi vid ezha iz Turkestana, *Hemiechinus microtis* [On a New Species of Hedgehog from Turkestan, *Hemiechinus microtis* sp. n.]. *Byulleten' Sredne-Aziatskovo Gosudarstvenovo Universiteta* (Tashkent), 8:66-70.
- Lay, D.M.  
1967. A Study of the Mammals of Iran. *Fieldiana: Zoology*, 54:1-282.
- Leche, W.  
1902. Zur Entwicklungsgeschichte des Zahnsystems der Säugethiere, zugleich ein Beitrag zur Stammesgeschichte dieser Thiergruppe. 2. Theil Phylogenie. 1. Heft. Die Familie der Erinaceidae. *Zoologica* (Stuttgart), 15:1-103.
- Lekagul, B., and J.A. McNeely  
1977. *Mammals of Thailand*. 758 pages. Bangkok: Kuruspha Ladpari Press.
- Lesson, R.P.  
1827. *Manuel de Mammalogie, ou Histoire Naturelle des Mammifères*. 432 pages. Paris.
- Linnaeus, C.  
1758. *Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis locis*. Edition 10, 824 pages. Stockholm.
- Ma, Y.  
1964. [A New Species of Hedgehog from Shansi Province, *Hemiechinus sylvaticus* sp. n.]. *Acta Zootaxonomica Sinica*, 5:212-213 [in Chinese], 214 [in English].
- MacPhee, R.D.E.  
1981. Auditory Regions of Primates and Eutherian Insectivores: Morphology, Ontogeny, and Character Analysis. In F.S. Szalay, editor, *Contributions to Primatology*, 18:1-282. Basel: S. Karger.
- Martin, W.C.L.  
1838 ("1837"). Description of a New Bat (*Rhinolophus landeri*) from Fernando Po, and a New Hedgehog (*Erinaceus concolor*) from Trebizond. *Proceedings of the Zoological Society of London*, 1837:102-103.
- McDowell, S.B.  
1958. The Greater Antillean Insectivores. *Bulletin of the American Museum of Natural History*, 115:113-214.
- Mearns, E.A.  
1905. Descriptions of New Genera and Species of Mammals from the Philippine Islands. *Proceedings of the United States National Museum*, 28(1402):425-460.
- Müller, S.  
1839-1840. Over de Zoogdieren van den Indischen Archipel. In C.J. Temminck, editor, *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche Bezittingen, Zoologie*, pages 1-57, 6 plates. Leiden: A. Arnz & Co.
- Niethamer, J.  
1969. Zur Taxonomie der Ohrnigel in Afghanistan (Gattung *Hemiechinus*). *Zeitschrift für Säugetierkunde*, 34:257-274.
- Novacek, M.J.  
1985. The Sespeductinae, a New Subfamily of Hedgehog-like Insectivores. *American Museum Novitates*, 2822:1-24.  
1986. The Skull of Leptictid Insectivorans and the Higher-level Classification of Eutherian Mammals. *Bulletin of the American Museum of Natural History*, 183:1-112.
- Novacek, M.J., T.M. Brown, and D. Schankler  
1985. On the Classification of the Early Tertiary Erinaceomorpha (Insectivora, Mammalia). *American Museum Novitates*, 2813:1-22.
- Nowak, R.M., and J.L. Paradiso  
1983. *Walker's Mammals of the World*. Volume 1, 4th edition, 568 pages. Baltimore: The Johns Hopkins University Press.
- Ognev, S.I.  
1928. *Zveri vostochnoi Evropyi Severnoi Azii* [Mammals of Eastern Europe and Northern Asia, volume 1: Insectivora and Chiroptera]. Moscow. [English translation 1962, Jerusalem.]  
1951. *Ob' ezkhakh (Erinacidae) [sic] Dal'nevo Vostoka*. [On the Hedgehogs (Erinaceidae) of the Far East.] *Byulleten' Moskovskovo Obshchestva Ispytatelei Prirody*, 56:8-14.
- Osborn, D.J., and I. Helmy  
1980. The Contemporary Land Mammals of Egypt (Including Sinai). *Fieldiana: Zoology*, new series, 5:1-579.

- Patterson, C.  
1982. Morphological Characters and Homology. In K.A. Joysey and A.E. Friday, editors, *Problems of Phylogenetic Reconstruction*, pages 21-74. London: Academic Press.
- Pavlinov, I.Ya., and O.L. Rossolimo  
1987. *Sistematika mlekopitayushchikh SSSR* [Systematics of Mammals of the USSR]. 284 pages. Moscow: Moscow University.
- Poduschka, W., and C. Poduschka  
1985. Beiträge zur Kenntnis der Gattung *Podogymnura* Meams, 1905 (Insectivora: Echinossoricinae). *Zeitschrift für Säugetierkunde*, 50: 1-21.
- Pomel, A.  
1848. Etudes sur les Carnassiers Insectivores (extrait), seconde partie: Classification des Insectivores. *Archives des Sciences, Physiques et Naturelle* (Géneve), 9:244-257.
- Puček, Z.  
1981. *Keys to the Vertebrates of Poland*. 188 pages. Warsaw: Polish Scientific Publishers.
- Puček, Z., and J. Raczynski  
1983. *Atlas of Polish Mammals*. 188 pages. Warsaw: Polish Scientific Publishers.
- Raffles, T.S.  
1822 ("1821"). Descriptive Catalogue of a Zoological Collection, Made on Account of the Honorable East Indian Company, in the Island of Sumatra and Its Vicinity, under the Direction of Sir Thomas Stamford Raffles, Lieutenant-Governor of Fort Marlborough, with Additional Notices Illustrative of the Natural History. *Transactions of the Linnaean Society of London*, 13(1):239-274.
- Ralls, K.  
1976. Mammals in Which Females Are Larger than Males. *Quarterly Review of Biology*, 51:245-276.
- Rich, T.H.V., and P.V. Rich  
1971. *Brachyerix*, a Miocene Hedgehog from Western North America, with a Description of the Tympanic Regions of *Paraechinus* and *Podogymnura*. *American Museum Novitates*, 2477:1-59.
- Robbins, C.B., and H.W. Setzer  
1985. Morphometrics and Distinctness of the Hedgehog Genera (Insectivora: Erinaceidae). *Proceedings of the Biological Society of Washington*, 98(1):112-120.
- Roberts, T.J.  
1977. *The Mammals of Pakistan*. xxvi + 361 pages. London: Ernest Benn.
- Ruprecht, A.L.  
1973. O rozmieszczeniu presedstawicieli rodzaju *Erinaceus* Linnaeus, 1758 w Polsce. *Przegląd Zoologiczny Wrocław*, 17:81-86.
- Satunin, K.  
1907 ("1906"). Über neue und wenig bekannte Igel des Zoologischen Museums der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Petersburg*, 11:167-190.
- Schmidt-Kittler, N.  
1981. Zur Stammesgeschichte der marderverwandten Raubtiergruppen (Musteloidea, Carnivora). *Eclogae Geologicae Helvetiae*, 74:753-801.
- Schrenck, L. von  
1859 ("1858"). *Reisen und Forschungen im Amur-Lande in den Jahren 1854-1856, Band I, Säugethiere des Amur-Landes, II: Insectivora*, pages 100-114. St. Petersburg: Commissionare der Kaiserlichen Akademie der Wissenschaften.
- Setzer, H.W.  
1957. The Hedgehogs and Shrews (Insectivora) of Egypt. *Journal of the Egyptian Public Health Association*, 32(1):1-17.
- Shaw, T.-H., and Wong Song [Wang Sung]  
1959. [A New Insectivore from Hainan.] *Acta Zoologica Sinica*, 11:422-425. [In Chinese; English summary.]
- Simpson, G.G.  
1945. The Principles of Classification and a Classification of the Mammals. *Bulletin of the American Museum of Natural History*, 85:1-350.
- Smith, A.  
1831. An Epitome of African Zoology: Or, a Concise Description of the Objects of the Animal Kingdom Inhabiting Africa, Its Islands and Seas. *South African Quarterly Journal*, 2:10, 29.
- Smithers, R.H.N.  
1983. *The Mammals of the Southern African Subregion*. 736 pages. Pretoria: University of Pretoria.
- Sokal, R.  
1986. Phenetic Taxonomy: Theory and Methods. *Annual Review of Ecology and Systematics*, 17:423-442.
- Sokolov, V.E.  
1973. *Sistematika mlekopitayushchikh* [Systematics of Mammals]. 430 pages. Moscow: Vysshaga Shkola.
- Stroganov, S.U.  
1957. *Zveri Sibiri: Nasekomoyadnye* [Mammals of Siberia: Insectivores]. 267 pages. Moscow: Akademia Nauk.
- Sundevall, C.J.  
1842 ("1841"). Ofversigt af släktet *Erinaceus*. *Kungliga Svenska Vetenskaps-Akademiens Handlingar*, 1841:215-239.
- Swofford, D.L.  
1984. *PAUP—Phylogenetic Analysis Using Parsimony, Version 2.4.1, User's Manual*. [Privately printed.]
- Thomas, O.  
1909 ("1908"). The Duke of Bedford's Zoological Exploration in Eastern Asia, XI: On Mammals from the Province of Shan-si and Shen-si, Northern China. *Proceedings of the Zoological Society of London*, 1908:963-983.  
1911. The Duke of Bedford's Zoological Exploration in Eastern Asia, XIII: On Mammals from the Provinces of Kansu and Szechwan, Western China. *Proceedings of the Zoological Society of London*, 1911: 158-180.  
1918. The Generic Division of the Hedgehogs. *Annals and Magazine of Natural History*, series 9, 1:193-196.
- Tilesius von Tilenau, W.G.  
1813 ("1812"). [Ericius.] *Denkschriften der Kaiserlichen Akademie der Wissenschaften zu München*, 1811-1812:75.
- Trouessart, E.L.  
1879. Catalogue des Mammifères Vivants et Fossiles... Insectivores. *Revue et Magasin de Zoologie*, 3(7):219-285.  
1909. *Neotetracus sinensis*, a New Insectivore of the Family Erinaceidae. *Annals and Magazine of Natural History*, series 8, 4:389-391.
- Van Valen, L.  
1967. New Paleocene Insectivores and Insectivore Classification. *Bulletin of the American Museum of Natural History*, 135:217-284.
- Wagner, J.A.  
1841. Die Raubthiere. In J.C.D. Schreber, *Die Säugethiere in Abbildungen nach der Natur mit Geschreibergern, Supplementband*, part 2, 558 pages. Erlangen: Walther.
- Watrous, L.E., and Q.D. Wheeler  
1981. The Out-group Comparison Method of Character Analysis. *Systematic Zoology*, 30:1-11.
- Wiley, E.O.  
1979. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. xv + 439 pages. New York: John Wiley and Sons.  
1981. Complex Groups and Consistent Classifications. *Systematic Botany*, 6:346-358.
- Woodward, M.F.  
1896. Contributions to the Study of Mammalian Dentition, Part II: On the Teeth of Certain Insectivora. *Proceedings of the Zoological Society of London*, 1896:557-594.



Wozencraft, W.C.

1989. The Phylogeny of the Recent Carnivora. In J.L. Gittleman, editor, *Carnivore Behavior, Ecology, and Evolution*, pages 495-535. Ithaca: Cornell University Press.

Wroughton, R.C.

1910. On the Nomenclature of the Indian Hedgehogs. *Journal of the Bombay Natural History Society*, 20(1):80-82.

Wyss, A.R.

1987. The Walrus Auditory Region and the Monophyly of Pinnipeds. *American Museum Novitates*, 2871:1-31.

Yates, T.L.

1984. Insectivores, Elephant Shrews, Tree Shrews, and Dermopterans. In S. Anderson and J.K. Jones, Jr., editors, *Orders and Families of*

*Recent Mammals of the World*, pages 117-144. New York: John Wiley & Sons.

Zaitsev, M.Y.

1982. *Sistematicheskii analiz taksonov podsemoeisva ezhovykh (Mammalia, Erinaceinae) fauny SSSR* [Systematic Analysis of the Taxa in the Subfamily of Hedgehogs ... of the Fauna of the USSR]. 22 pages. Leningrad: Avtoreferat, Minist. Vyssh. i Spred. Spets. Obraz. RSFSR.

1984. K sistematike i diagnostike eshei podroda *Erinaceus* (Mammalia, Erinaceinae) fauny SSSR [On Systematics and Diagnosis of Hedgehogs of the Subgenus *Erinaceus* ... of the Fauna of the USSR]. *Zoologicheskii Zhurnal*, 63:720-730.

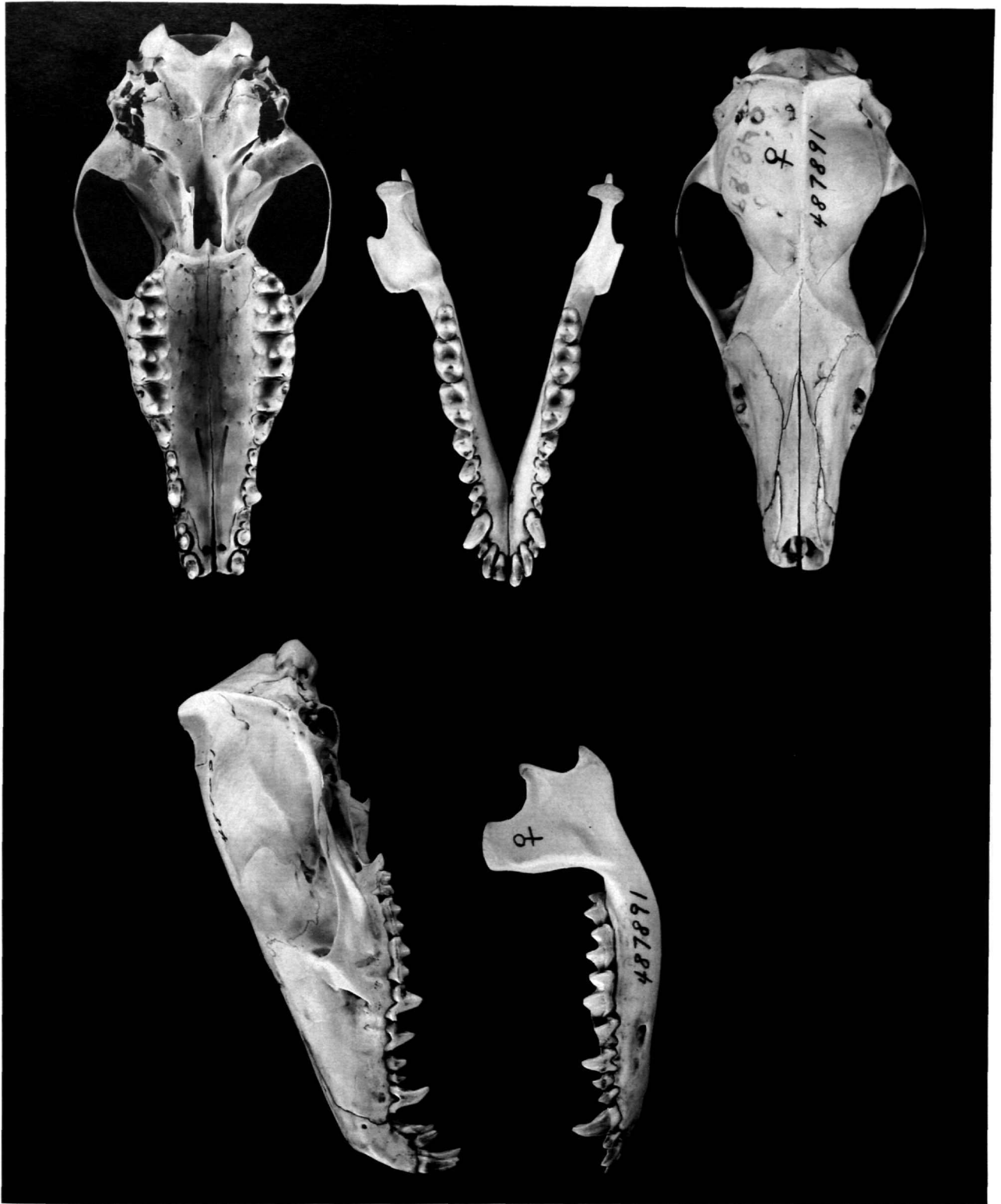


PLATE 1.—*Echinorex gymnura*, USNM 487891, ♀. Malaysia: Selangor; Klang; Tanjong Duablas, Kuala Langat Forest Reserve, Bukit Mandol (2°55'N, 101°34'E). CBL = 73.45 mm.

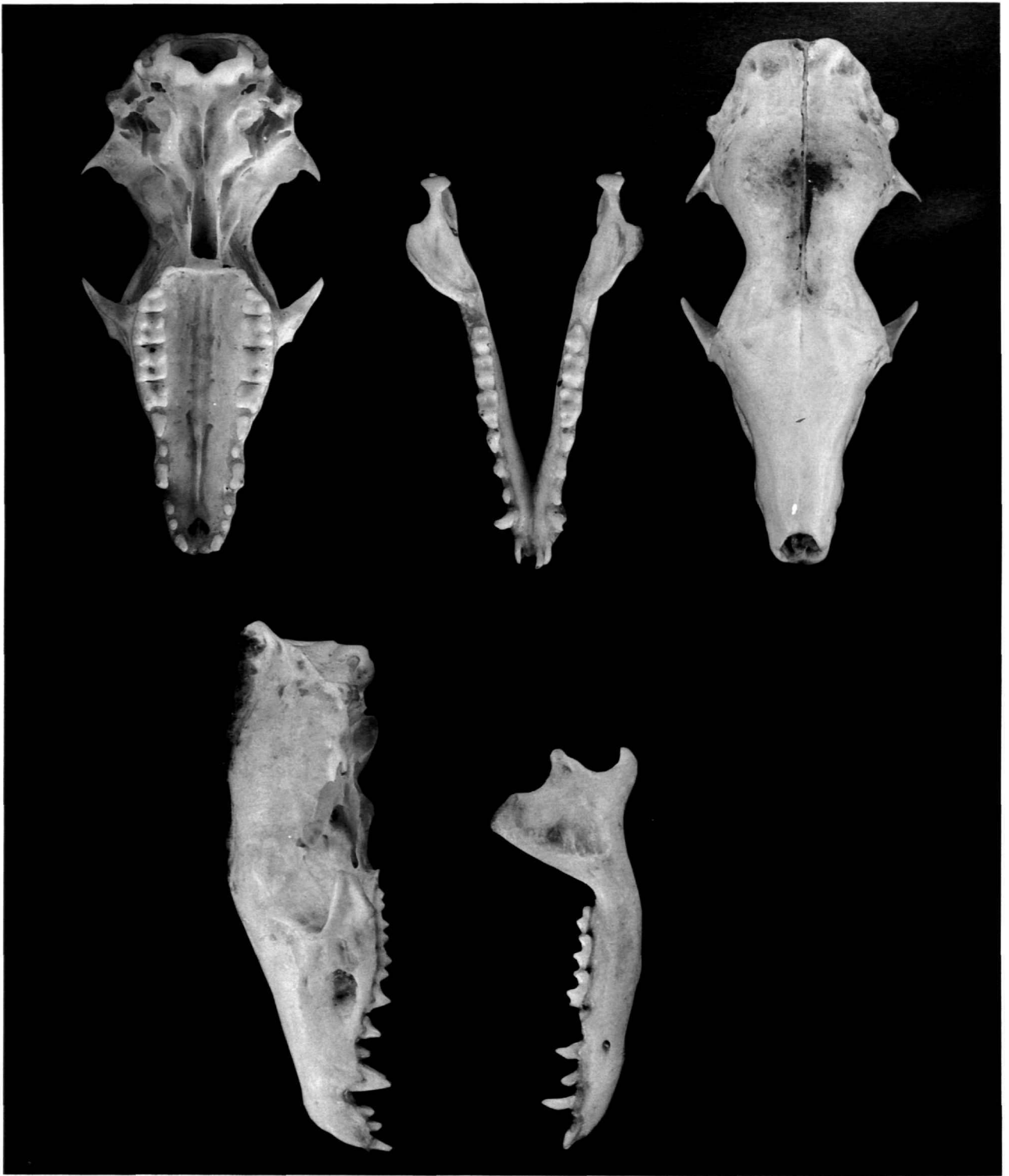


PLATE 2.—*Podogymnura aureospinula*, UPBL 3753, ♂. Philippine Islands: Dinagat Island; Loreto Municipality, Balitbiton. CBL = 52.02 mm.

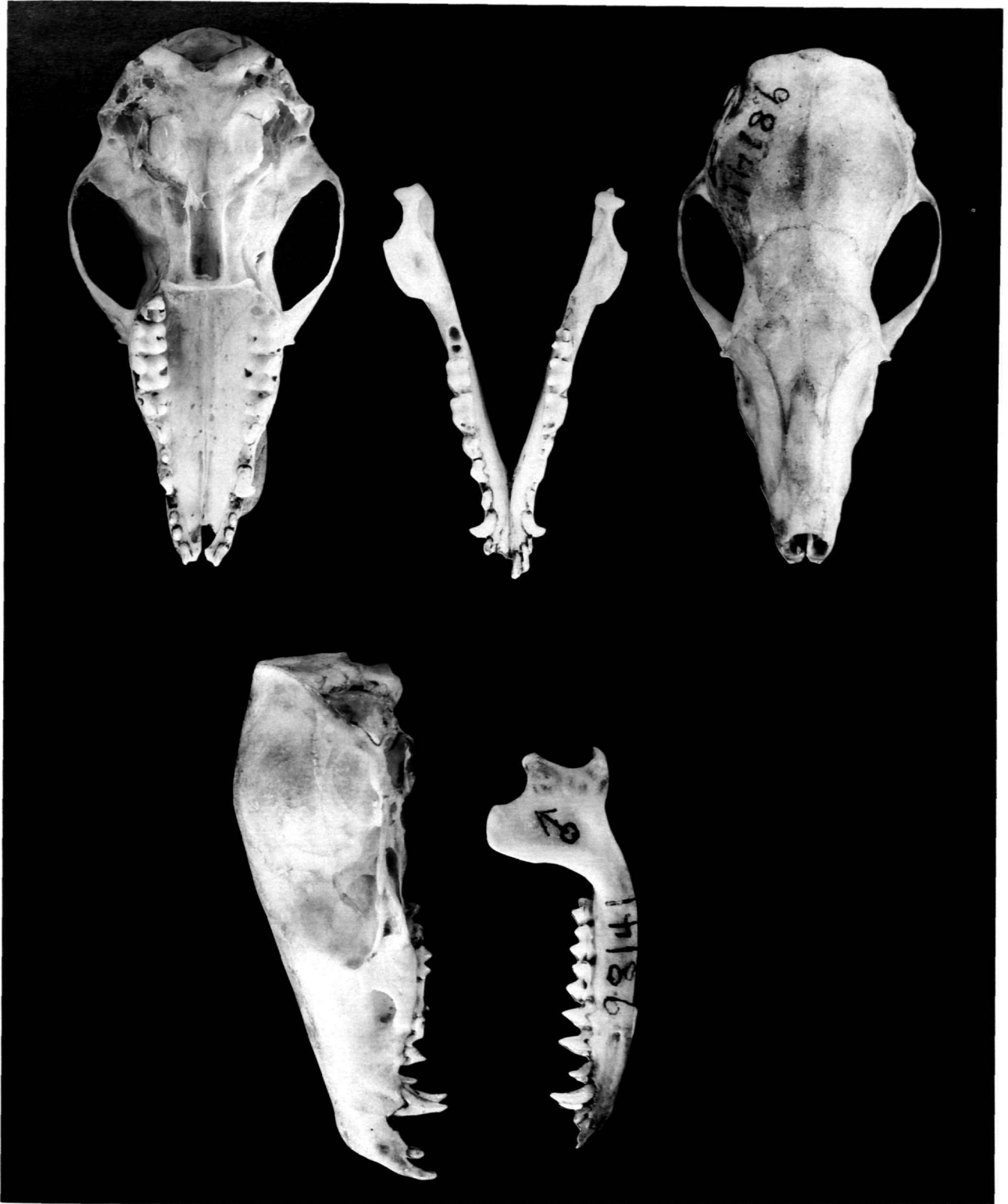


PLATE 3.—*Podogymnura truei*, KU 98141, ♂. Philippine Islands: Mindinao Island. CBL. = 38.25 mm.



PLATE 4.—*Hylomys hainanensis*, BEIJ 70875, ♂. China: Hainan Dao. CBL = 34.82 mm.



PLATE 5.—*Hylomys sinensis*, USNM 241402, ♂. China: Yunnan; Ho Mu Shu Pass, on main Yung-Chang to Teng-yueh Road. CBL = 28.34 mm.



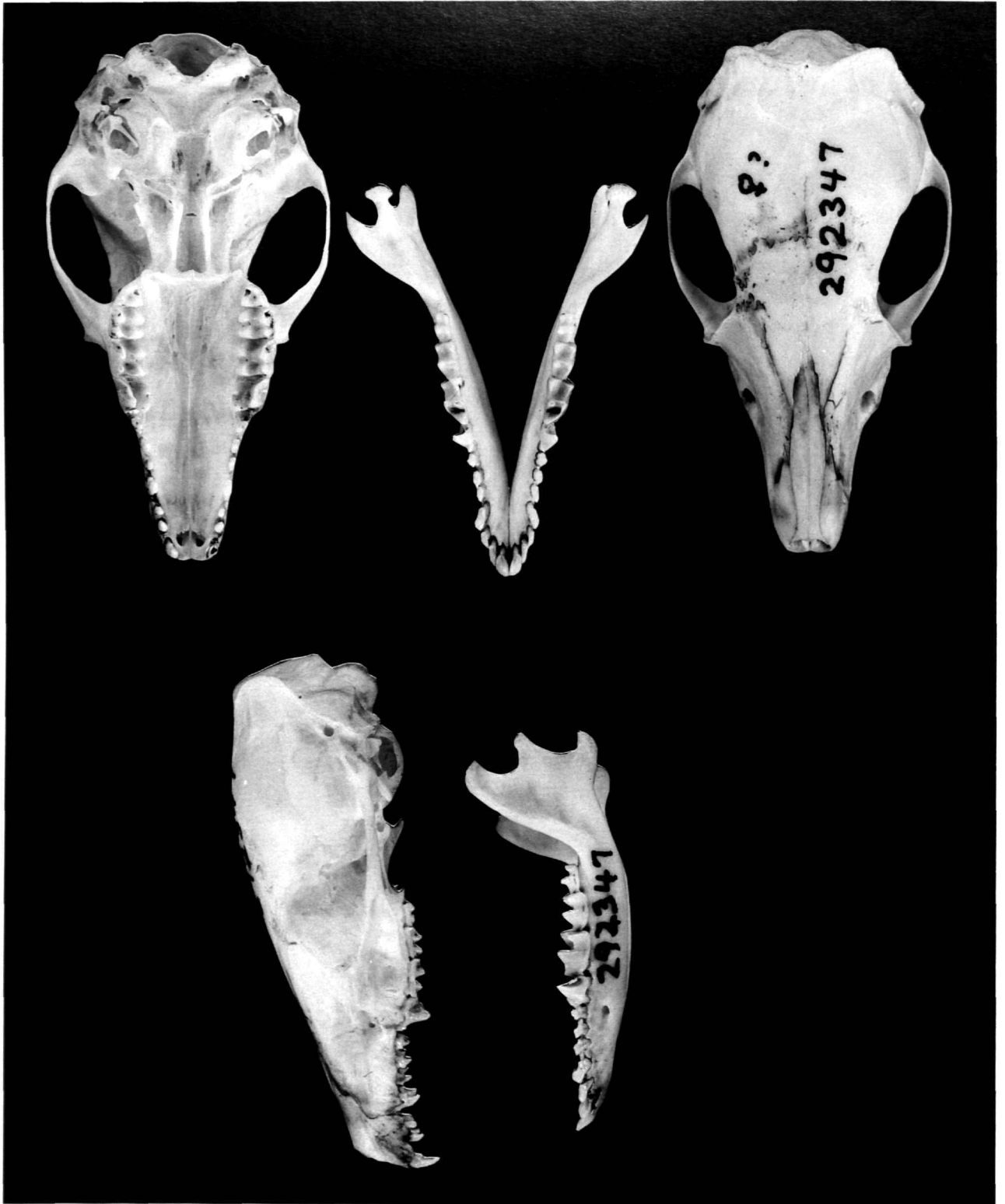


PLATE 6.—*Hylomys suillus*, USNM 292347, ♀. Malaysia: Sabah; Mount Kinabalu; Bundu Tuhan. CBL = 34.00 mm.



PLATE 7.—*Atelerix albiventris*, USNM 181442, ♀. Kenya: South Nguasso Nyiro; Loita Plains. CBL = 40.20 mm.

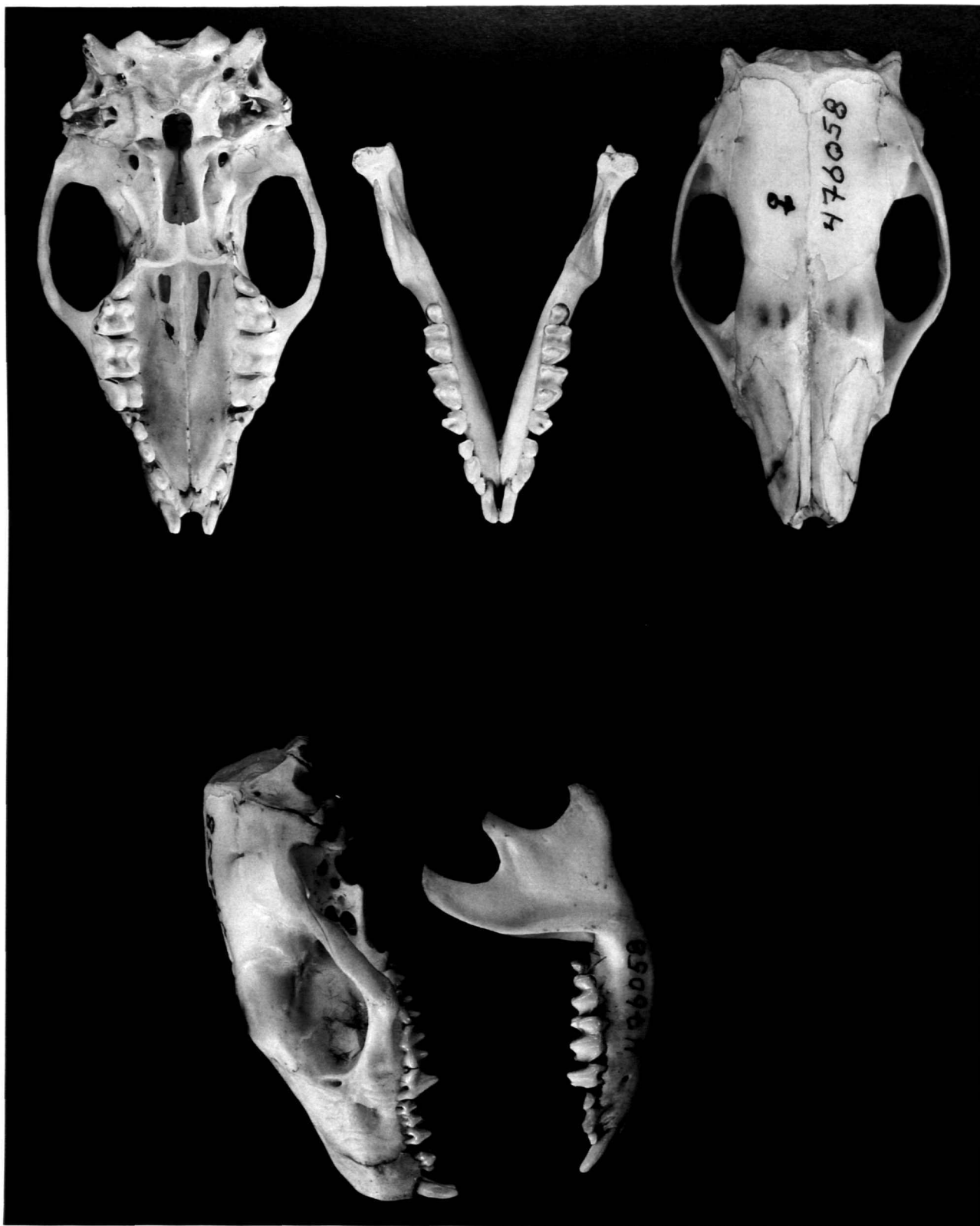


PLATE 8.—*Aterix algirus*, USNM 476058, ♀. Morocco: Agadir, 8 km N of Tamri (30°20'N, 9°50'W). CBL = 57.62 mm.

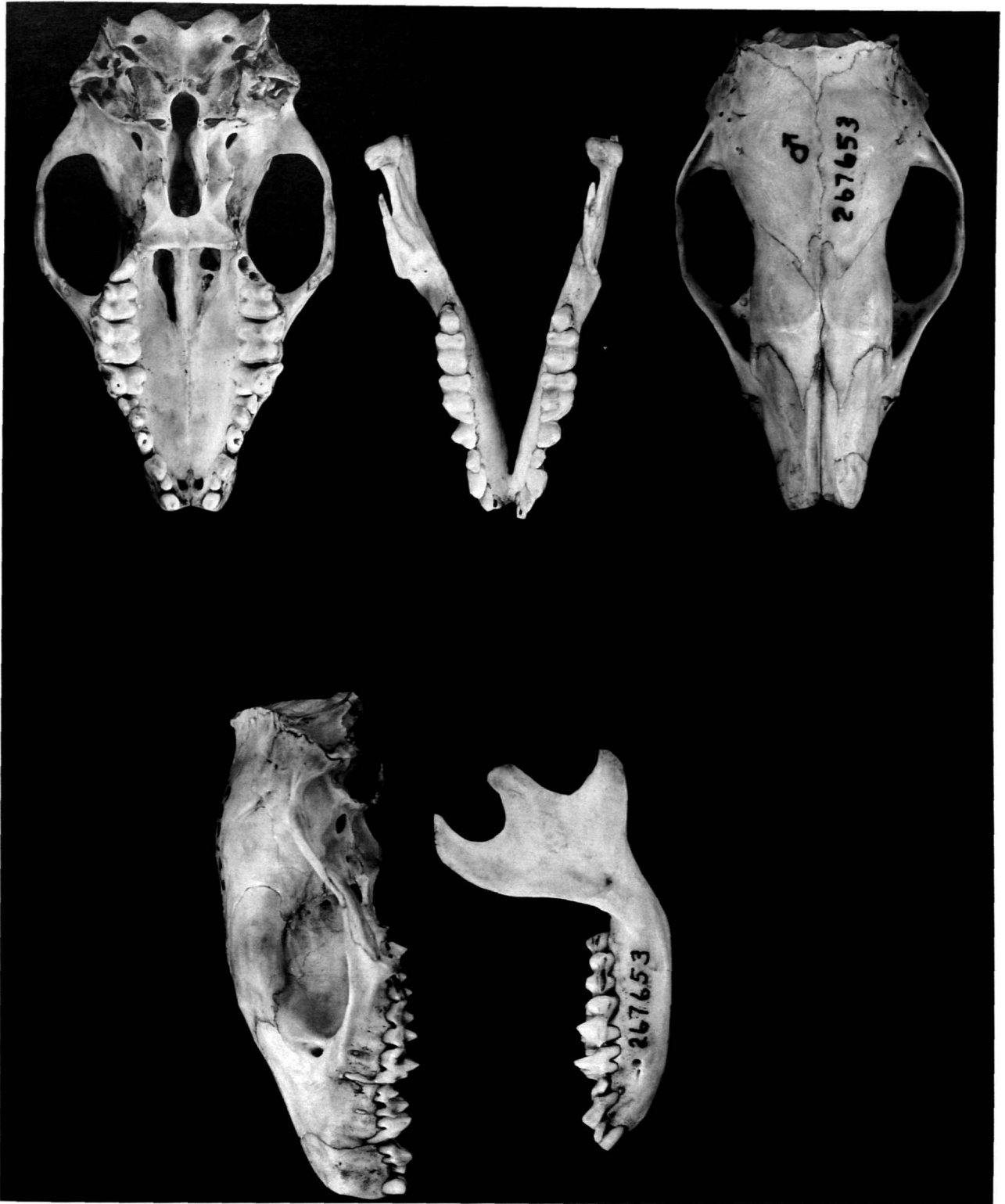


PLATE 9.—*Atelerix frontalis*, USNM 267653, ♂. South Africa: Transvaal; Pretoria District. CBL = 47.41 mm.

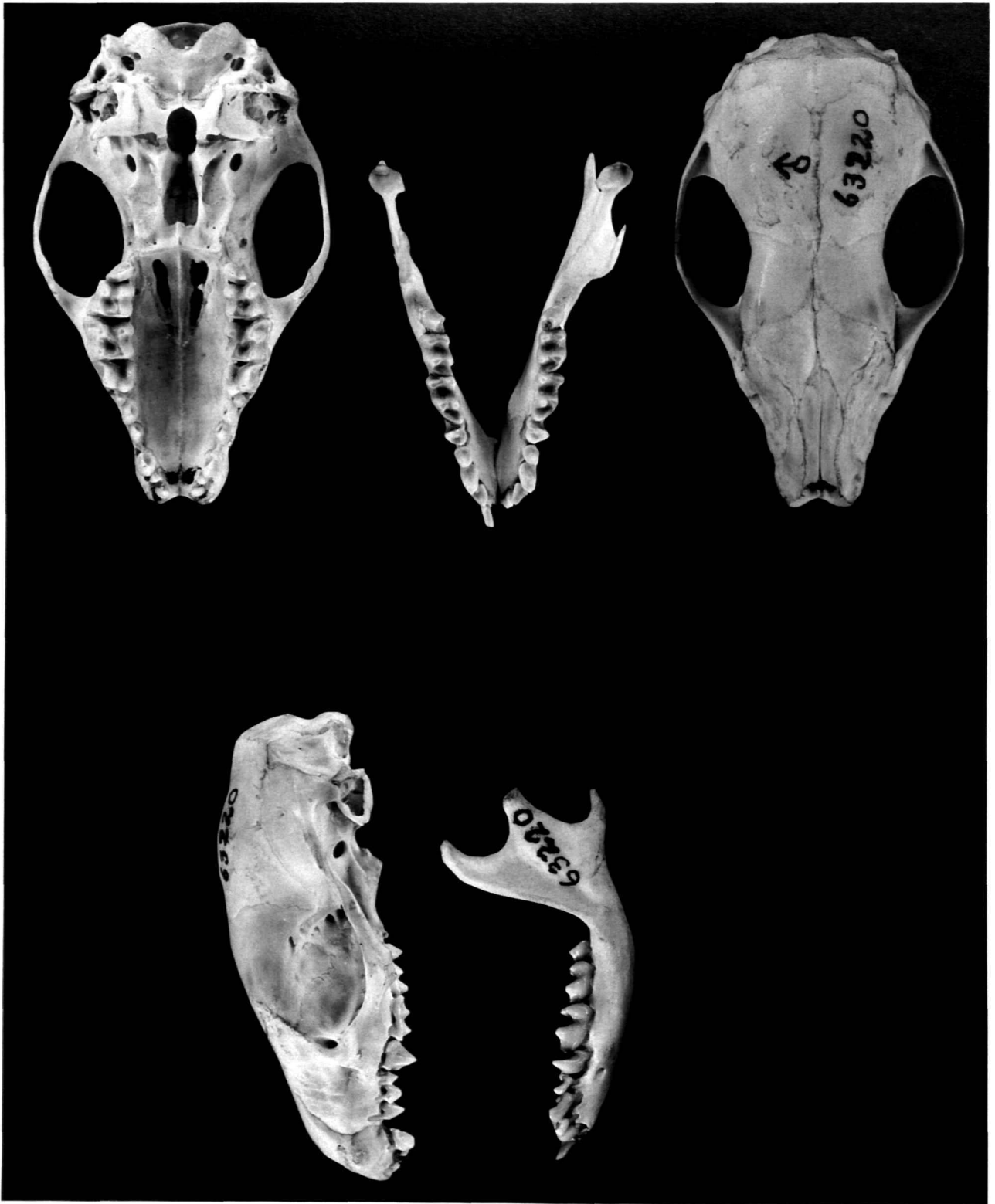


PLATE 10.—*Aterix sclateri*, USNM 63220, ♂. Somaliland: Berbera. CBL = 39.85 mm.



PLATE 11.—*Erinaceus amurensis*, USNM 197779, ♀. China: Kirin [Manchuria]; 60 mi SW on Sungaree River.  
CBL = 48.80 mm.





PLATE 12.—*Erinaceus concolor*, USNM 369533, ♂. Iran: Khuzistan; Dorud, 5 km NW. CBL = 58.91 mm.



PLATE 13.—*Erinaceus europaeus*, USNM 153410, ♂. United Kingdom: England; Surrey. CBL = 55.70 mm.

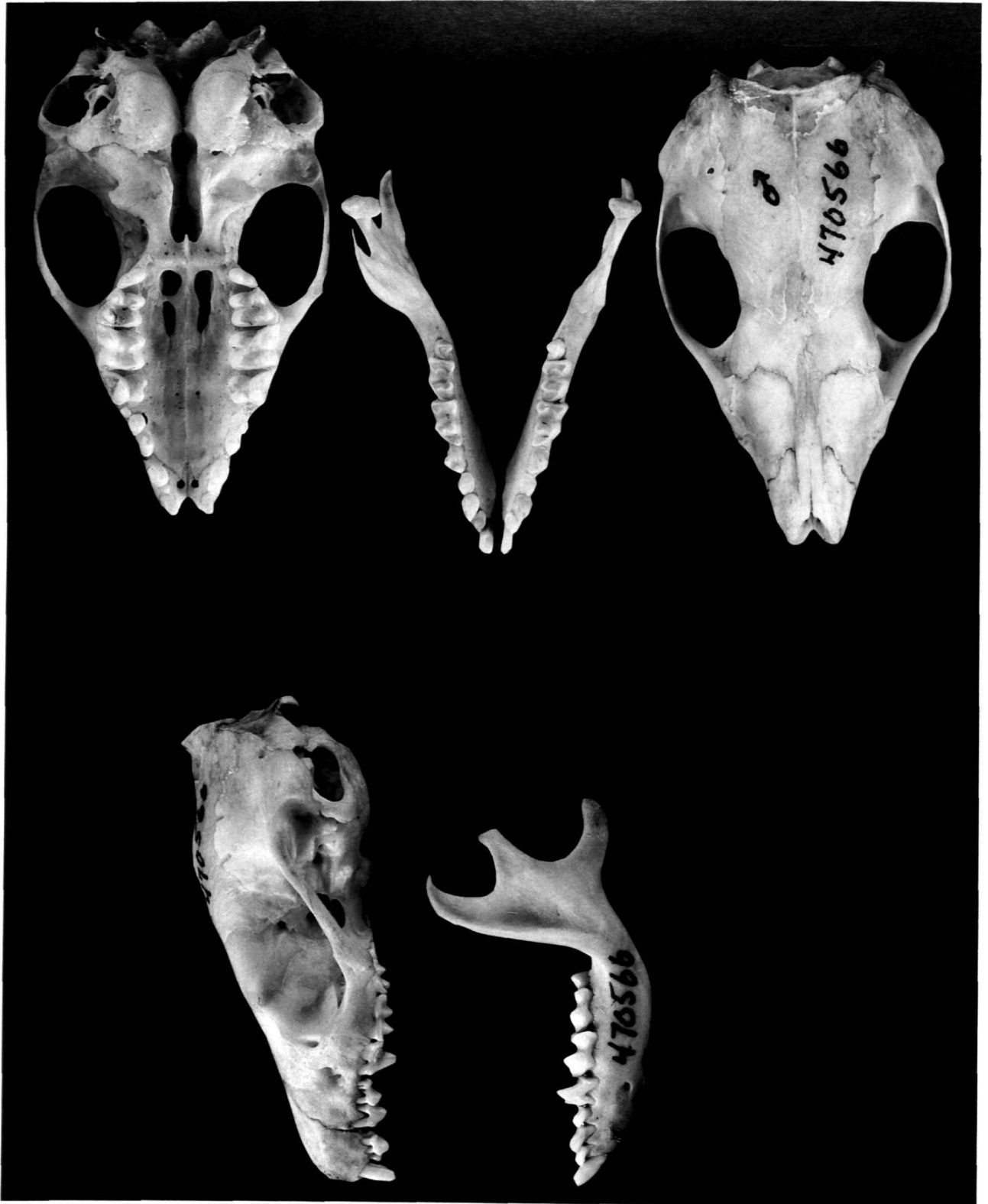


PLATE 14.—*Hemiechinus aethiopicus*, USNM 470566, ♂. Morocco: Ouarzazate; Tazarine, 3 km NW (30°48'N, 5°36'W). CBL = 48.90 mm.



PLATE 15.—*Hemiechinus auritus*, USNM 340933, ♂. Iran: Mazanderan; 28 km W of Gorgan, on Su River near Gharareh. CBL. = 49.40 mm.

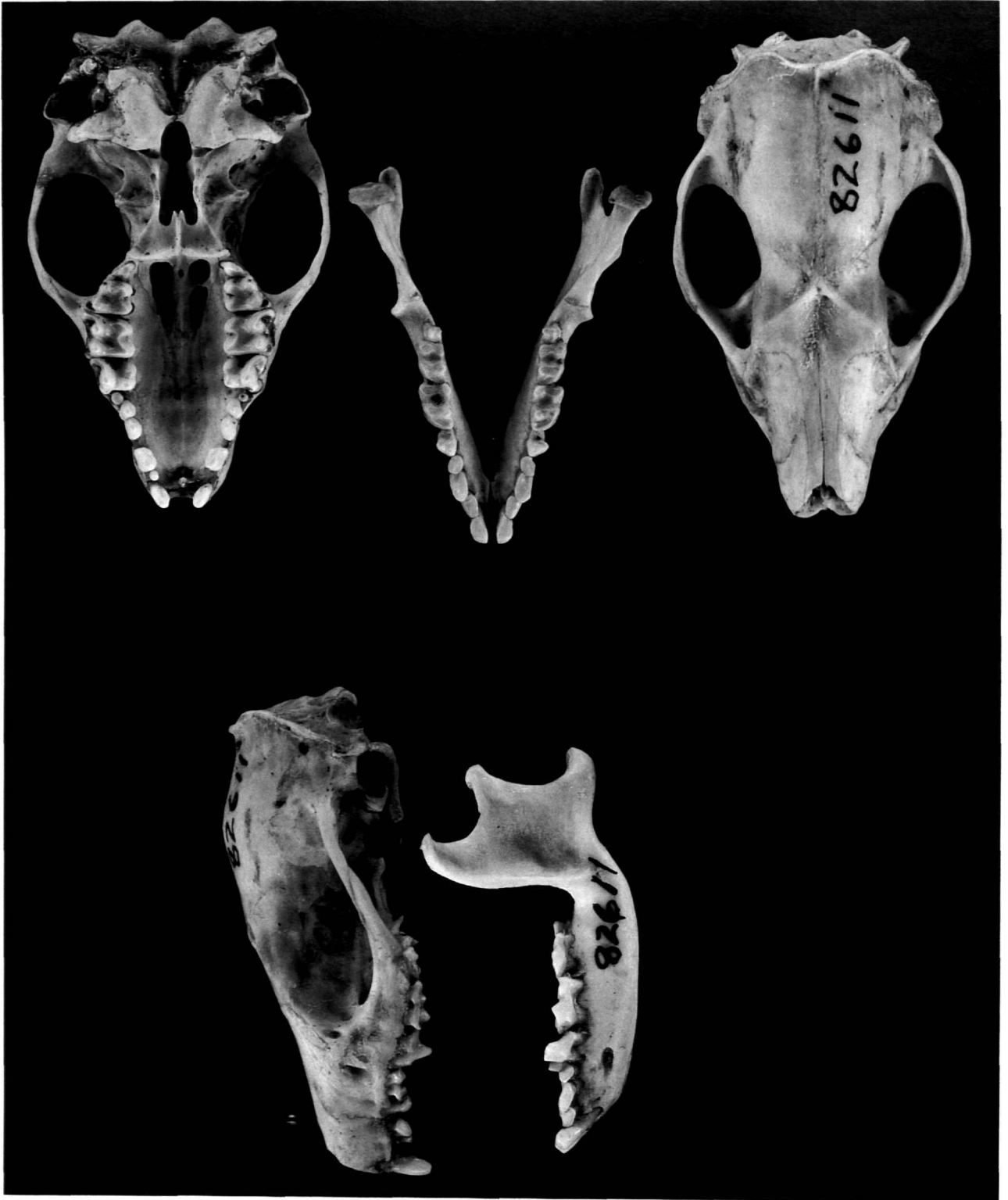


PLATE 16.—*Hemiechinus collaris*, FMNH 82611, ♂. India: Gujerat. CBL = 47.40 mm.

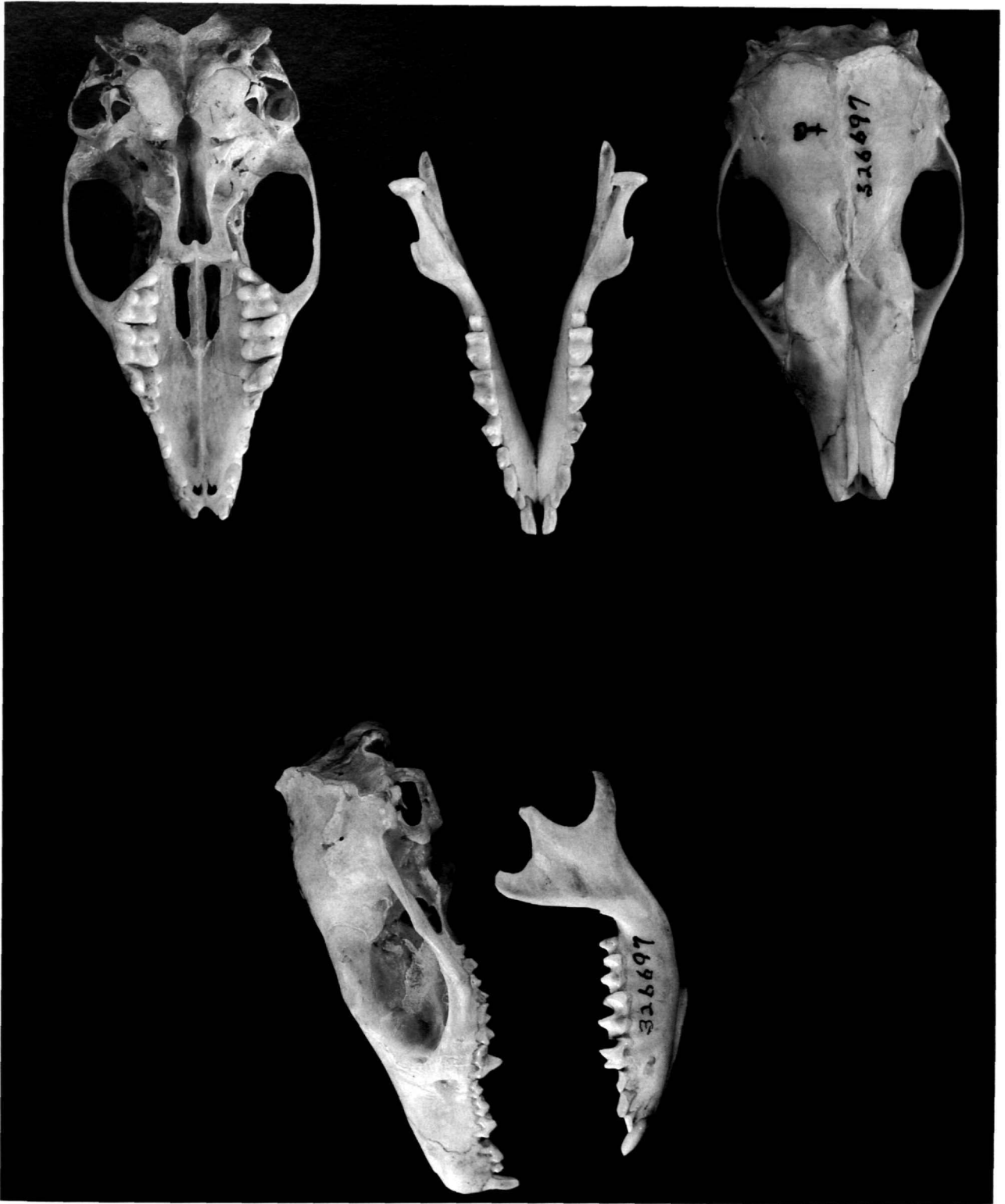


PLATE 17.—*Hemiechinus hypomelas*, USNM 326697, ♀. Iran: Khurasan; Turbat-i-Haidari. CBL = 54.90 mm.





PLATE 18.—*Hemiechinus micropus*, FMNH 82605, ♀, India: Kathiawar. CBL = 44.60 mm.



PLATE 19.—*Mesechinus dauuricus*, USNM 270539, ♂. China: Inner Mongolia; Northern Manchuria; Barga, Dalai Nor Lake at the mouth of the Urshun River. CBL = 49.65 mm.







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