THE SKULL OF LEPTICTID INSECTIVORANS AND THE HIGHER-LEVEL CLASSIFICATION OF EUTHERIAN MAMMALS

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CONTENTS

"The history of classification warns us against
taking superordinal groupings too seriously."
Gregory, 1910, p. 462

"The problem of relative affinities of various orders of
placental mammals is one on which the study of the
development of the skull can unfortunately throw but little
light, and when it comes to attempt a grouping of the various
orders *inter se,* grave difficulties are encountered."

DeBeer, 1937, p. 468

ABSTRACT

The excellent cranioskeletal representation of Early Tertiary leptictids permits broad comparisons with major groups of living and better preserved fossil mammals. Such comparisons reveal that leptictids are indeed closely related to lipotyphlan insectivorans. This conclusion supports interpretations dating back to the beginning of this century. Such interpretations were abandoned in the last two decades in favor of the view that leptictids were an isolated eutherian clade with no clear affinity to a particular eutherian order. Other eutherian higher categories supported by cranial homologies are an edentate-pholidotan group, a dermopteran-chiropteran group, a glires (rodent-lagomorph) group, a glires-macroscelidid group, an ungulate (sans tubulidentate) group, and a subset of ungulates comprising hyracoids, proboscideans, and sirenians. There is some evidence that the edentate-pholidotan clade represents a very remote branch of the Eutheria, and that all other major groups of eutherians form a monophyletic clade (cohort Epitheria). A higher-level classification of the Eutheria that reflects the stronger associations is proposed.

INTRODUCTION

Leptictids are an archaic group of eutherian mammals implicated in the origin and relationships of many higher taxa. The group is represented by a diverse fossil record from the North American Early Tertiary. Earliest bona fide members of the group (*Prodiacodon*) occur in early Paleocene faunas and last occurring taxa (*Leptictis*) extend to the late Oligocene (Novacek, 1977a). Cranial and skeletal remains are extremely abundant for *Leptictis* (now a senior synonym of *Ictops,* see Van Valen, 1967; Novacek, 1976). This wealth of information has attracted much attention from paleontologists.

Early studies (Gregory, 1910) established leptictids as an ideal example of a primitive placental mammal, well suited for close relationship with, or possible ancestry to, modern hedgehogs. This impression was strengthened by the notion that leptictids were "basal" lipotyphlan insectivorans and insectivorans were, in turn, the "stem" group for most of the eutherian orders. That notion was first explicitly criticized by Butler (1956). His comparisons showed that leptictids lacked many special cranial traits shared by "true" lipotyphlan insectivores. These conclusions were independently reached by McDowell (1958), who allied leptictids with tree shrews. Butler (1972) later claimed that leptictids were a distinct eutherian clade having no obvious phylogenetic connection with lipotyphlans or tree shrews, an interpretation widely endorsed (McKenna, 1975; Novacek, 1977a; Szalay, 1977; Kielan-Jaworowska et al., 1979).

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The title of this work bears more than coincidental resemblance to P. M. Butler's (1956) influential "The skull of *Ictops* and the classification of the Insectivora." Ultimately, it was a renewed consideration of that paper that prompted me to consider the problem of leptictid relationships from a new perspective. My interests in leptictids began with dissertation research that produced several publications (Novacek, 1976, 1977a, 1980, 1982a). At that time I was so convinced by Butler's (1956, 1972) separation of leptictids from lipotyphlans that I looked elsewhere for leptictid relationships. This pursuit led up several blind alleys (Novacek, 1980, 1982b). However, a recent comparison of mammalian skull features (Novacek, 1985) suggested that the case against insectivore-leptictid relationships was not yet closed. A more detailed attack of the problem was warranted. I thus commenced a detailed description of each element of the leptictid skull. Unlike previous studies, this paper accounts for the cranial and dental variation among leptictid genera, and provides a more comprehensive review of the homology of skull features through comparison with a rather broad sampling of mammalian taxa (table 3). These comparisons led me to venture some proposals for the higher-level classification of eutherian mammals, as discussed in the last section of this paper.

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cellent preparation of some cranial material. Bruce Haugh (formerly of the Department of Invertebrates, American Museum of Natural History) prepared the cranial sections (figs. 24, 25) with an annular rotary saw. Lisa Lomauro and Lorraine Meeker did the final layout and labeling of all figures.

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TERMINOLOGY

The nomenclature for molar crown morphology adopted here follows that of Van Valen (1966, p. 7–9) as modified by Rich (1971, p. 4). The term "premolariform" is usually expressed with explanation in the text. I follow Krishtalka's (1976, p. 5) designations: a premolariform last lower premolar is dominated by a single major cusp (protoconid) and a short, usually unicuspid, talonid. A premolariform last upper premolar bears only two major cusps, a protocone and a paracone. The notation for leptictid dental formula adopted here follows that proposed by McKenna (1975): I_3^{2-3} C_1^1 dP_1^1 P_2^2 P_4^4 P_5^5 M_1^1 M_2^2 M_3^3 (see justification in Novacek, 1977a, and below).

Skull terminology is basically the same as that used in McDowell (1958). This author provided a valuable list of definitions (pp. 121–129) for various cranial terms which, hitherto, had acquired diverse and often confusing meanings. Earlier definitions were provided by Klaauw (1931), Gregory (1910), Schaeffer (1942), and DeBeer (1937).

Nomenclature for the auditory cavity basically follows MacPhee (1981), who presented a very comprehensive glossary of terms for both embryonic and adult structures in the auditory region. Other sources of auditory terminology are MacIntyre (1972), Bugge (1974), Szalay (1975), Cartmill (1975), Archibald (1977), and Novacek (1977b).

The terminology used in many early studies of fossil endocasts is utterly confusing. Discussions on the problem of homologies and terminology of brain surface features by Sanides (1970) and Radinsky (1970, 1972) are very useful. However, a standardized nomenclature is clearly needed in this area of research (see also comments in Novacek, 1982a). I generally follow designations given by Radinsky (1972) and Jerison (1973).

Discussions of postcranial elements herein generally follow familiar anatomical texts (e.g., Romer, 1970). Details of the astragalo-calcaneal complex are based on the terminology used in Szalay and Decker (1974), and Szalay (1977) as modified by Cifelli (1983). Davis's (1964) monograph on the giant panda provides a detailed nomenclature for various aspects of mammalian anatomy.

Particular problems of anatomical terminology will be considered in the context of the comparative discussions below.

ABBREVIATIONS, ANATOMICAL

Teeth

C, canine
I, incisor
M, molar
P, premolar

Elements

AS, alisphenoid
BS, basisphenoid
B-OCC, basioccipital
DEN, dentary
DEN (Asc. Ramus), ascending ramus
DEN (Hor. Ram.), horizontal ramus
ECT, ectotympanic
ECT (c.-Sq.), caudal squamosal foot of the tympanic
ECT (r.-Sq.), rostral squamosal foot of tympanic
ENT, entotympanic
ETH, (mes)ethmoid
ETURB I, ectoturbinal I
ETURB I (Ex. Conch), locus of external conch of ectoturbinal I

ETURB I (Int. Conch), locus of internal conch of
ectoturbinal I
ETURB II (Int. Conch), locus of internal conch of
ectoturbinal II
EX-OCC, exoccipital
FR, frontal
JU, jugal
LA, lacrimal
MX, maxilla
MXTURB, maxillo turbinal (scar on internal
maxilla)
NA, nasal
NTURB, nasoturbinal
NTURB (ex. Conch), locus of external conch of
nasoturbinal
OS, orbitosphenoid
PA, parietal
PL, palatine
PMX, premaxilla
PR, petromastoid
PRS, presphenoid
PT, pterygoid
S-OCC, supraoccipital
SQ, squamosal
STAP, stapes
VO, vomer
VO (Post. W.), posterior wing of the vomer

Foramina, Fossae, Sulci

Acoust. F., acoustic foramen
Alis. Ca., alisphenoid canal
Ant. Pal. F., anterior palatine foramen
Ca. Int. V., canal for internal jugular vein
Ca. Spme. V., canal for suprameatal vein
Cond. Ca., condyloid canal
Cond. F., condyloid foramen
Do. Nas. Me., locus of dorsal nasal meatus
Epitym. Rec., epitympanic recess
Ept. Fos., ectopterygoid fossa
Eth. F., ethmoidal foramen
Eust. Ca., eustachian canal
Eust. F., eustachian foramen
Fallop. F., fallopian foramen
Fen. Oval., fenstra ovalis
Fen. Rot., fenestra rotunda
For. Mag., foramen magnum
For. Ov., foramen ovale
For. Subov., foramen subovale
Fos. Mm. Tens. Tymp., fossa for tensor tympani
muscles
Fos. Stap. Mm., fossa for stapedius muscle
Glas. Fis., Glaserian fissure
Glen. Fos., glenoid fossa
Hyp. F., hypoglossal foramen
Inc. F., incisive foramen
Inc. Vom., incisive vomeris
Infra. Ca., infraorbital canal

Infra. Ca. (Ant. O.), locus of anterior opening of
infraorbital canal
Infra. Ca. (Post. O.), locus of posterior opening of
infraorbital canal
Infra. F., infraorbital foramen
Ju. F., jugal foramen
Lacr. D., groove for lacrimal duct
Lacr. F., lacrimal foramen
Lev. Plp. Sup., pit for levator palbebrae superioris
Mas. F., mastoid foramen
Mass. Sc., masseteric scar
Mm. Inf. Obl., pit for inferior oblique muscles
Mx. Ant., maxillary antrum
Opt. F., optic foramen
Opth. F., ophthalmic foramen
Opth. Sulc., ophthalmic sulcus
Petr. F., petrosal foramen
Phar. Sulc., pharyngeal sulcus
Post. Lac. F., posterior lacerate foramen
Post. Vid. F., posterior vidian foramen
Postglen. F., postglenoid foramen
Postmas. F., postmastoid foramen
Postpal. F., postpalatine foramen
Sph. F., sphenopalatine foramen
Sphenorb. Fis., sphenorbital fissure
Spme. F., suprameatal fissure
Spme. Fos., suprameatal fossa
SQ. (Sin.-Ca.), squamosal sinus-canal
Sq. Tym. Fis., squamosotympanic fissure
Styl. F. Def., stylomastoid foramen (definitivum)
Styl. F. Prim., stylomastoid foramen (primitivum)
Subarc. Fos., subarcuate fossa
Sulc. Inf. Petr., sulcus of the inferior petrosal sinus
Sulc. Int. Car. A., sulcus for internal carotid artery
Sulc. Med., sulcus medialis (of petromastoid)
Sulc. Mm. Digas., sulcus for the digastric muscle
Sulc. Prom. A., sulcus for promontory artery
Sulc. Stap. A., sulcus for stapedial artery
Sulc. Tym., sulcus tympanicus
Supr. F., supraorbital foramina
Ven. F., venous foramen
Ven. Nas. Me., ventral nasal meatus
Vid. F., vidian foramen

Processes, Sutures, Septa

Ang. Pr., angular process
AS (Ect. Cr.), ectopterygoid crest of the alisphe-
noid
AS (Preot. Cr.), preotic crest of the alisphenoid
Cond. Pr., condyloid process
Cor. Pr., coronoid process
Cor. Sut., coronal suture
Crib. Pl., cribriform plate
Cris. Gal., crista galli
Do. Atlan. Fac., dorsal atlantal facet
Dors. Sel., dorsum sellae
ECT (Mal. Plt.), mallear plate of tympanic

FR (Orb. Pr.), orbital process of frontal
JU (Ant. Pr.), anterodorsal process of the jugal
JU (Do. Ant. Pr.), dorsal anterior process of the jugal
JU (Post. Sp.), posterior spine of jugal
JU (Ven. Ant. Pr.), ventral anterior process of jugal
Lacr. Tub., lacrimal tubercle
Lambd. Cr., lambdoidal crest
LA (P-orb. Cr.), preorbital crest of the lacrimal
Mas. Pr., mastoid process
Mas. Tub., mastoid tubercle (including tympanohyal)
Med. Cr. Supraocc., median crest of supraoccipital
Med. Petr. Cr., median petrosal crest
Met. Sut., metopic suture
Mm. Stap. Cr., crest for stapedius muscle
MX (Zyg. Pr.), zygomatic process of the maxilla
Occ. Cond., occipital condyle
Occ. Cond. (Do.), dorsal occipital condyle
Occ. Cond. (Ven.), ventral occipital condyle
OCC (Int. Pr.), interparietal process of occipital
Para. Cr., parasagittal crest
Parocc. Pr., paroccipital process
PA (Sq. Fac.), squamosal facet of parietal
PL (Ant. Orb. Pr.), anterior orbital process of the palatine
PL (Pars Per.), pars perpendicularis of the palatine
PMX (Rost. Pr.), rostral process of the premaxilla
PMX (Vom. Pr.), vomerine process of the premaxilla
Postglen. Pr., postglenoid process
Postpal. Sp., postpalatine spine
Postpal. Tor., postpalatine torus
Postym. Pr., posttympanic process
PR (Mas.)., mastoid exposure of petromastoid
PR (Mas. Pr.), mastoid process (of petromastoid)
Prom. Coch., promentorium cochleae
PR (Sq. Fac.), squamosal facet of petromastoid
PT (Ent. Cr.), entopterygoid crest (of pterygoid)
PT (Ham.), pterygoid hamulus
Postzyg. Cr., postzygomatic crest
SQ (Me. Su.), suprameatal surface of the squamosal
SQ (Preot. Cr.), preotic crest of the squamosal
SQ (Zyg. Pr.), zygomatic process of squamosal
Teg. Tymp., tegmen tympani
Tub. Sel., tuberculum sellae
VO (Sh.), shaft of vomer
Zyg. Pr., zygomatic process

Nerves, Arteries, Veins

Basil A., basilar artery
Cav. Sin., cavernous sinus
Cerebr. A., cerebral artery
Ch. Tymp., chorda tympani
Circ. Wil., circle of Willis
Cond. V., condyloid vein

Ex. Ju. V., external jugular vein
Inf. Petr. Sin., inferior petrosal sinus
Int. Car. A., internal carotid artery
Intcav. Sin., intercavernous sinus
Int. Ju. V., internal jugular vein
Int. Max. A., internal maxillary artery
Ling. N., lingual nerve
Mas. V., mastoid vein
Mm. Stap., stapedius muscle
M. Pal. F., middle palatine foramen
N. II, optic nerve
N. III, oculomotor nerve
N.V (mand.), mandibular branch of trigeminal nerve
N. VII, facial nerve
N. IX, glossopharyngeal nerve
N. X, vagus nerve
N. XI, spinal accessory nerve
N. XII, hypoglossal nerve
Occ. Sin., occipital sinus
Opth. A., ophthalmic artery
Opth. V., ophthalmic vein
Phar. A., pharyngeal artery
Phar. N., pharyngeal nerve
Pt. Can. A., artery of the pterygoid canal
Prom. A., promontory artery
Ram. Inf. Stap. A., ramus inferior of the stapedial artery
Ram. Sup. Stap. A., ramus superior of the stapedial artery
Sag. Sin., sagittal sinus
Spme. V., suprameatal vein
Sq. Sin., squamosal sinus
Stap. A., stapedial artery
Sup. Petr. Sin., superior petrosal sinus
Tens. Tymp. Mm., tensor tympani muscle (cut)
Trans. Sin., transverse sinus
Tymp. Plxs., tympanic plexus
Vert. A., vertebral artery
Vid. N., vidian nerve

ABBREVIATIONS, INSTITUTIONAL

AMNH, American Museum of Natural History
CMNH, Chicago Field Museum of Natural History
F:AM, Frick Collections; American Museum of Natural History
MCZ, Museum of Comparative Zoology, Harvard University
SDSM, South Dakota School of Mines
USNM, United States National Museum

METHODS

The basis for any inquiry into relationships among organisms is the discovery of homology. The term homology has multifarious

meanings in the biological literature. Herein, homology means the relation that characterizes monophyletic or natural taxa (Patterson, 1982; Stevens, 1984). Cast in evolutionary terms, homology implies the equivalence of features derived by common descent in related organisms (Tomlinson, 1984). This concept of homology merges with classical definitions of homology as essential structural correspondence (Owen, 1843) under one condition: that the taxonomic level of the structural correspondence is specified (Patterson, 1982). Hence, homologies are structural similarities that distinguish a given set of organisms from a more inclusive set. Other uses of homology concern iterative (serial, sexual, and antimeric) similarities (Ghiselin, 1976; Roth, 1984).

Owen (1843, 1848) was perhaps the first to explicitly distinguish homology from analogy. Analogy—which refers to resemblance in form and function derived from different sources—is akin to the phylogenetic usage of convergence and parallelism. Convergences are not homologies because they do not define monophyletic groups; they are misleading indicators of such groups. Despite Owen's concern for this problem, many currently used classifications—including several reviewed herein—do not reflect the consistent use of homologies to define groups. In other words, many groups (e.g., "reptiles" and "insectivores" in the classical, traditional sense) are paraphyletic; they are recognized for the *absence* of homologies.

The method of classification that seems most sensitive to the consistent use of homologies is phylogenetic systematics, or cladistics (Hennig, 1966). This is because homologies at specified levels can be equated with Hennig's (1966) synapomorphies—derived characters that define monophyletic taxa. The greatest contribution of Hennig's approach is its rigorous emphasis on synapomorphy and monophyly and its abandonment of paraphyly.

Cladistics is amply explained in many sources. Aside from Hennig's (1966) treatise, it is the subject of three recent textbooks (Eldredge and Cracraft, 1980; Wiley, 1981; Nelson and Platnick, 1981). It is also well represented in articles published between in 1973 and 1982 in the Journal of Systematic Zoology. A new journal, Cladistics, treats mod-

ern theory and application of Hennig's method. A few remarks here address issues of particular relevance to this study.

Hennig (1966) depicted organismic relationships in the form of branching diagrams or cladograms. Many authors accept cladograms as efficient summaries of character evidence, but they decry the conversion of this information into explicit, hierarchical classifications (see Mayr, 1974). This objection stems from a repellance to the proliferation of formal categories and highly unstable, complex classifications. However, the issue is not that classifications have too many names. The issue is simply whether or not the names represent groups that are reasonably supported by evidence of homology. In this light, it is odd that some students who shun supposedly unstable hierarchical classifications would continue to recognize and name paraphyletic groups (e.g., Carroll, 1982). Such groups, devoid as they are of any character definition, would hardly be expected to contribute to stable classifications.

Higher-level classifications of mammals traditionally lack hierarchical organization (but see McKenna, 1975). This lack of organization mirrors a poor understanding of genealogy, not just a resistance to the profligate use of formal names. Many superordinal names proposed by workers in the late 19th century and early 20th century have since been abandoned because they represent groups of doubtful validity. These names are readily available, assuming their use is justified by the discovery of stronger evidence for monophyly. If a pattern of phylogenetic relationships is well-corroborated by characters, it is *best* represented by a hierarchical classification.

Another problem that has foiled attempts to fashion higher mammalian classifications is the ambiguity of similarities between different orders. Hence Gregory (1910), mindful of Owen's (1843) distinction between homology and analogy, expressed doubts concerning apparent specializations shared by certain orders. Were these similarities the result of true homology or convergence? Very few mammalian orders are themselves defined by a large number of homologous characters. One might suspect that the same applies to any superordinal category recognized. How is this problem resolved? In cladistics,

the distinction of homologous structures from convergence takes the form of a parsimony argument. The hypothesis of relationships favored is the simplest, in the sense that it requires the fewest ad hoc explanations to protect it from contradictory evidence (Platnick, 1977). The contradictory data in this case are features consistent with alternative patterns of relationships. The ad hoc explanation is that such contradictory characters are, in reality, instances of homoplasy (character convergence, parallelism, or reversal). Hence the most parsimonious statement of relationships for any set of comparative data is that allowing the fewest instances of homoplasy.

Some biologists (Felsenstein, 1978; Cartmill, 1981) dispute this formulation, arguing that parsimony may be a misleading indicator of phylogenetic relationships. This claim usually stems from one or more of the following premises: (1) parsimony cannot be a scientific procedure in accord with definitions of science established by certain philosophers (Cartmill, 1981); (2) acceptable models of evolution are better inferred by statistical measures of maximum likelihood (Felsenstein, 1978); (3) rampant homoplasy, and thus unparsimonious evolution, is a biological reality (Hecht, 1976; Kirsch, 1982; Kirsch and Archer, 1982); and (4) a direct analysis of parsimony ignores the relative phylogenetic weight of different features (Kirsch, 1982).

Some of these premises, while conceivably valid at certain levels, do not lead one to abandon parsimony as a method in systematics. Weighted characters, for example, can be analyzed parsimoniously. Farris (1983) has skillfully addressed criticisms of parsimony and does not find them effective. Indeed, it is difficult to claim that parsimony is dispensable in the absence of any foreknowledge or presumption about true genealogy (Sober, 1983). The issue of character weighting and parsimony bears directly on matters arising in this study, and the issue will be considered briefly here.

It is difficult, perhaps absurd, to claim that all kinds of features are equally reliable as evidence for relationship. Some traits are more likely to arise independently and more frequently than others. Historical events (e.g., mutation or heterochrony in ontogeny) may effect certain character transformations more readily than others. This acknowledgment is, however, far from accepting an argument for the a priori weighting of characters (e.g., Hecht, 1976). Such arguments fail to convince. To say, for example, that biomolecular and physiological characters have a higher phylogenetic weight than anatomical characters (Kirsch, 1982) presupposes theories of evolutionary change that are, at best, highly contentious (Goodman et al., 1982). The only convincing case for a priori weighting applies strictly to characters of little information content. For example, the absence of a trait in adult organisms, inferred as a "loss" character, is ambiguous. With little or no developmental information, it cannot be established whether the condition represents a derived loss or simply the retention of the state preceding the acquisition of the character (Hecht, 1976).

Does some program of character weighting have a place then in systematic analysis? Given the current lack of evolutionary explanations, the only conceivable basis for weighting comes from the distributions of the characters themselves. Characters that seem to unite many species into large monophyletic groups and repeatedly resist contradiction (the vertebrate eye, bird feathers, mammal ear ossicles) are compelling as features of "high-weight" (Patterson, 1982). Conversely, characters that pop up in apparently unrelated taxa, or if used as evidence for monophyly face strong contradiction, are characters of low weight. Hence, homologies weigh themselves (Riedl, 1979; Patterson, 1982) and their relative strengths are shown by distributions of relevant characters. The strength of the character evidence can be measured for its ability to produce branching sequences that very efficiently describe the distributional pattern of the characters (figs. 31, 32). The resulting hypothesis of relationships is further corroborated if the addition of many other characters fails to contradict the original geometry of the branching pattern (cf. figs. 32 and 33 and Appendix).

PREVIOUS WORK

The following inauspicious notice appeared in the Proceedings of the Academy of Natural Sciences of Philadelphia (1868, p. 315):

"Dr. Hayden, in his trip to the Mauvaises Terres of White River, Dakota, in the summer of 1866, discovered the remains of two genera of insectivorous mammals, which appear to be peculiar, but related to the hedgehogs."

The author of that report, Joseph Leidy, continued with a brief description of the genera, which he named *Leptictis haydeni* and *Ictops dakotensis*. Gill (1872) was uncertain of the relationships of leptictids, indicating their position within the Insectivora as incertae sedis. However, many other workers endorsed Leidy's interpretation; the affinities of leptictids with erinaceids were recognized by Schlosser (1887), Matthew (1903, 1918, 1937), Gregory (1910), Abel (1928), Scott and Jepsen (1936), and Simpson (1945). Gregory (1910) included leptictids, erinaceids, and dimylids in his section Erinaceomorpha (see table 1). The superfamily Erinaceoidea of Scott and Jepsen (1936) and Simpson (1945) was essentially similar in content to Gregory's Erinaceomorpha. Matthew (1903) further emphasized leptictid-hedgehog relationships by recognizing leptictids as a subfamily of the Erinaceidae.

Early workers did not restrict the possible affinities of leptictids to a consideration of erinaceoids. Schlosser (1887) and Winge (1917) noted resemblances to tupaiids. Gregory (1910) made detailed comparisons of the skull of *Leptictis* (=*Ictops*) with other insectivores and concluded that leptictids were more primitive than erinaceids and showed affinities with *Solenodon* and tenrecids. Cope (1884) was also impressed with the similarities between leptictids and *Solenodon* and *Potamogale*. Resemblances to marsupials and carnivores were observed by Leidy (1869a, 1869b), and by Cope (1884), who placed *Leptictis* in the creodont family Proviverridae.

In his review of the early taxonomic work on leptictids, Simpson (1945, p. 177) made the following statement:

The peculiar †leptictids have been supposed to show relationships with the †creodonts and with the primates. The former resemblance is now shown to be surely misleading, as regards any ordinal affinity. The resemblance to the primates seems to be more real and deep-seated, but it is unlikely that it indicates anything more

than that primitive insectivores of more or less erinaceoid stamp gave rise to primates. That the †leptictids are most closely related to the erinaceids is now a well-supported theory. Several fossil genera might equally well be referred to either family on present knowledge, and the sorting of the varied genera referred with greater or less confidence to the †Leptictidae is not yet satisfactorily accomplished.

Saban (1954) basically endorsed Simpson's inclusion of the Leptictidae within the superfamily Erinaceoidea.

It was not until the late 1950s that the alleged close relationship of leptictids with erinaceids was seriously questioned. Following a detailed analysis of the skull of *Leptictis* (including *Ictops*), Butler (1956) concluded that leptictids were much more primitive than any known erinaceid and at the same time possessed several uniquely derived (autapomorphous) characters which separated them from the latter. Butler (ibid.) claimed that the characters leptictids share with erinaceids are nearly entirely primitive and not indicative of special relationship. Accordingly, he removed the Leptictidae from the Erinaceoidea and placed it in a separate superfamily, the Leptictoidea. According to the phylogenetic hypothesis argued by Butler (1956), the Leptictoidea was the earliest divergent lineage of the order Lipotyphla, a more restricted category of "insectivores" that excluded macroscelidids and tupaiids. He divided the Lipotyphla into the suborder Erinaceomorpha, a primitive group consisting of the Leptictoidea and Erinaceoidea and the suborder Soricomorpha, a specialized group comprising the Tenrecoidea, Soricoidea, and Chrysochloroidea (table 1). In an addendum, Butler (1956) commented that, because of McDowell's assessments (1958 and unpublished MS), he was less convinced of his association of leptictids and lipotyphlans.

McDowell developed a comparative study of the skull of *Leptictis*, but he abandoned this work when he learned of the completion of Butler's study (McDowell, 1958, and personal commun.). McDowell was in basic agreement with Butler on the lack of erinaceoid-leptictid relationships. Moreover, he excluded leptictids from the Lipotyphla altogether and argued that they were closely

related to the Tupaiidae and should be placed either with that family, or, as he preferred, with the Menotyphla.

McKenna (1966) examined the basicranial anatomy of leptictids and concluded that that family, along with tupaiids, microsyopids, apatemyids, and mixodectids were nonprimates, but were close to the stock from which the primates originated at the beginning of the Tertiary Period.

Members of the Leptictidae were thought to be the possible "ultimate ancestors" of both tupaiids and primates by Van Valen (1965). Reasons for putative tupaiid-leptictid affinities were shared features (1) in the reduction of the medial internal carotid artery, (2) the entotympanic bulla, and (3) the retention of the major branches of the lateral internal carotid artery. Van Valen (1965) noted, however, that these features may be present in skulls of Paleocene or Eocene erinaceoids yet to be discovered. He acknowledged that derivation of tupaiids from erinaceoids was equally likely. The direct leptictid-primate relationship was, in Van Valen's (1965, p. 148) words, "even less secure," and he entertained McKenna's (1960) suggestion that the Microsyopidae perhaps represent "collateral ancestors" of primates.

In his formal classification of the order Insectivora, Van Valen (1967, pp. 258–259) allocated the Leptictidae (including *Procerberus* and *Gypsonictops*) to Romer's (1966) "waste-basket" suborder, the Proteutheria. Also included within this group were the Zalambdalestidae, Anagalidae, Paroxyclaenidae, Tupaiidae, Pantolestidae, Ptolemaiidae, Pentacodontidae, and Apatemyidae. Thus Van Valen (1967) implied that leptictids bore only a remote affinity with erinaceids, although he suggested a possible ancestor-descendant relationship between leptictids and erinaceids via the poorly characterized and misnamed "Adapisoricidae" (see Novacek, 1982c; Bown and Schankler, 1982).

Szalay (1968a, 1968b) argued, however, that leptictid ancestry for the Apatemyoidea and Erinaceoidea (sensu Van Valen, 1967) was unlikely, maintaining that leptictids have several dental characters more advanced than the molar construction in either apatemyids or erinaceoids. He further suggested the independent origin of leptictoids and erinaceoids from separate Cretaceous stocks, and advocated this separation on the ordinal or subordinal level (although Van Valen, 1967, had already taken the latter action).

In his review of the Microsyopidae and Mixodectidae, Szalay (1969, p. 319) remarked that primates may have evolved during the latter part of the Cretaceous from one of three possible groups: (a) unknown stocks of leptictids; (b) erinaceoids, or (c) primitive condylarths. Szalay (1969) argued that any phyletic connection between *Procerberus* (recognized as an early leptictid by Van Valen, 1967, but later included in the Palaeoryctidae by Lillegraven, 1969) and earliest primates was improbable. The basicranial similarities between tupaiids, microsyopids, and leptictids were also observed by Szalay (1969, p. 311), but, like other workers, he was conservative in weighting such characters heavily in phylogenetic determinations because of the lack of good specimens representing late Cretaceous to early Paleocene leptictids and primates.

According to McKenna (1969, p. 233), the Leptictidae occupied a central role in eutherian evolution and diversification. McKenna recognized the leptictids to be plausible ancestors of tupaiids, microsyopids, primates, "proto"-rodents, pantolestids, and other mammalian lineages. Lillegraven (1969, p. 59) believed the oldest North American leptictid taxon, *Gypsonictops,* to be the possible ancestor of erinaceids, pantolestids, primates, and rodents, thus espousing a taxonomic view generally in agreement with McKenna (1969) and Van Valen (1965, 1967).

The recent discovery of additional fossils of Late Cretaceous eutherians from the Gobi Desert, Mongolia, reopened the question of leptictid origins. Among these were *Kennalestes* Kielan-Jaworowska (1969) and more complete material of *Zalambdalestes* Gregory and Simpson (1926) (see Kielan-Jaworowska et al., 1979). Both genera were allocated to the superfamily Leptictoidea by Kielan-Jaworowska (1969), but *Zalambdalestes* has since been removed from this grouping by Kielan-Jaworowska et al. (1979). *Kennalestes* was, however, separated from unquestioned leptictids because of its more

primitive features in the premolars and in the development of the nasal elements.

Butler (1972) modified his earlier (1956) views regarding leptictid affinities by excluding the family from the suborder Erinaceomorpha and order Lipotyphla. He reemphasized that features of the ear region and orbital wall in leptictids preclude their relationship with erinaceoid Lipotyphla, and the similarities between the two groups were, in the main, primitive eutherian features. Butler (1972, p. 263) also doubted the leptictid affinities of *Gypsonictops* and endorsed Lillegraven's (1969) reallocation of *Procerberus* to the Palaeoryctidae. Butler (1972) placed the Leptictidae, along with plagiomenids, palaeoryctids, apatemyids, and pantolestids in the waste-basket order Proteutheria, acknowledging that better fossil material and further study might lead to the dissolution of this category.

The affinities of *Gypsonictops* were examined in detail by Clemens (1973), who suggested that this Cretaceous genus was possibly a member of a leptictid subgroup that was ancestral to erinaceoids, apatemyids, pantolestids, pentacodontids, and primates. He emphasized, however, the attendant problems and uncertainties in deriving any of these relationships. Subsequently, Clemens (1974) expressed agreement with Szalay (1968a) that leptictids were not good candidates for the ancestry of primates because of their dental specializations (including extensive molarization of the last premolars, sharp differentiation of the postcingulum from the protocone, basic functional differences in occlusion, and anteroposterior compression of high trigonids).

Return of leptictids to the proximity of primate ancestry was, however, suggested by Bown and Gingerich (1973). These authors argued that the diagnostic features of primate molar morphology evolved from a molar condition approximated in leptictids before the characteristic primate petrosal bulla was acquired. Thus they implied that the earliest primates departed from leptictids in molar specializations but retained leptictid basicranial features, particularly an entotympanic bulla. Their hypothesis rests on the much contested ordinal affinities of microsyopids, a group that shows a combination of both leptictid and primate features.

In a review of tarsal morphology in Late Cretaceous eutherians and Paleocene primates, Szalay and Decker (1974) concluded that a broadly defined palaeoryctid-leptictid group probably gave rise to pantolestids, rodents, taeniodonts, and tupaiids, but excluded the group from either affinities or ancestry to condylarths, primates, carnivores, hyaenodontids, and anagalids.

Bugge (1974) proposed a classification of insectivores and other eutherian orders based on variation in the cephalic arterial system in which leptictids were regarded as a basal lineage of the Lipotyphla, retaining a basically primitive eutherian pattern in carotid circulation.

A radical reorientation of views on eutherian interrelationships has recently appeared with McKenna's (1975) phylogenetic classification of the Mammalia. One significant departure from former classifications was McKenna's (ibid.) recognition of a major eutherian clade, the magnorder Ernotheria, distinguished by differences in the hypothetical pattern of dental replacement and morphology, from most other eutherians. McKenna's Ernotheria comprises the Mongolian Cretaceous taxa *Kennalestes, Asioryctes,* and *Zalambdalestes*; anagalids (described and reviewed most recently by Szalay and McKenna, 1971); macroscelidids; and leptictids (table 1). Thus leptictids were made a sister lineage of other ernotheres and were removed from close relationship with tupaiids, primates, erinaceoid insectivores, and other "non-ernotherian" groups.

Szalay (1977) presented a mammalian classification that accounted for his excellent review of structure and variation in the proximal tarsus. In his arrangement, Szalay argued against a close relationship of leptictids with anagalids, macroscelidids, and lagomorphs (McKenna's 1975 Ernotheria) because of basic differences in dental and foot structure. He united leptictids with their supposed derivatives, the Pantolestidae and Taeniodonta, in the order Leptictimorpha. Szalay (1977) further maintained that *Cimolestes,* a genus McKenna (1975) interpreted to be allied with carnivores and creodonts, was more closely related to "bona fide" leptictids *Leptictis, Prodiacodon,* and *"Myrmecoboides,"* based on shared-derived astragalocalcaneal features. Thus Szalay's (1977) Lep-

TABLE 1
**Previous Higher-Level Classifications of the
Leptictidae and Selected Eutherian Groups**

1. Gregory (1910)
   Order Insectivora
     Section Erinaceomorpha
       Family †Leptictidae
       Family †Dimylidae
       Family Erinaceidae
2. Simpson (1945)
   Order Insectivora
     Superfamily Erinaceoidea
       Family †Zalambdalestidae
       Family †Leptictidae
       Family Erinaceidae
       Family †Dimylidae
     Superfamilies †Deltatheroidea, Tenrecoidea,
       Chrysochloroidea, Macroscelidoidea, Sori-
       coidea, †Pantolestoidea, †Mixodectoidea
3. Butler (1956)
   Order Lipotyphla
     Suborder Erinaceomorpha
       Superfamily †Leptictoidea
       Superfamily Erinaceoidea
     Suborder Soricomorpha
       Superfamilies Tenrecoidea, Soricoidea, Chrys-
         ochloroidea
4. McDowell (1958)
   Order Lipotyphla (including Erinaceomorpha and
     Soricomorpha)
   Order Menotyphla
     Family Tupaiidae
     Family †Zalambdalestidae
     Family Macroscelididae
     Family †Leptictidae
     Family †Pantolestidae
5. Van Valen (1967)
   Order Insectivora
     Suborder Proteutheria
       Superfamily Tupaioidea
         Families †Leptictidae, †Zalambdalestidae,
           †Anagalidae, †Paroxyclaenidae, Tu-
           paiidae, †Pantolestidae, †Ptolemaiidae,
           †Pentacodontidae
       Suborders Macroscelidea, Dermoptera (includ-
         ing Mixodectidae), Erinaceota (includ-
         ing Erinaecidae, †Dimylidae, Talpidae,
         Soricidae)
     Order Deltatheridia
       Suborders Hyaenodonta (including †Palaeoryc-
         tidae), Zalambdodonta (including Tenreci-
         dae, Chrysochloridae, Solenodontidae)
6. Butler (1972)
   Order Lipotyphla
     Suborders Erinaceomorpha (including †Adapi-
       soricidae, Erinaceidae, †?Dimylidae), Sori-
       comorpha (including Soricidae, Talpidae,
       and several extinct families), Tenrecomor-
       pha, Chrysochlorida

TABLE 1—*(Continued)*

   Order Scandentia (Tupaiids)
   Order Macroscelidea
   Order Proteutheria (including †Palaeoryctidae,
     †Plagiomenidae, †Apatemyidae, †Pantolesti-
     dae, †Leptictidae)
7. McKenna (1975)
   Magnorder Ernotheria
     Superorder †Kennalestida
     Superorder Leptictida
       Grandorder Ictopsia
       Grandorder Anagalida
         Order Macroscelidea
         Order Lagomorpha
   Magnorder Preptotheria
     Superorder †Deltatheridia
     Superorder Tokoþeria
       Grandorder Ferae (including some †palaeoryc-
         tids [*Cimolestes*], †didelphodontids,
         †pantodontids, †pantolestids, †apate-
         myids, and †taeniodontids)
         Order †Creodonta
         Order Carnivora
       Grandorder Insectivora
         Order Erinaceomorpha
         Order Soricomorpha
       Grandorder Archonta
         Orders Scandentia, Dermoptera, Chiroptera,
           Primates
     Eutheria, incertae sedis
       Order Rodentia
8. Szalay (1977)
   Cohort Glires
     Order Leptictimorpha (including the †Leptictin-
       ae and the †Palaeoryctinae as Leptictidae,
       the †Pantolestidae, †Taeniodontidae, and
       possibly †Microsyopidae)
     Order Rodentia
     Order Lagomorpha

tictimorpha included the Late Cretaceous
Cimolestes, Procerberus, and *Gypsonictops,*
even though other students, notably Lille-
graven (1969) and McKenna (1975), regard-
ed the first of these as palaeoryctoid insec-
tivorans. Among the other mammalian
orders, only the Rodentia was believed by
Szalay (1977) to be possibly closely related
to Leptictimorpha. However, he emphasized
that the specializations in the astragalocal-
caneal complex shared by the two orders could
be the result of convergence.

In an excellent review of Cretaceous eu-
therian mammals, Kielan-Jaworowska et al.
(1979) allocated *Gypsonictops* and *Kenna-
lestes* to the superfamily Leptictoidea, and

placed this grouping within the "waste-basket" order Proteutheria. These authors acknowledged Novacek's (1977a) removal of *Gypsonictops* from the Leptictidae, but they did not establish a new family for this genus.

Novacek (1980) considered the relationships of leptictids in a review on tupaiid affinities. He identified three derived features shared by leptictids, tupaiids, and macroscelidids (entotympanic bulla, superior astragalar foramen absent, and position of the lacrimal foramen). These similarities were in conflict with specialized characters shared by macroscelidids and tupaiids with other major eutherian clades. The resulting cladogram (Novacek, 1980, fig. 26) thus showed very poor resolution.

Table 1 lists some of the classifications reviewed above. These are, of course, derived from different premises and criteria. Some classifications are basically limited to fossil taxa, while others group leptictids with Recent orders. Only McKenna's (1975) classification might be considered cladistic—it allows a "read-out" of a more highly resolved cladogram. Many of McKenna's groupings were, however, undefined (see Hecht, 1976; Szalay, 1977; and remarks below).

COMPARATIVE MORPHOLOGY

The purposes of this section are to summarize the morphological variation within leptictids and to establish, where possible, a basis for homology through comparisons with other mammalian groups. These comparisons form the evidence for the closing sections on leptictid affinities and eutherian classification.

A major obstacle to broad-based morphological comparison is the uncertainty in characterizing a higher-level taxon by the homologous features that root all its members. Long-term misunderstandings have resulted from the mistaken representation of a group by members showing a more derived condition. Studies of tupaiids, for example, often focus exclusively on *Tupaia* and ignore the character evidence from *Ptilocercus*, which, in many aspects, is more primitive than its famous relative (Gregory, 1910; McKenna, 1966; Novacek, 1980). In the comparisons to follow, higher-level groups are character-

ized by their presumably primitive (more generally homologous) features. Characterizations of groups of lower diversity are naturally less troublesome than those for highly diverse groups. In groups where generalization is unwarranted, features of both or several subgroups are noted.

Throughout this comparative section, the term lipotyphlan insectivorans of Butler (1972) and earlier workers is used. These groups traditionally comprise Erinaceidae, †Dormaaliidae, Soricidae, †Dimylidae, †Geolabidiidae, †Plesiosoricidae, †Micropternodontidae, Talpidae, †Nyctitheriidae, Tenrecidae, Solenodontidae, †*Nesophontes*, Chrysochloridae, and, perhaps, †Apternodontidae and †Palaeoryctidae (sensu stricto).

The interrelationships within early Leptictidae were reviewed most recently by Novacek (1977a). A revised classification that includes Oligocene forms as well as new Paleocene and Eocene genera is forthcoming. For the present purpose, published information (see Van Valen, 1967; Novacek, 1976, 1977a) provides adequate reference. The best cranial material is found in *Leptictis*. A new, unnamed Oligocene genus is also represented by excellent skulls, but it differs from *Leptictis* only in a few unique specializations which do not affect the conclusions drawn herein. Skull material of *Palaeictops* does, however, show a number of primitive traits altered in Oligocene forms. Unlike previous publications, differences between *Palaeictops* and *Leptictis* are explicitly cited. Other leptictids (*Myrmecoboides, Prodiacodon*) are not represented by extensive cranial material.

DENTAL FORMULA

There is good evidence that the Late Cretaceous leptictid relative, *Gypsonictops,* had at least five lower premolars (Lillegraven, 1969; Clemens, 1973; Novacek, 1977a). A small premolar, designated by Lillegraven (1969) as P_c is present in the middle of the premolar series of *Gypsonictops* and is flanked on each side by teeth or alveoli for at least two premolars (Clemens, 1973; Novacek, in press). McKenna (1975) designated this tooth as P_3 and proposed that the premolar formula for *Gypsonictops* is $(d)P_1 \ P_2 \ P_3 \ P_4 \ P_5$. That eutherians primitively had five premolars has

been questioned (Butler, 1980; Luckett and Maier, 1982). However, the presence of five or more premolars in several Mesozoic mammals (Simpson, 1928; Trofimov in Beliajeva et al., 1974; Clemens and Kielan-Jaworowska, 1979; Crompton and Jenkins, 1979) and Eocene sirenians (Domning et al., 1982) strongly supports the five premolar theory (Novacek, in press).

Gypsonictops, known only from jaws and dentitions, is excluded from leptictids by its lack of several derived dental traits. However, this genus is clearly the closest "fossil-tooth" relative of leptictids (Novacek, 1977a, and remarks below). Assuming that the tooth lost in the derivation of leptictids was P_3, McKenna's notation for the leptictid dental formula seems most correct. This formula is: $I_1 \ I_2^2 \ I_3^3 \ C_1^1 \ dP_1^1 \ P_2^2 \ P_4^4 \ P_5^5 \ M_1^1 \ M_2^2 \ M_3^3$. The discussion that follows reflects this formal change. Leptictid dP_1^1, P_2^2 equals teeth traditionally designated as P_1^1, P_2^2; P_4^4, P_5^5 equals traditionally designated P_3^3, P_4^4.

<center>INCISORS, CANINES
(figs. 1–5)</center>

In only a few of the described leptictid species are incisors well represented. The lower incisors are small and spatulate, and moderately procumbent with I_2 exceeding the size of I_1 or I_3 in *Prodiacodon tauricinerei.* Most other Paleocene and Eocene leptictids show three closely spaced alveoli suggesting that incisors were small in these species as well. In *Leptictis* the small spatulate lower incisors closely resemble those of *Prodiacodon,* but the I_1, I_2, and I_3 are of nearly equal size (fig. 1).

Only two upper incisors are known in leptictids. The homologies of these teeth are uncertain but a gap at the anterior extremity of the snout suggests that I^1 has been lost. The two single-rooted incisors present are small, rounded in lateral outline, and laterally compressed (fig. 1). $I^{?2}$ is slightly larger than $I^{?3}$. This condition is basically similar in *Prodiacodon tauricinerei, Leptictis,* and a new Paleocene genus (Novacek and Shubin, in prep.). Upper incisors in other species of *Prodiacodon,* in *Palaeictops,* and in *Myrmecoboides* are unknown, although the type of *Palaeictops bicuspis* shows the presence of two al-

veoli for incisors on each side of the upper jaw (fig. 3).

The lower canines in leptictids are generally procumbent, and single rooted (fig. 1). C_1 is moderately larger than $(d?)P_1$ in most leptictids, but in *Leptictis dakotensis* the latter tooth is secondarily enlarged.

The upper canines, where known, vary little in structure. In *Prodiacodon tauricinerei, Palaeictops matthewi, Palaeictops bicuspis,* and *Leptictis,* they are enlarged, sharp, and piercing with a single transversely compressed root (figs. 1–3, 5). A small posterior accessory cuspule on the upper canine is variably developed.

The phylogenetic significance of incisor and canine morphology in leptictids is unclear, mainly because of the great variation in morphology of these teeth among early eutherians and their generally poor representation in many fossil taxa. The presence of only two upper incisors is undoubtedly derived, but other features are less easily recognized as specializations. The canine is usually double rooted in primitive erinaceoid insectivorans, *Kennalestes, Asioryctes,* most didelphid marsupials, macroscelidids, and other eutherian groups and this two-rooted condition is primitive relative to the single-rooted canine of leptictids (table 2).

<center>PREMOLARS
(figs. 1–5)</center>

The premolar morphology in leptictids varies considerably and often proves diagnostic at the species and generic level. The morphotypical condition for leptictid premolars is plausibly represented in most features of *Prodiacodon puercensis* and *P. tauricinerei.* Although $(d)P_1$ is poorly known in *Prodiacodon,* it is a simple, unicuspid, single-rooted tooth in *Myrmecoboides, Palaeictops,* and *Leptictis.* P_2 is a trenchant two-rooted tooth with three or four cusps usually much higher than P_1 (figs. 1–3). P_4 (=traditional P_3) is similar in construction to P_2 with sometimes as many as five cusps (fig. 4). It is usually higher than P_2 but often subequal in height to P_5. P_4 has a greatly enlarged central cusp in *Palaeictops matthewi, Palaeictops multicuspis,* and *Leptictis dakotensis.* This feature appears to be a secondary specialization. The

reduced, mitten-shaped P_1, P_2, P_4 seen in "*Prodiacodon*" *concordiarcensis* and "*P.*" *furor* are specialized traits that ally these taxa more properly with a new Paleocene genus (Novacek and Shubin, in prep.).

P_5 (=traditional P_4) is a large tooth whose molariform character represents the most commonly cited diagnostic feature of the Leptictidae. In *Prodiacodon, Myrmecoboides, Palaeictops multicuspis,* and *Leptictis* this tooth has a talonid with four cusps. In other leptictid species there are usually three talonid cusps, the paraconid is variable in relative size and position, and the transverse alignment of the metaconid and protoconid shows marked differences. However, the basic molariform structure of this tooth as typified by *Prodiacodon puercensis* is a consistent character of the family. DP_5 is similar in structure to P_5, primarily differing in having a more distinctly developed, anteriorly projecting paraconid.

P^1 is a small tooth, somewhat button shaped and bi- or tricuspid with cusps aligned anteroposteriorly (figs. 1, 4). This tooth is single rooted in *Prodiacodon tauricinerei, Prodiacodon puercensis,* and *Palaeictops bicuspis,* but double rooted in *Leptictis dakotensis, L. haydeni,* and *Palaeictops matthewi.* It is not certain as to whether the single- or double-rooted condition is primitive for the family.

P^2 is small and two-rooted with a large anterior cusp and a smaller posterior accessory cusp (figs. 1–3). Little variation in this construction is seen among most Paleocene and Eocene leptictids, but in *Leptictis dakotensis* the P^2 is nearly caniniform in appearance with a greatly enlarged, projecting anterior cusp (figs. 1, 2).

P^4 (=traditional P^3) is most characteristically triangular in outline with distinctly developed metacone, paracone, and protocone, and small anterior and posterior accessory cusps (figs. 1–5). The structure, size, and position of the protocone and the expansion of the paracone vary markedly among species. In *Prodiacodon puercensis* and *P. tauricinerei* the protocone and paracone are moderately developed. The protocone is shifted posteriorly and reduced in some species of Oligocene leptictids and is missing altogether in *Leptictis haydeni.* The paracone is swollen at its base and much higher than the other P^4 cusps in *Palaeictops matthewi, P. bicuspis,* and *Leptictis haydeni.*

As in its occlusal counterpart, P^5 (=traditional P^4) is molariform with a distinctly developed paracone, metacone, protocone, hypocone, conules, and anterior cingulum (figs. 1–5). *Palaeictops,* and *Leptictis* are characterized by a much stronger hypocone on P^5. Again the variation in morphology of this tooth among leptictids does not obscure its consistent molariform construction. As in the lower last premolar, P^5 has historically proven to be a useful diagnostic character of the Leptictidae.

DP^{4-5} (=traditional DP^{3-4}) are similar to their replacement teeth, but show a more pronounced development of conules and hypocones.

Doubtless, the complexity of the posterior premolars in leptictids has phylogenetic significance, but the polarity of this condition in respect to eutherian evolution is difficult to assess. Butler (1956, p. 467) judged this condition to be a "leptictid specialization," a view with which I concur. The evidence for this judgment is that a last premolar of simple construction (dominated by a single large cusp; upper premolars lacking distinct metacones, hypocones, pre- and postcingula; lower premolars with poorly developed paraconids, talonid basins, and talonid cusps) is present in a variety of primitive eutherians including species of *Cimolestes, Batodon, Asioryctes,* primitive erinaceomorphs, and other fossil and Recent insectivorans. *Kennalestes* has more molariform last premolars than the above taxa but it does not approach the condition in *Gypsonictops* and leptictids. "Molarization" of the posterior premolars is a character also found in Mixodectidae, certain pantolestids, Macroscelididae, Dermoptera, certain primates, and many condylarths. The tendency of this tooth for independent "molarization" in various lineages seems quite certain.

This discussion assumes, of course, a basic homology among the last premolars of these various taxa. Alternatively, McKenna (1975) proposed that in some of the above, the traditionally designated M_1^1 are actually retained DP_5^5 and the M_3^3 are lost, yielding a cheek tooth formula of $(d)P_1^1$ P_2^2 P_3^3 P_4^4 DP_5^5 M_1^1 M_2^2.
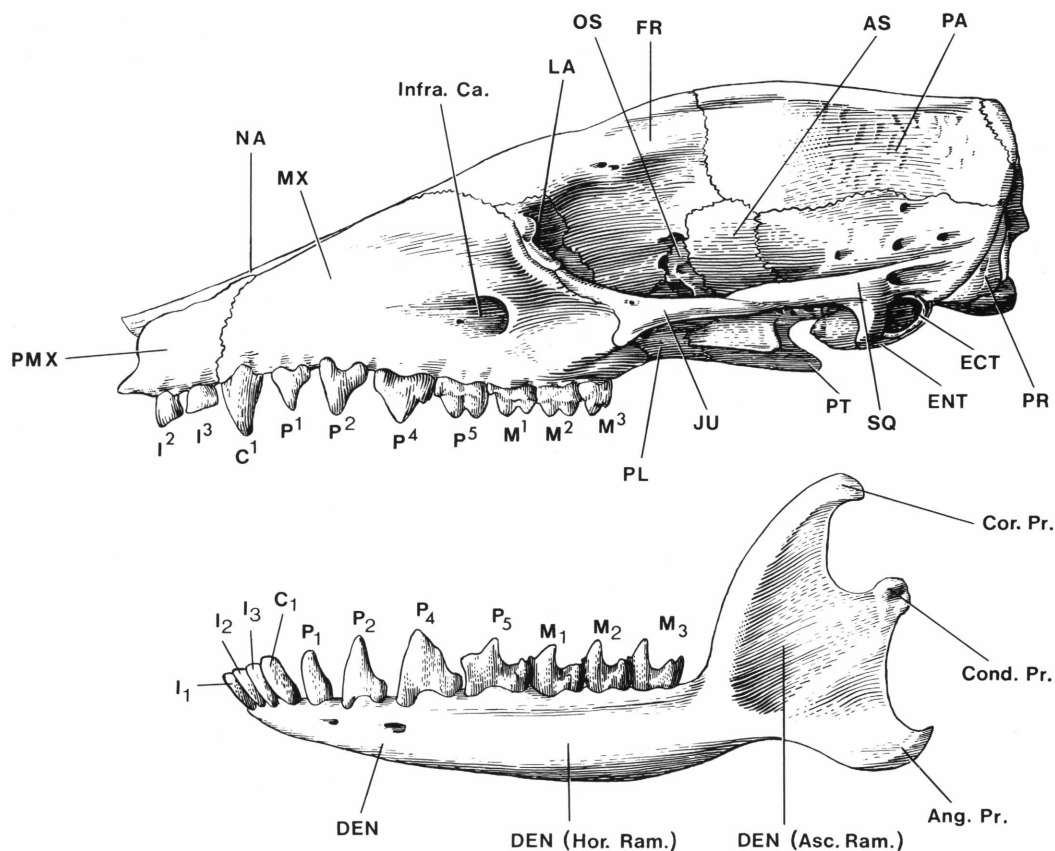
FIG. 1.   Lateral view of *Leptictis dakotensis* skull and jaws. For abbreviations see pp. 5–7.

Hence the leptictid P_5^5 would not be homologous to the last premolar (P_4^4) of primitive erinaceomorphs or other lipotyphlans. However, I think the reduction to the four-premolar, three-molar formula of these latter taxa through loss of P_3^3 is more plausible (Szalay, 1977; Novacek, in press), a transformation matching that for leptictids.

MOLARS
(figs. 1–5)

The primitive plan of molar structure in leptictids is, with a few exceptions, typified by *Prodiacodon*. In this form, the upper molars are transverse with rather high piercing cusps. The ectocingulum is narrow, but present, and parastylar and metastylar spurs are prominent. The conules are set lingually and the precingulum is long, extending to the anterolingual corners of the crown. A hypocone is present but greatly exceeded in elevation by the protocone. The paraconule is usually positioned more lingually than the metaconule. The upper molar paraconules are doubled and the M^2 markedly transverse, but these are interpreted as derived features of the genus. The other molar characters are variously modified in *Leptictis* and *Palaeictops*.

The lower molars have tall trigonids with high, piercing cusps. Aside from variation in the number of talonid cusps, the position and development of the paraconid, length of the heel on M_3, and the aberrant molar trigonids in *Myrmecoboides,* the lower molars do not show significant differences among leptictid taxa.

Copious literature on molar evolution in early eutherians includes consideration of character polarity based on comparative anatomy, functional analysis, and stratigraphic occurrence. Readers are referred to

treatments by Simpson (1951), Slaughter (1965), Patterson (1956), Szalay (1968a, 1968b), Lillegraven (1969), Crompton (1971), Turnbull (1971), Butler (1972), Clemens (1973) and Kielan-Jaworowska (1975). These represent only a small sample of the many relevant papers. A particularly useful synthesis is provided by Fox (1975).

FIG. 2.   (A) Dorsal, (B) ventral, (C) lateral, (D) posterior views of F:AM 108194, skull of *Leptictis dakotensis*. Photographs of epoxy cast of original specimen.

DENTAL COMPARISONS WITH ERINACEOMORPHS

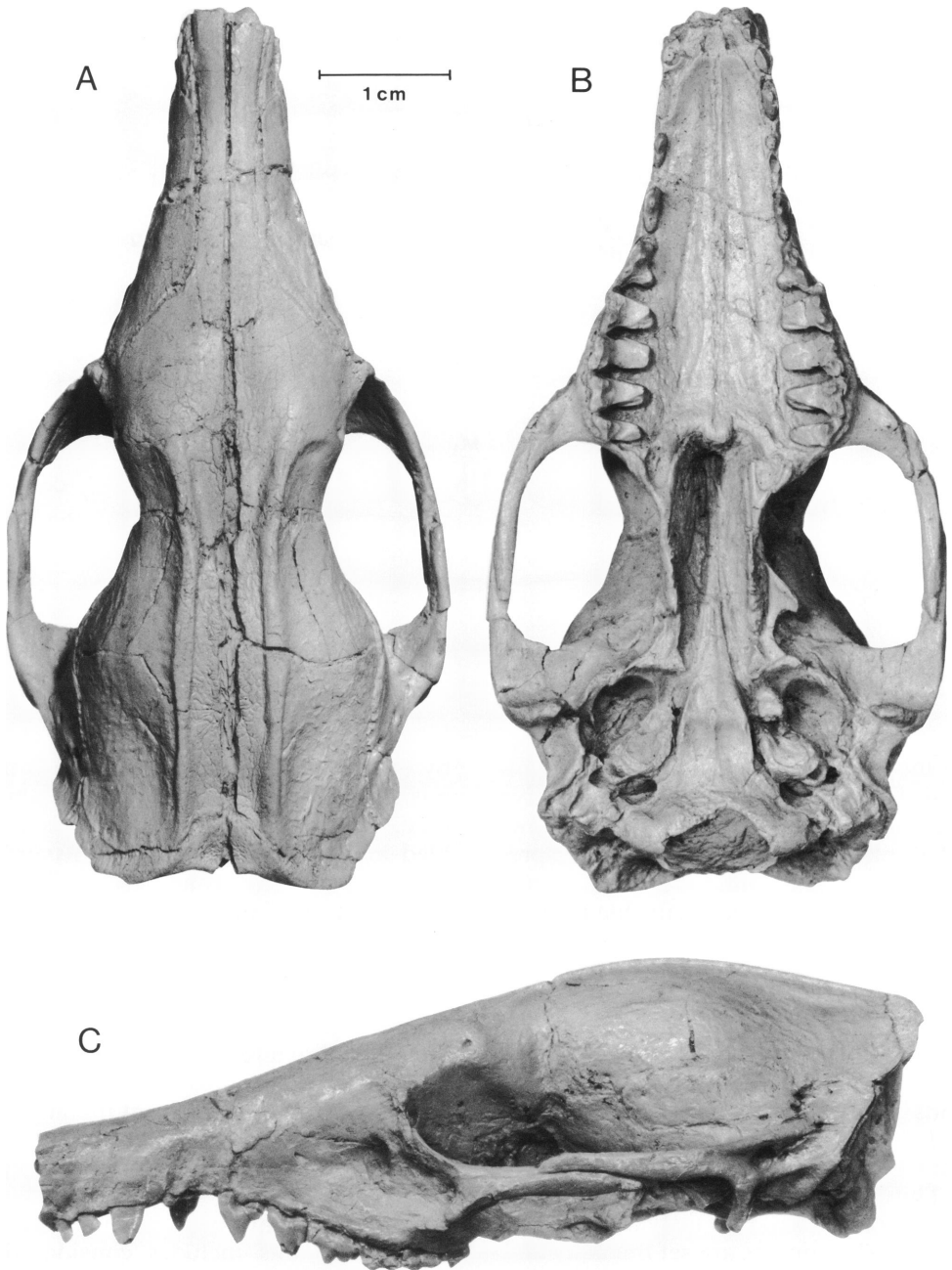Many of the above studies have been cited in arguments for a close leptictid-insectivoran relationship, a grouping based on the alleged dental resemblance between primitive erinaceomorphs (see Novacek, 1982c), and early leptictids (*Prodiacodon*). However, major dental differences exist between these two groups (see table 2):

1. There are three upper incisors in many erinaceomorphs (for example *Echinosorex,* Butler, 1948) but there is indication of only two upper incisors in primitive leptictids (although *Prodiacodon tauricinerei* may have three).

2. The lower canines in leptictids (where known) are small, procumbent, and single rooted, while these teeth in erinaceomorphs are somewhat larger and more trenchant. A smaller more canted, lower canine evolved secondarily in some erinaceomorphs.

3. In erinaceomorphs the anterior premolars are usually small with button-shaped crowns; they are subequal in height and consist primarily of a large anterior cusp and a small posterior cuspule. The first lower postcanine tooth is usually small and single rooted, while the succeeding premolars are double rooted. All upper premolars are normally double rooted. In most leptictids the anterior premolars are markedly more complex, more disparate in size, more trenchant, and show a proliferation of crown cusps. The first postcanine tooth is small, spatulate, and single rooted, as in erinaceomorphs. The procumbent, reduced, mitten-shaped anterior premolars of "*Prodiacodon*" *concordiarcensis* and "*P.*" *furor* are probably secondary features.

4. The posterior premolars (P^4, P^5_5?) in erinaceomorphs do not show the addition of cusps, talonid basins, or cingula typical of leptictids. The lower last premolar (P_5? or P_4?) in some erinaceids is premolariform; there is a single dominant protoconid, an extremely short, unicuspid talonid, and a small paraconid. The metaconid may be present but is poorly differentiated from the protoconid. In some early erinaceomorphs (Krishtalka, 1976), the last lower premolar is "semimolariform"—the talonid is much narrower but nearly as long as that on M_1 and usually bears two or three small cuspules, the paraconid is distinct, but smaller than in primitive leptictids. This condition is shown in "*Mckennatherium ladae*" (Krishtalka, 1976). The upper last premolar is "premolariform" to "semimolariform" in erinaceomorphs; the metacone, if present, is never well developed; it is often only a small rise on the metastylar crest. Pre- and postcingula are usually absent. The contrasting features in leptictid last premolars are sufficiently described above.

5. Leptictid upper molars differ from those in erinaceomorphs in being more transverse and in having smaller hypocones, smaller metacrista (especially on M^1), longer anterior cingula, higher and more piercing cusps, longer external shearing surfaces (surfaces 1 and 2 of Crompton, 1971), and much narrower ectocingula.

6. Leptictid lower molars differ from those of erinaceomorphs in having more erect trigonids, higher, more piercing trigonid cusps, relatively higher protoconids, paraconids that are cuspate rather than bladelike and more anteriorly isolated from protoconids and metaconids, and more elongate talonids on M_3. Some early erinaceids also show a marked progressive reduction in size from M_1 to M_3.

In items 1, 2, and 4 leptictids seem more specialized than erinaceomorphs; whereas in 3, 5, and 6 the latter group seems dentally more derived, although differences in molar structure comprise both primitive and derived characters. This brief comparison suffices in illustrating the marked dental differences between leptictids and erinaceomorphs,

Fig. 2. (*Continued*).

but does not necessarily vitiate a close relationship between leptictids and erinaceomorphs or other insectivoran groups.

JAWS
(fig. 1)

Few aspects of the jaw in leptictids seem highly specialized. The basic features of the jaw apparatus are the following:

1. The dentary is long and slender, with a gently convex ventral border. Its deepest section is below M_1 in all taxa. The number and position of the mental foramina vary. In *Leptictis*, the anterior mental foramen is below the P_1, the posterior below the anterior root of P_4 (fig. 1). In *Palaeictops* the anterior foramen is below P_1, the posterior below the posterior root of P_4. In *Prodiacodon*, the anterior mental foramen is below a point between C and P_1; the posterior, below the anterior root of P_5.

2. The mandibular condyles are transversely wide, projecting medially and laterally beyond the vertical plane of the mandible.

3. The articular surface of the condyle is cylindrical, being curved in the sagittal plane, but its transverse convexity is slight.

4. There is a depression on the head of the posterolateral surface for the ligament connecting the posterior edge of the meniscus.

5. The condyle does not fill the glenoid fossa, allowing for some horizontal movement of the jaw joint.

6. The postglenoid process is well developed.

7. The masseteric fossa is moderately deep.

8. The posterior border of the masseteric fossa is marked by a crest running anteroventrally from the side of the condyle.

9. The angular process is a broad, thin flange, and distally "hooked" in *Leptictis*.

10. There is a horizontal flange on the inside of the condyle for insertion of the internal pterygoid muscle.

11. The coronoid process is well developed and inclined at an angle of approximately 50–65° to the tooth row. The process is broader dorsally in *Palaeictops* but more constricted with a hooklike dorsal apex in *Leptictis*.

12. The zygomatic arch is generally narrow.

13. The area for origin of temporal muscle seems large, and there is a well-developed sagittal crest (divided supratemporal crests appear in Oligocene forms).

Some of these features were considered in detail by Butler (1956) in his comparisons of *Leptictis* with selected mammal groups. Jaw specializations occur within leptictids but do not characterize the family as a whole. Perhaps the posterior masseteric crest (character 8 above) is a derived eutherian trait (see also Butler, ibid.), but the distribution of this condition includes tenrecid insectivorans, certain fossil primates, anagalids, and zalambdalestids. This character alone fails, therefore, to distinguish the leptictid jaw apparatus.

This basically primitive plan has correspondent functional implications. Any biomechanical analysis of the leptictid jaw apparatus is obviously speculative, owing to the lack of evidence for muscle mass and fiber orientation. Nonetheless, the skeletal similarity of the leptictid jaw apparatus to that in *Didelphis* and *Echinosorex* makes it possible to draw analogy with Turnbull's (1970) "generalized group." This category was defined by a large temporalis muscle, smaller masseter, and reduced pterygoid muscle complex, where dominance of the temporalis muscles in masticatory action does not approach that in true carnivores (Turnbull's specialized group 1). As in *Didelphis* and *Echinosorex*, the long effort lever arm represented by the leptictid lower jaw requires a significant force exerted by backward and upward pull of the temporalis muscles for biting force of the enlarged canines. The well-developed masseteric fossa in the leptictid lower jaw also suggests that the masseter muscles functioned with the pterygoids in moving the jaws transversely and anteroposteriorly. In this connection, Butler (1956) noted the mandibular condyle does not entirely occupy the glenoid fossa, allowing for some horizontal movement of the jaw joint.

Although not well preserved in earlier leptictids, the postglenoid process in *Leptictis* is prominent and has a distinctly semilunar, concave glenoid fossa for articulation with the mandibular condyle. This suggests that there was a significant stress on the jaw joint not necessarily balanced by the opposing forces of the jaw closing muscles. In other
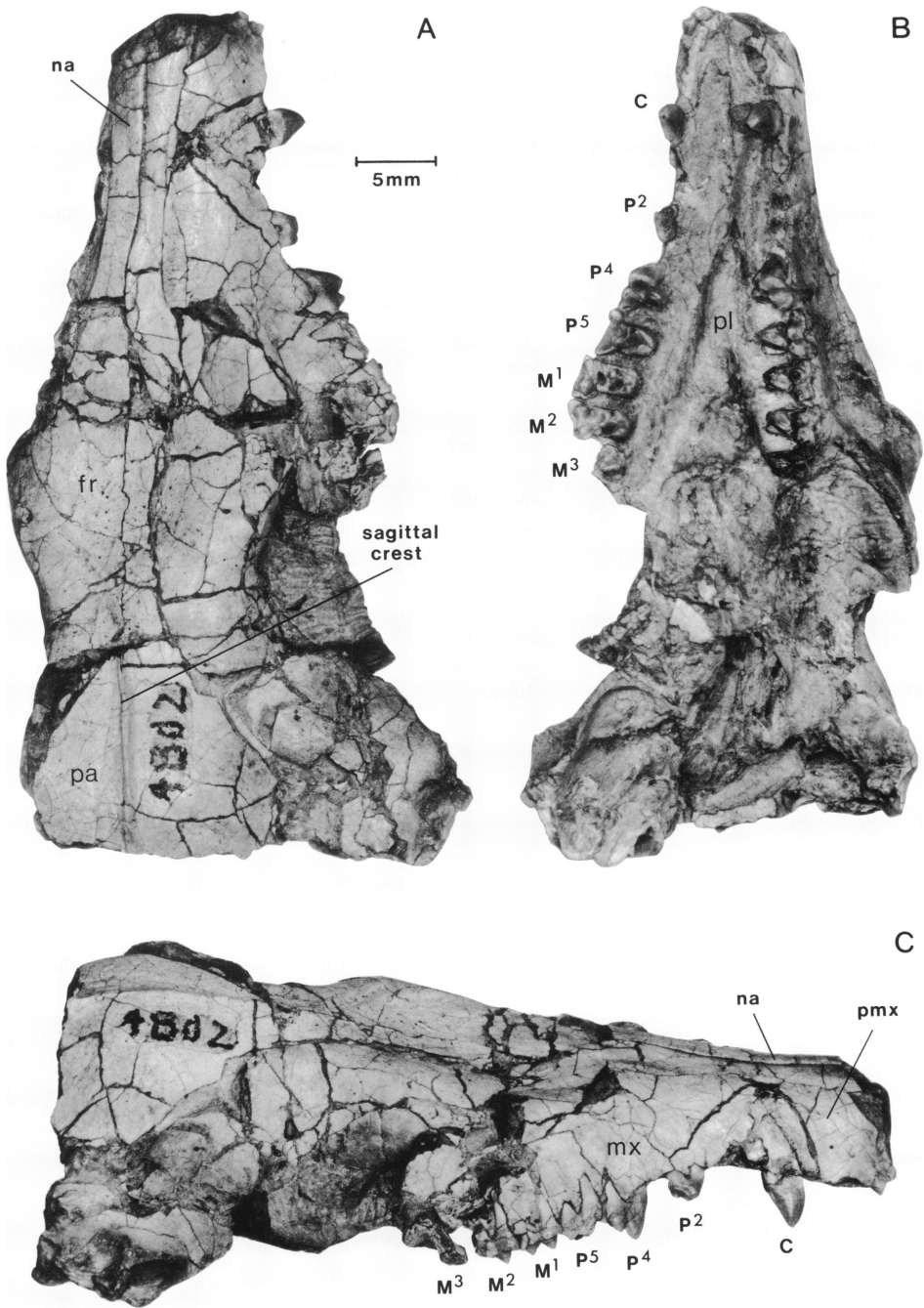
FIG. 3. (A) Dorsal, (B) ventral, (C) lateral views of AMNH 4802 (type). Skull of *Palaeictops bicuspis*. For abbreviations see pp. 5–7.

words, the resultant temporalis force on the craniomandibular joint (CMJ) did not equal and directly oppose that of the combined masseter and pterygoideus muscles. In car-nivorous mammals where the temporalis is the dominant jaw-closing muscle, the rear of the glenoid fossa receives the greatest stress. This stress is correlated with the enlargement

TABLE 2
Comparative Dental Features of Leptictids and Several Other Eutherian Taxa
Suggested derived eutherian character states are in *italics*.

Leptictidae	Gypsonictops	Kennalestes	Procerberus	Zalamb-dalestes	Erinaceo-morpha[a]
1. *Two upper incisors*	—	three	—	three	three
2. Upper incisors not greatly enlarged	small	small	—	*enlarged*	small
3. *Upper canine single rooted*	—	two-rooted	—	two-rooted	two-rooted
4. Lower canine small, *procumbent, single rooted*	enlarged, *single rooted*	enlarged, two-rooted	—	smaller, two-rooted	enlarged, two-rooted
5. Diastema between anterior premolars and canine short or absent[a]	absent	absent	absent	*present*	absent
6. *P¹ single rooted*	—	two-rooted	—	two-rooted	two-rooted
7. *Four molar premolars*	five	*four*	?*four*	*four*	*four*
8. *(d)P₁ single rooted*	?two-rooted	two-rooted	—	two-rooted	*single rooted*
9. Anterior lower premolars trenchant, with three or more cusps	—	bicuspid	?trenchant, cusps variable	bicuspid, trenchant, slightly procumbent	*simple button-shaped crowns, one or two cusps*
10. P⁴ paracone not greatly enlarged; but piercing or sectorial[b]	slightly larger, sectorial	greatly enlarged, sectorial	not enlarged, sectorial	enlarged, sectorial	P⁴ (=?P³) paracone not greatly enlarged
11. *P⁴ with metacone, conules, and lingual cingula*[b]	extra cusps, cingula weak, absent	weak, absent	*metacone present, cingula weak, absent*	*metacone small, conules, cingula absent*	weak, absent
12. *P⁵ with metacone*[b]	*metacone present*	absent	*present*	present, but small	P⁵ (=?P⁴) metacone weak, absent
13. *P⁵ with narrow stylar shelves*[b]	*narrow stylar shelves present*	shelves wider	*shelves narrow*	*shelves narrow*	*shelves narrow*
14. *P⁵ with lingual cingula and conules*[b]	*cingula and conules present*	*present*	weak or absent	absent	P⁵ (=?P⁴) without distinct lingual cingula
15. *P₅ paraconids large*[b]	smaller	vestigial or absent	*large*	smaller	P (last) with small paraconids
16. *P₅ with three trigonid cusps, three or more talonid cusps*[b]	*3 trigonid, 3+ talonid cusps present*	talonid unicuspid	*talonid cusps present*	unicuspid talonid	talonid unicuspid or with small extra cuspules
17. *P₅ protoconid conical, bulbous*[b]	conical	conical-sectorial	laterally compressed, sectorial	conical-sectorial	*conical, swollen, or bulbous*

TABLE 2—(*Continued*)

Lepticidae	*Gypsonictops*	*Kennalestes*	*Procerberus*	*Zalamb-dalestes*	Erinaceo-morpha[a]
18. *P₅ talonid open or basined, with distinct entoconid*[b]	talonid trenchant	trenchant, unicuspid	*basined*	broad, but not basined	short, unicuspid, not deeply basined
19. Upper molars transverse in occlusal outline	transverse	transverse	transverse	*markedly transverse*	*more semirectangular in outline*
20. *Upper molars with narrow stylar shelves*	stylar shelves slightly wider	wider	*narrow*	wider	slightly wider
21. *Upper molars hypocones consistently present*	variably present or absent	weak or absent	weak or absent	absent	*present, well developed*
22. *Upper molars with lingual cingula*	*present*	*present*	variably present or absent	absent	*present*
23. *Metacrista on M¹⁻² low, rounded*	metacrista elevated, sharp	*weaker*	sharp, elevated	*lower*	variable but more pronounced than in lepticids
24. Prevallum, postvallum shearing surfaces subequal in height	subequal	subequal	subequal	*prevallum notably higher following differential wear*	subequal
25. Pre- and postprotocrista wear not extensive, confined to ridges	not extensive	not extensive	not extensive	*wear extensive, forming a large, lingual, concave facet*	not extensive
26. *Lower molar trigonids "closed" due to closely approximated paraconid and metaconid*	trigonids "open," paraconid salient	*trigonids "closed"*	trigonids open	*trigonids "closed"*	*notably closed due to closely approximated, bladelike paraconid*
27. Lower molar trigonids erect, tall relative to talonids	erect, tall	erect, tall	erect, tall	*slightly procumbent, not markedly taller than talonids*	*procumbent, not markedly taller than talonids*
28. Lower molar paraconids cuspate, conical, *well developed*	cuspate, small	cuspate, small	cuspate, conical, *well developed*	*bladelike*	*notably compressed, bladelike*
29. M₃ *talonid elongate with enlarged hypoconulid*	shorter, hypoconulid small	*elongate, hypoconulid small*	*elongate, hypoconulid large*	shorter	shorter

[a] The characters listed for the Lepticidae and Erinaceomorpha are taken to be primitive features of these groups. For discussion of Erinaceomorpha, see Novacek (1982c).

[b] Comparisons of P₄, P₃ features (numbers 10–18) in lepticids with those in *Procerberus, Zalambdalestes,* and erinaceomorphs are impeded by the lack of certainty concerning the homology of the posterior premolars in the latter taxa—see text.
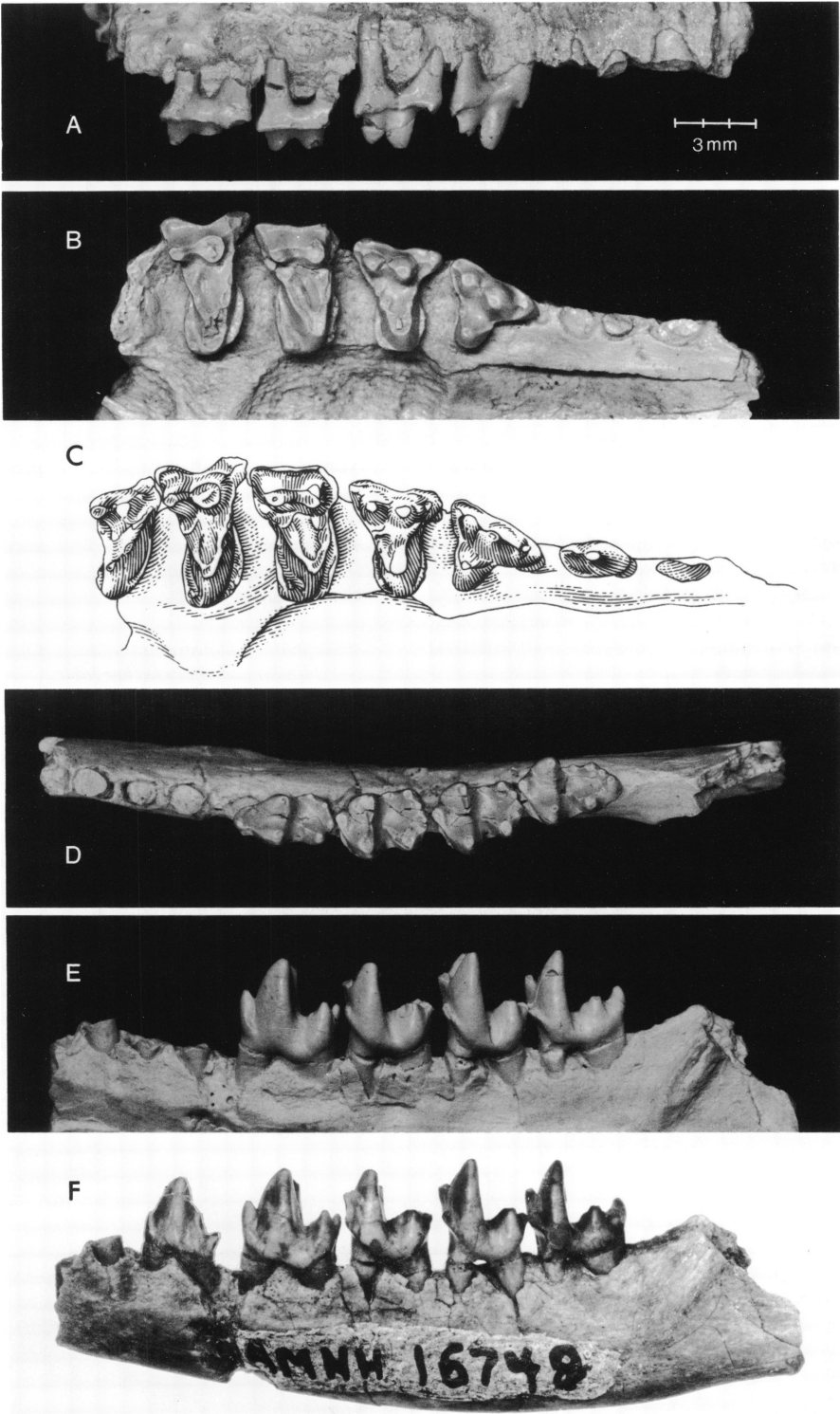
of the carnivore postglenoid process (Davis, 1955; Turnbull, 1970). Using a bifulcral model, Bramble (1978, p. 281) described the "postglenoid hook" in placental carnivores as a passive bony stop to offset large negative rotational loads on the CMJ. Such forces are generated with contraction of the temporalis and a powerful bite with the posterior cheek teeth. In *Leptictis* the postglenoid process is robust and its distal end partly cradles the ventral moiety of the mandibular condyle (figs. 1, 2, 5). The "postglenoid hook" in these animals does not, however, encapsulate the condyle so completely as in many carnivores. This suggests that stress on the CMJ in *Leptictis* was expressed primarily as posteriorly directed, positive translational (t+) forces and ventroposteriorly directed, negative rotational (r−) forces.

Possibly connected with changes in the masticatory apparatus are the divergence of the paired supratemporal crests (figs. 2, 6) in *Leptictis*. This condition clearly contrasts with the more primitive (single-sagittal crest) condition in *Palaeictops*. Variation in the separation patterns of the paired temporal crests in *Urocyon, Vulpes,* and certain other canids shows that these modifications coincide with braincase expansion and reorientation of fiber direction of the temporalis to align more closely with the vertical plane of jaw closure. The functional implications of these correlated traits are not clearly understood.

SKULL SHAPE AND PROPORTIONS
(figs. 1–3, 5, 6)

Leptictis is represented by superb cranial material, but such is not the case for other leptictids. The nearly complete skull of *Palaeictops bicuspis* is compressed and details of the orbital and basicranial regions are obscured. In this and other sections on the cranium, descriptions will focus on *Leptictis,* and refer to variation shown in crania of *Palaeictops.*

The principal work on the leptictid skull is Butler's (1956) description of *Leptictis* (referred to as *Ictops* by Butler). This author (ibid.) provided excellent comparisons between *Leptictis* and a variety of insectivore groups. Butler's description, however, omitted certain cranial details. It is clear from McDowell's figures of *Leptictis* that this author's unpublished study contains details either overlooked by Butler or not preserved in the material available to him. McDowell's figures are composites from several specimens of *Leptictis*. Careful review of the illustrations against original material demonstrates their accuracy, although variation in allometric proportions among specimens cannot be appreciated by reference solely to the drawings. McDowell's figures provide excellent anatomical diagrams for *Leptictis,* and they are gratefully reproduced here.

The most distinctive aspect of the skull shape in *Leptictis* is the long, tapering snout. Butler (1956) compared the general form of the *Leptictis* skull to *Echinosorex*. However, the snout in the former is relatively narrower and more elongate, the orbital section of the skull (between the facial-zygoma contact and the craniomandibular joint) is relatively longer. The slender snout of *Leptictis* is more reminiscent of that in the tupaiid, *Urogale*.

In dorsal view, the braincase of *Leptictis* is broadest above the zygomatic process of the squamosal. The mean ratio of braincase width to condylocanine length is 0.38 for 13 skulls of *Leptictis dakotensis*. In dorsal view, the posterior occipital shows a slight flaring, owing to the development of the lambdoidal crest. Exclusive of the nasal region, the skull is narrowest between the zygomatic arches at a point crudely differentiating the orbital and temporal fossa. As Butler (1956, p. 455) noted, the greatest width of the olfactory capsules is at least 75 percent of the greatest width of the braincase.

In the region of the glenoid fossa the brain-

←

FIG. 4. *Prodiacodon puercensis,* AMNH 16748 (type). **(A)** Lateral, **(B)** occlusal views of cast of right maxilla with P$^{4-5}$, M$^{1-2}$. **(C)** Drawing of original specimen with P$^{2,4-5}$, M$^{1-3}$. **(D)** Occlusal, **(E)** lateral views of cast of left ramus with P$_5$, M$_{1-3}$. **(F)** Lateral view of original specimen with P$_5$, M$_{1-3}$ (P$_4$ from right ramus reversed).
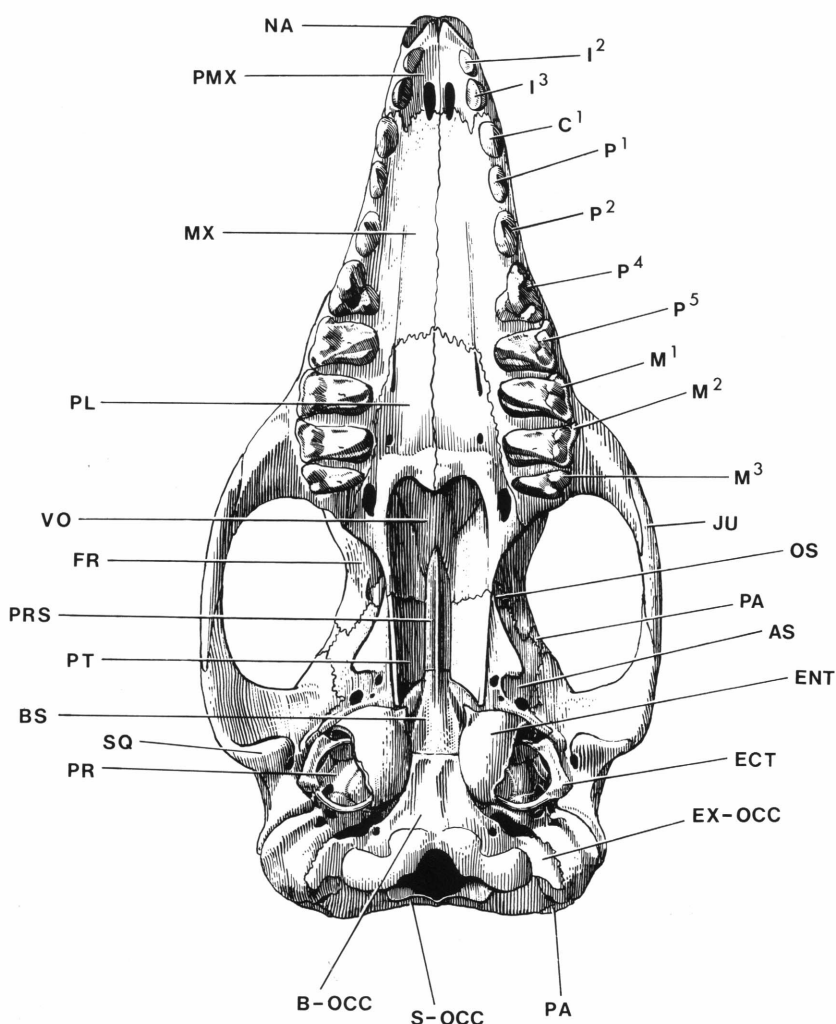
FIG. 5. Ventral view of *Leptictis dakotensis* skull. For abbreviations see pp. 5–7.

case wall gradually changes from an anterior slightly concave surface to a rounded, convex surface. No doubt, the area of the origin of the temporalis was large, as indicated by the extensive ornamentation for musculature on the surface of squamosal and parietal.

In ventral view, the snout of *Leptictis* shows a slight "pinching" opposite the space between P^2 and P^4, so the ventral outline of the snout shows less than even curvature. The palate in *Leptictis* emarginates between M^3s. The middle part of the basicranium, between the palate and the tympanic chamber, is relatively longer than in the Erinaceidae.

As Butler (1956) noted, the basicranium posterior to the glenoid fossa is relatively more elongate in *Leptictis* than that in some erinaceids but comparable to that in *Erinaceus*. The relative length of the posterior basicranium is also similar to that in the tupaiid *Urogale*.

The cranial proportions above noted are not markedly different in the Eocene *Palaeictops*. The exact dimensions of the snout cannot be determined in skulls of these species, although the snout seems somewhat shorter and broader. The braincase seems somewhat less expanded than in the Oligocene taxa. Skull material of the new Paleocene genus (Novacek and Shubin, in prep.) is damaged, but
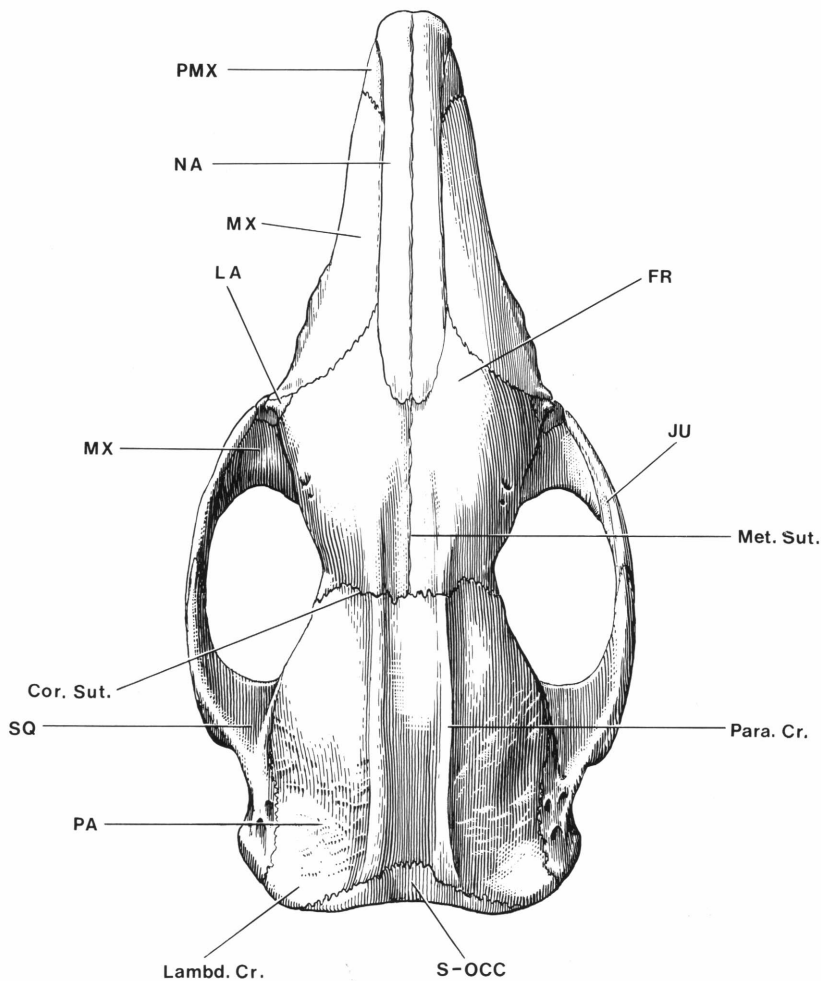
FIG. 6.   Dorsal view of *Leptictis dakotensis* skull. For abbreviations see pp. 5–7.

its proportions are comparable to those in *Palaeictops*. Maxillary and premaxillary fragments in *Palaeictops matthewi* and *Prodiacodon tauricinerei* suggest that the rostrum was also slender in these species. Thus, a long, tapered snout is plausibly a primitive condition for the family.

NASAL
(figs. 1–3, 6)

The nasals in *Leptictis* are elongate and slender, decreasing slightly in width after their junction with the maxillary-frontal suture (figs. 2, 6). By contrast, the nasals in *Palaeictops bicuspis* show a distinctly broader out-

line, although the nasal-frontal suture is partly obscured by damage (Novacek, 1977a, fig. 1; and fig. 3 here). The latter condition is seen in didelphid marsupials and *Kennalestes* and is probably primitive for mammals.

The anterior process of the nasal is poorly preserved in most taxa. In *Leptictis* the nasals extend beyond their point of contact with the anterior edge of the premaxilla (figs. 1, 2). In dorsal view, the anterior nasals are spatulate and their anterior border is distinctly convex. There is no evidence of retraction of the nasals as seen in erinaceids, macroscelidids, and tupaiids, as well as larger mammals (elephants, tapirs, etc.). Hence, leptictids prob-

ably lacked a long nasal cartilage. However, there is indirect evidence in *Leptictis* for well-developed snout muscles and a small, mobile proboscis (see below).

PREMAXILLA
(figs. 1, 5, 6)

In *Leptictis* the premaxilla is a small element with a rudimentary posterodorsal process (see also Scott and Jepsen, 1936; Butler, 1956). The premaxillary-maxillary suture runs from a point just anterior to the canine to a junction with the nasal suture above the posterior edge of the canine (fig. 1). In palatal view the premaxillary-maxillary suture runs anteriorly for a short distance from the canine to a point opposite the anterior edge of I^3. Confined to the small palatal exposure of the premaxilla are a pair of incisive foramina. These openings are barely longer than the alveoli for I_1^2 (fig. 5). Some specimens (MCZ, 19678, USNM 214548) show a small rostral process of the premaxilla that protrudes about as far forward as the nasals overhanging the external bony nares. In lateral view, the anterior (narial) border of the premaxilla is strongly concave (fig. 1). The premaxilla in *Palaeictops* is poorly preserved, but it appears to resemble closely that element in the Oligocene taxa.

The development of the premaxilla and incisive foramina varies greatly in mammals. The small size of this element in leptictids is comparable to the condition in erinaceids (e.g., *Echinosorex*), although in the latter the posterodorsal process is usually more pronounced. Certain mammals (rodents, lagomorphs, plesiadapids) show marked expansion of the premaxilla, an undoubtedly specialized condition correlated with the enlargement of the upper incisors. By contrast, chiropterans show a divergently specialized trait; this element is small or rudimentary. This condition correlates well with any or all of the following: reduction or loss of upper incisors, increased surface area for facial muscles, and enlargement of the canine. The premaxillary condition in leptictids is therefore what might be expected in a primitive eutherian.

Similar conclusions obtain for the incisive foramina. In didelphid marsupials these openings are longer than in leptictids, but the palatal wing of the premaxilla is also better developed than in the latter. The incisive foramina are very small in erinaceids, solenodontids, and tenrecids, but larger or more elongate in tupaiids and some macroscelidids. Most marked is the elongation of these foramina in lagomorphs and rodents, where the Jacobson's organs are well developed (see Novacek, 1985).

In lateral view, the anterior rim of the premaxilla is distinctly concave. This emargination of the bony nares suggests that the cartilaginous lateral nasal process in the embryo is not fully fused to the median nasal process, a condition similar to that in strepsirhine primates.

NASAL CAVITY
(figs. 7, 8, 15, 16, 30)

Several elements surround the nasal cavity. These are the nasal, premaxilla, maxilla, palatine, lacrimal, and frontal. The nasal cavity extends from the external nares to the cribriform plate and is divided bilaterally by a median septum formed by parts of the nasals and mesethmoid. The cavity is also intruded by the vomerine shaft and the turbinals contributed by the ethmoid and maxilla (figs. 7, 8). The contributions of these elements are difficult to describe because the matrix filling the cavity cannot be removed without some damage to the nasal elements. Fine preparation, cross sections, and endocranial casts of *Leptictis* allow partial description. These features are not known in other leptictids.

The vomer is obscured ventrally by the cribriform plate and cannot be clearly separated from the ethmoid. Presumably, these elements and the palatines form a transverse lamina that isolates the choanae from the more dorsal olfactory chamber.

The cribriform plate is distinctly inclined in an anterodorsal orientation when the nasal cavity is viewed laterally or in sagittal section. The posterior face of the plate is distinctly concave and pitted with small foramina. The median septum formed by the mesethmoid and dividing the plate has a well-developed crista galli (figs. 8, 15).

The nasal septum appears to be formed by the median convergence of the ventral wings
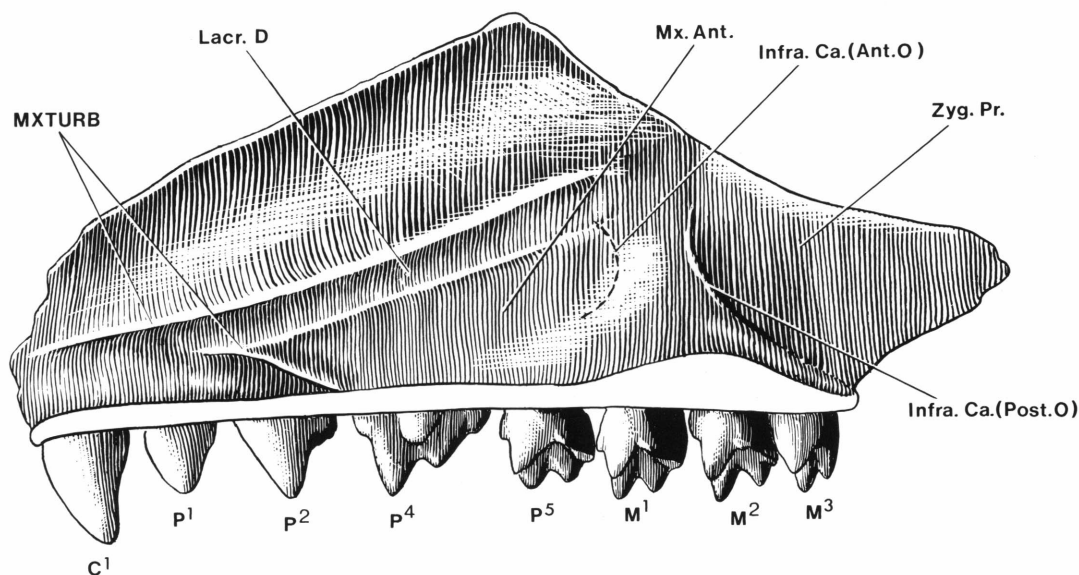
FIG. 7.   Internal view of right maxilla of *Leptictis dakotensis* showing scars for features of the nasofacial cavity. For abbreviations see pp. 5–7.

of the paired nasals. The septum at its most anterior end is triangular and pointed. The lateral surfaces of the nasal septum are distinctly concave and thus represent the median walls of the first endoturbinal (or nasoturbinal). It is likely that, posteriorly and more ventrally, the nasal septum is formed by the mesethmoid, although the contribution of this element is not clearly seen in any specimen.

The internal surface of the maxilla reveals a distinct groove for the nasolacrimal duct. The groove runs obliquely from the internal rim of the orbit above M^1 to a more ventral position above the alveolar border in the region of P^1 (fig. 7). In this anterior area the groove appears to coalesce with a shallow recess that probably represents a scar of the maxilloturbinal (fig. 7).

Above the cribriform plate the nasal cavity expands into a broad chamber, the posterior superior recess, which is roofed by the frontal. The recess is divided by the median septum. The recess on each side of this septum contains at least three conchae, or scrolls, formed by the nasoturbinals and two ectoturbinals (figs. 8, 30). The ectoturbinals are derivatives of the thin ethmoidal lattice. Each ectoturbinal has an internal and external conch.

The features of the nasal cavity described above are typical of many insectivorans. In the latter, the nasal septum is also formed largely by the union of the paired nasal elements. The number of ectoturbinals in marsupials and insectivorans varies but there are at least two or three ectoturbinals on each side of the median septum. In primates where the posterior superior recess is present, the number of ectoturbinals is reduced. In Recent carnivorans and ungulates the ectoturbinal number is usually more than three.

MAXILLA
(figs. 1, 5–11)

All leptictids show basic similarity in the form of the maxilla. This bone occupies nearly all of the facial region, owing to the weak posterior extension of the premaxilla and the elongation of the snout. In *Palaeictops* the sutures of the maxilla are poorly defined although its contact with the nasal is discernible (see above). Sutures are very well preserved in *Leptictis*. In these genera the maxillary-frontal contact is a somewhat coarsely interdigitated suture that arcs (concave forward) from the dorsal junction with the nasal to the junction with the lacrimal. The maxillary-lacrimal suture is well marked
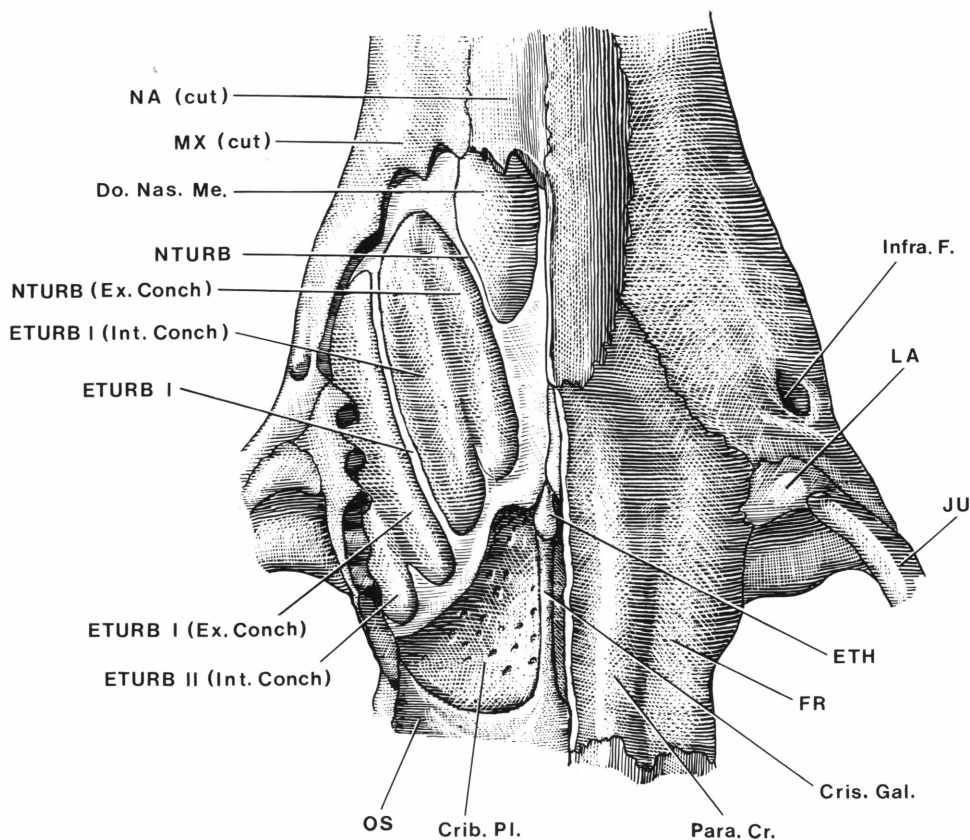
Fig. 8. Dorsal view of nasofacial region of *Leptictis dakotensis*. Bone removed on left side to reveal internal structures of nasofacial cavity. For abbreviations see pp. 5–7.

on the antorbital rim of the root of the maxillary zygomatic process. The lacrimal is thus poorly exposed on the facial region (see below).

The infraorbital canal is of similar form and caliber in all leptictid genera in which this feature is preserved. The canal is short in length and large and nearly circular in cross section. In life the infraorbital canal transmits the infraorbital nerve (branch II of the trigeminal nerve), artery, and vein. The anterior opening of the canal lies above M^1 (figs. 1, 2, 10). Its posterior opening is a large, circular foramen at the anterior apex of the orbit behind the zygomatic process of the maxilla. This opening lies wholly within the orbital wing of the maxilla but just lateral to the triple junction of the maxilla, lacrimal, and palatine (figs. 9, 11). On the anterior surface of the zygomatic process of the maxilla is a

well-excavated antorbital fossa. This fossa is bordered ventrally by a ridge for the zygomaticus and buccinator muscles which run above M^2 along the anterior border of the root of the zygoma. The lateral border of the antorbital fossa is marked by the Y-shaped prominence formed by the anterior bifid process of the jugal (figs. 1, 2, 10). The antorbital fossa in *Leptictis* shows deeper excavation than in *Palaeictops*. The fossa serves as a site of origin for snout muscles (levator alae nasi) and the muscles of the supralabial vibrissal pad (levator labii superioris). The marked excavation of this fossa and the large diameter of the infraorbital canal suggest that the vibrissal and snout muscles were well developed.

The palatal process of the maxilla is extensive due to elongation of the snout, the small premaxilla (see above), and the pos-

terior position of the palatine. The maxillary-palatine suture runs from the posterior edge of the palate following a course slightly medial to the lingual edge of the cheek teeth. The suture runs roughly parallel to the dental row, until, opposite the anterior edge of M^1, it arcs in an irregular suture to the median line of the palate (figs. 2, 5). The suture intersects this medial line at a point opposite the embrasure between P^5 and P^4. The posterior boundary of the maxilla, as marked by this suture is clearly seen in *Leptictis* but is obscured in *Palaeictops*. In palatal view, the root of the zygomatic process of the maxilla arises opposite M^{2-3}.

Internal features of the maxilla are described above in conjunction with other features of the nasal cavity and the posterior superior recess.

The orbital process of the maxilla, clearly seen in *Leptictis,* is well developed, but exposed only in the anterointernal wall of the orbital fossa because of the marked intrusion of the palatine. The maxilla in this region is bounded dorsally by the posterior and medial surfaces of the jugal and the posterior (orbital) face of the lacrimal (figs. 9, 11). Medially, the maxilla orbital wing adjoins the palatine. Thus, the maxilla is effectively excluded from contact with the frontal, although on one side of a specimen of *Leptictis dakotensis* (SDSM 332) there is a very small process of the maxilla that joins the frontal and separates, by 2 mm, the palatine from the lacrimal. This condition seems anomalous as the opposite side of the same specimen shows the typical condition described above (fig. 11). The maxilla is clearly separated by a suture from the ventral edge of the orbital wing of the palatine and the large, posterior palatine foramen lies wholly within the latter bone.

Noteworthy features of the maxilla, then, are its broad contact with the frontal on the dorsolateral surface of the facial region, the rather short and broad infraorbital canal, the deep antorbital fossa, the extensive palatal process, and the exclusion of the orbital wing of the maxilla from contact with the frontal by the intrusion of a large orbital process of the palatine.

The broad maxillary-frontal contact is, as noted above, correlated with the poor facial exposure of the lacrimal. In didelphids, the lacrimal nearly meets the posteriorly expanded nasals, permitting only a narrow connection between the maxilla and the frontal. Possibly, but by no means certainly, this is a primitive therian condition (see discussion of lacrimal below). There is a broad frontal-maxillary contact in erinaceids, and the arc-like suture in *Echinosorex* is very similar to that in *Leptictis*. The maxillary-frontal contact is usually narrower in tenrecids and other insectivorans where the suture is not obscured by early fusion of cranial elements. This constricted contact is, however, more marked in tupaiids, macroscelidids, and *Cynocephalus* (table 3) where there is strong expansion of either the lacrimals (facial wing), the orbital rim, or the posterior nasals.

The infraorbital canal in leptictids closely resembles that in galericine erinaceids, where it also has a large, somewhat circular cross section. The canal in galericines is also of moderate length. In erinaceines, the canal is shorter with a more slitlike anterior orifice. The infraorbital canal is very short and of large diameter in tenrecomorphs, soricomorphs, and macroscelidines (in part) but the canal is generally longer and narrower in tupaiids, rhynchocyonines, dermopterans, and some primates. Butler (1956) cited the variation in length of the infraorbital canal as important character evidence for relationships among insectivorans and other eutherians, but the polarity represented by different conditions is still open to question. Muller (1934) recognized the elongate infraorbital canal as a primitive mammalian character based on Broom's (1915) observation of this condition in cynodont skulls. Osborn (1902) noted that shorter infraorbital canals occur in dolicephalic skulls, while Butler (1956, p. 470) attributed the shortening of the canal to emargination of the facial musculature.

Butler (1956) discussed the phylogenetic implications of the deep antorbital fossa in *Leptictis*. He noted that, unlike the condition in erinaceids and tenrecids, the origin of nasolabial muscles in *Leptictis* does not extend to areas of face above the orbit. A correlative feature is the less dorsally extensive process of the maxilla in *Leptictis*. Perhaps a more interesting feature in leptictids is the deep excavation of the antorbital fossa and the position of the fossa on the anterior face of the

zygomatic process of the maxilla. This suggests that, unlike erinaceids, leptictids have the nasolabial muscles attached distinctly behind and lateral to the anterior opening of the infraorbital canal. However, the deep antorbital fossa may not be a primitive condition for the leptictid clade, as the fossa is somewhat shallower in *Palaeictops* (see above). The latter shows only a slight concave depression on the anterior zygomatic process. This condition is likely a generalized one; in didelphids, tupaiids, some erinaceids (*Echinosorex*), and tenrecids the antorbital fossa (on the anterior zygomatic process) is poorly excavated. The fossa is comparably deep and similarly positioned in *Leptictis,* some macroscelidines (*Elephantulus, Petrodromus*), and galericine erinaceids (*Hylomys, Neotetracus*). In *Rhynchocyon,* the fossa shows a very deep funnel-shaped pit, well marked dorsally, ventrally, and posteriorly by muscle ridges. Although such development exceeds that in *Leptictis,* one might suppose that the latter had a mobile proboscis. This is further suggested by the slight expansion and protrusion of the anterior nasals described above.

The extensive palatal process of the maxilla in leptictids seems to be the result of a number of developmental and allometric factors mentioned above. The size relationships of the bones on the ventral palate are, in fact, very similar in *Echinosorex* and other long-snouted insectivorans. It is only in animals where the premaxilla is greatly enlarged (rodents, lagomorphs) or the palate is lengthened or shortened that this relationship is altered.

The development of the maxilla in the orbit and its relation to other bones of the orbital mosaic is a feature of some systematic interest. Butler (1956) observed, incorrectly, that the maxilla in *Leptictis* has extensive contact with the frontal and excludes the palatine from the anterior orbital wall and from contact with the lacrimal. This error has since been corrected (McDowell, 1958; Novacek, 1980). What Butler (1956, p. 471) illustrated in his figure 7 as the orbital expansion of the maxilla is, in reality, the expanded dorsal process of the palatine. Butler (1956) cited the marked expansion of the maxilla in the orbit to the exclusion of the palatine as an important specialization shared by erinaceids and leptictids. In an addendum, Butler (1956, p. 481) agreed with McDowell (1958) who noted that both leptictids and tupaiids have a large orbital process of the palatine and a restricted maxilla in the orbital wall. The leptictid condition is, in fact, intermediate between those in erinaceids and tupaiids, and the matter of polarity for the three different conditions is of importance.

The problem of transformation of the orbital mosaic has been considered in several studies (reviewed in Novacek, 1980). It has been argued that the expanded maxilla in the orbit and its contact with the frontal is a primitive eutherian condition (Le Gros Clark, 1959). However, most authors agree that this arrangement is derived (Butler, 1956; Van Valen, 1965; Novacek, 1980). The maxilla is virtually excluded from the orbital wall and the palatine is, by contrast, large and broadly in contact with the frontal in a variety of mammals, including morganucodontids, "polyprotodont" marsupials, tupaiids, macroscelidids, hyaenodontids, and some artiodactyls and carnivores (Haines, 1950; Butler, 1956; Van Valen, 1965; Kermack and Kielan-Jaworowska, 1971). The development of the maxilla in the orbit of leptictids is therefore somewhat specialized but not to the degree seen in lipotyphlan insectivorans. Relevant evidence from the Cretaceous mammals *Kennalestes, Asioryctes,* and *Zalambdalestes* is lacking as the orbital sutures in these taxa are poorly preserved.

Muller (1934) effectively argued that the expanded maxilla in the anterior orbital wall was a developmental pattern related to the posterior expansion of the nasal capsule. Novacek (1980, fig. 3) viewed this pattern as influenced by the differential expansion of the nasal capsule, the eye, and the neopallium. A problem with the latter model is the variable pattern in primates. Certain forms show an expanded maxilla and frontal-maxillary contact in the orbit (e.g., indriids, daubentoniids, adapids, *Plesiadapis,* cheirogalines, and certain lemurs). Cartmill (1975) argued, quite reasonably, that this condition is primitive for primates, and that the expansion of the palatine in the orbit of certain primates is secondary. This idea is attractive because
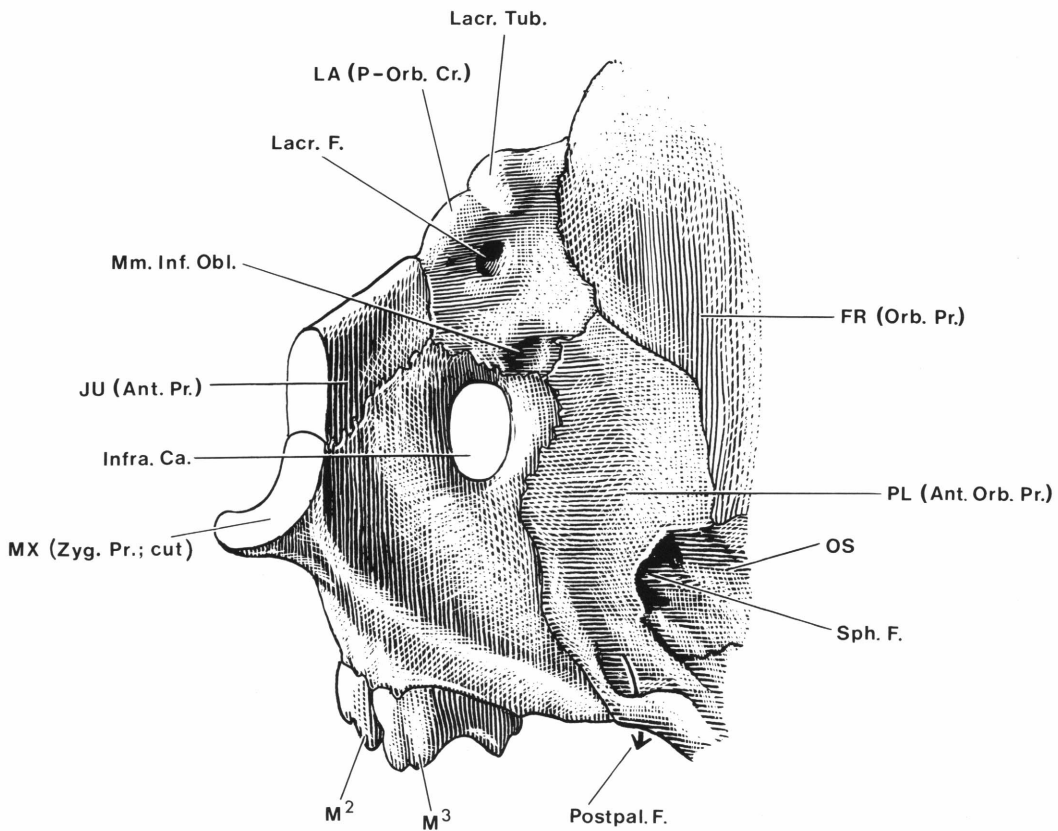
Fig. 9. Posterior view of the anterior left orbital wall of *Leptictis dakotensis* showing relationships of maxilla, palatine, and other elements. For abbreviations see pp. 5–7.

it also suggests a sharing of derived orbital traits between primitive primates and erinaceomorphs (Cartmill, 1975; Novacek, 1982b), and thus offers some clue to the identity of primate relatives. If Cartmill's (1975) argument is correct, transformational hypotheses for the orbital mosaic (e.g., Muller, 1934; Novacek, 1980) must account for the secondary reversion to a presumed general condition—namely the large orbital wing of the palatine—in certain primates and other mammals. Further, it is important to consider more carefully whether the occurrence of a large palatine contribution to the orbital wall is simply a retention of the primitive state rather than a secondary modification (e.g., paedomorphosis) influenced by the ontogeny of the brain, sensory system, and adjacent elements of the cranium.

PALATINE
(figs. 1, 5, 9–12, 14)

As in the case of many other skull elements, the detailed features of the palatine are clearly seen only in *Leptictis,* although a few features are detectable in *Palaeictops.* The palatine is a small, somewhat trapezoidal bone on the surface of the palate. Its lateral and anterior edges are clearly separated from the surrounding maxilla by a jagged suture (fig. 5, and description above). There is a small, oval anterior palatine foramen at the point opposite P[4] where the maxillary-palatine suture runs medially. This foramen opens anteriorly into a shallow trough continuous with a long, faint sulcus that runs anteroposteriorly for most of the length of the palatal process of the maxilla (fig. 14). Posterior and somewhat
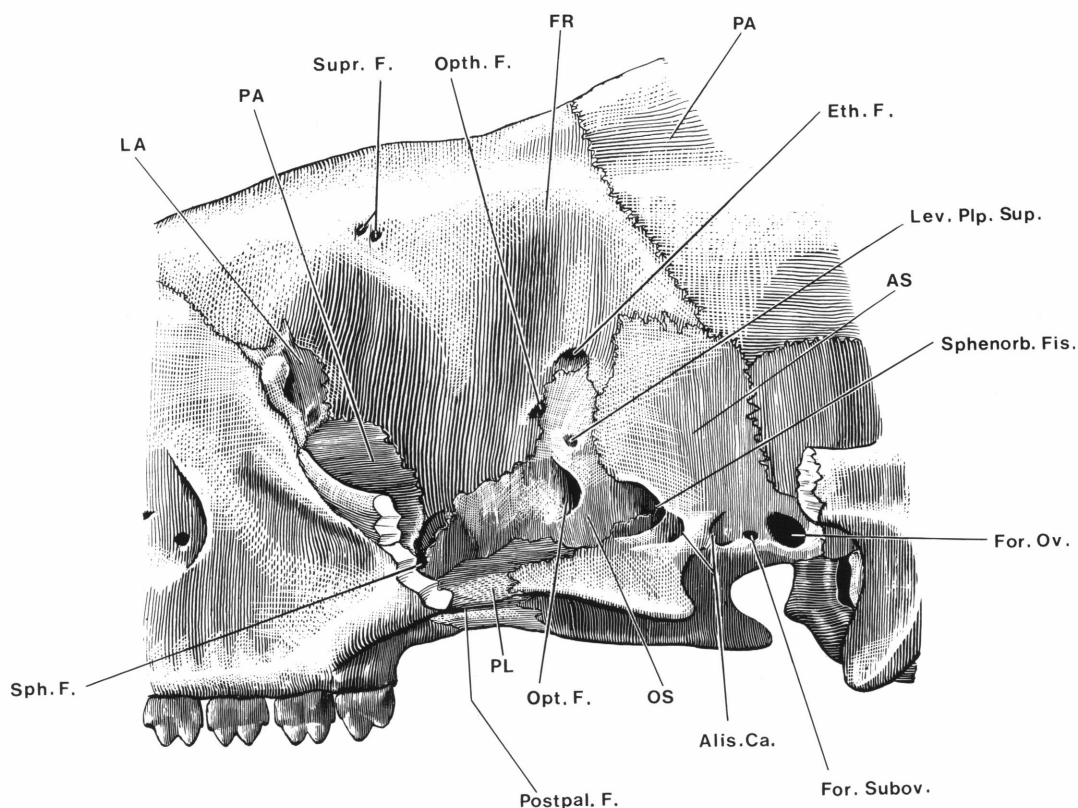
FIG. 10.   Lateral view of left orbital wall of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

medial to the anterior palatine foramen is the middle palatine foramen. Both these palatine foramina are ill-defined in most skulls, and their position and size vary. Such is not the case for the posterior palatine canal; it is consistently a large, oval opening flanking the postpalatine torus and situated far posterior to M³. This canal is barely one at all, as it opens dorsally in the palatine flange that forms the floor of the orbital wall. In living mammals the posterior palatine canal transmits the descending palatine vein and it is often a notch rather than a canal as it lacks a lateral bridge of the palatine or the maxilla (see below).

The posterior emargination of the palate is formed by a rounded lip, the postpalatine torus (figs. 2, 5, 14), that curves in classic art nouveau lines, giving the edge of the palatine a biconcave outline that evokes the delicate heart-shaped boundaries of the cameo. The wings of the postpalatine torus converge at the median line of the palate to form a rounded prominence that projects posteriorly over the choanal orifice. This delicate appendage, the postpalatine spine, marks the apex of curvature of the edge of the palate—a tiny inflexion at the top of the "M" (fig. 14). Its position varies slightly with respect to the cheek teeth but it is usually situated opposite M³ or the embrasure between M² and M³.

In some specimens of *Palaeictops* (AMNH 96250), the posterior palate shows the strong biconcave curvature and the large opening for the posterior palatine canal present in Oligocene leptictids. The postpalatine torus is weak, but the postpalatine spine is present. Other features of the palatine are obscured by damage.

Posterior to the posterior palatine canal, the ventral palatine converges as a narrow splint that contacts the pterygoid behind (fig.

14). The median process of the ventral palatine forms part of the wall and roof of the choanal exit. It is bounded anteriorly and medially by the vomer, more posteriorly and medially by the presphenoid, and posteriorly by the pterygoids (fig. 14).

The orbital (lateral vertical process) of the palatine has been discussed above in relation to its contact with the maxilla. In this region, the palatine is not merely confined to the floor of the orbit. Its ventralmost exposure is defined by sutures with the maxilla and the pterygoid. Dorsal to this ventral wall, the palatine forms a more horizontally directed shelf into which opens the posterior palatine canal (figs. 5, 10–12). Posterior to the canal the palatine is slightly constricted by the forward projection of the alisphenoid, but above this point the palatine expands posteriorly between the orbitosphenoid and alisphenoid. Still more dorsally, the palatine is a narrow bridge in the vertical wall of the orbit. Most of this area is occupied by a recess for two foramina (figs. 9–12). A small, circular dorsal palatine foramen (for the descending palatine artery and nerve) opens posteriorly into a shallow trough in the floor of the recess. A larger, elliptical sphenopalatine foramen (transmits the sphenopalatine nerve, artery, and vein) opens in the medial wall of the recess, its posterior border marked by the leading edge of the orbitosphenoid. Above the sphenopalatine recess, the palatine expands into a broad flange (figs. 9, 11) that makes, via an irregular suture, extensive contact with the frontal (dorsally and posteriorly), lacrimal (dorsally and anteriorly), and the maxilla (anteriorly). Only in a few specimens of *Leptictis* (SDSM 332, ANSP 11042, AMNH 38919) are these boundaries clearly defined by intact sutures.

The dorsal (intranasal) features of the palatine are described above in combination with other features of the nasal chamber.

For comparative purposes, the following features of the palatine stand out: the presence of anterior and middle palatine foramina, the large, short posterior palatine canal, the posterior emargination of the palate as a (posteriorly) biconcave boundary between the last molars, the well-developed postpalatine torus and spine, the large recess for a separate sphenopalatine foramen and dorsal palatine foramen, and the broad contact of the orbital process of the palatine with the frontal and lacrimal.

The anterior and middle palatine foramina are variably present in lipotyphlans. In galericines, these openings are very small or absent; in erinaceines, they coalesce to form a large, elongate pair of openings; in tenrecids the number of foramina varies between several and none; in *Solenodon* there is a more posteriorly situated medial palatine foramen but no obvious anterior foramen. The leptictid condition most resembles that in *Rhynchocyon* where the anterior foramina are continuous with elongate palatal grooves. In this form, however, the middle palatine foramina are absent. Hence, the presence and number of these openings vary considerably at or below the familial level and offer little evidence for higher-level relationships.

By contrast, the posterior border of the palatine provides less variable characters. The emargination of the palate in leptictids is far forward of that in erinaceids (see also Butler, 1956). Further, the palatal margin in erinaceids is either straight or has a simple curve. Although there is a thickening of the palatal margin (postpalatine torus), it is not sinusoidal as in leptictids. The posterior palatine canal is very small in most erinaceids and, even if somewhat larger (as in *Echinosorex*), is always anterior rather than lateral to the postpalatine torus. The strong biconcave curvature of the palatal margin is seen in *Cynocephalus,* but here the posterior palatine canal is a very small opening anterior to the palatal rim, and the choanae exit far forward, between the first molars. In tupaiids the palatal margin is nearly straight or has a slight curve, the torus is weak or absent, and the posterior palatine canal is not entirely enclosed by bone.

Three groups show the closest resemblance to leptictids with respect to the posterior palate. These are *Solenodon,* an elephant shrew (*Rhynchocyon*), and the Rodentia. Yet, even here, some differences are apparent. In *Solenodon,* the postpalatine spine is weaker and the posterior palatine canal is somewhat smaller and less elongate than in leptictids. In *Rhynchocyon* the postpalatine spine is
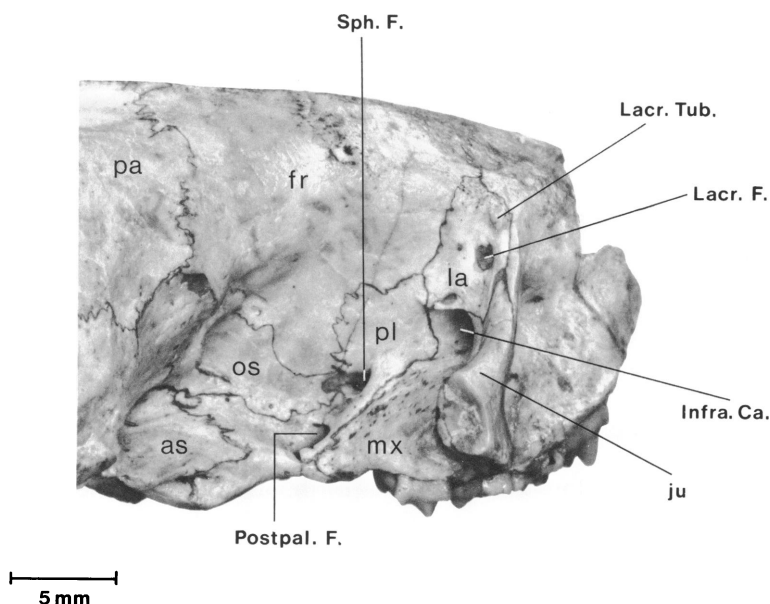
FIG. 11. Oblique view of right orbital wall of SDSM 332 of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

strong but the posterior palatine foramina are openings in the vertical edge of the palatal margin. In rodents, the postpalatine spine extends forward for a short distance as a raised keel, and the posterior palatine canal is variable in size and position. In *Paramys, Sciuravus, Leptotomus,* and *Prosciurus* the posterior palatine canal is often incomplete, forming a notch that is not bounded laterally by a ring of bone (in rodents, usually the maxilla). In *Ischyromys,* aplodontids, and a diversity of later rodents the notch is enclosed as a short canal similar, though sometimes smaller in caliber, to that in leptictids. Despite these differences, it is worth emphasizing that the posterior palate of leptictids bears a striking resemblance to that of Tertiary and Recent rodents (e.g., *Marmota*) that represent the more generalized cranial plan (see Wahlert, 1974) for this order.

Based on comparisons with a variety of therian mammals, including Cretaceous Mongolian genera (Kielan-Jaworowska et al., 1979), the following traits of the posterior palate seem primitive for the subclass: posterior emargination straight or slightly curved, occurring notably behind last upper molars; posterior palatine canal short, ellipsoidal, and anterior to postpalatine torus; postpalatine

spine weak or absent. As described above, leptictids depart from this condition in several ways (table 3) and resemble other groups, particularly rodents, in these modifications.

The large recess for the sphenopalatine and dorsal palatine foramina in *Leptictis* is reminiscent of the basic condition in lipotyphlan insectivorans. In the latter, however, the recess for these foramina opens more directly posteriorly into a funnel-shaped sulcus at the edge of the maxillary-palatine suture in the orbit. Accordingly, the posterior flange of the maxilla forms a lateral wall of the recess.

In rodents, the sphenopalatine foramen is usually a circular opening not hidden by a deep recess and the dorsal palatine foramen is well separated and situated somewhat more posteriorly in the palatine. The sphenopalatine foramen is small and well exposed in macroscelidids and tupaiids and, as in the case of didelphids, its opening appears to be combined with that of the dorsal palatine canal. The relationships of these foramina are not clearly seen in *Asioryctes, Kennalestes,* and certain other "key" early eutherians.

The presence of a deep recess for the separate openings of the sphenopalatine and dorsal palatine foramina in leptictids, as in the case of lipotyphlans, is probably an eutherian
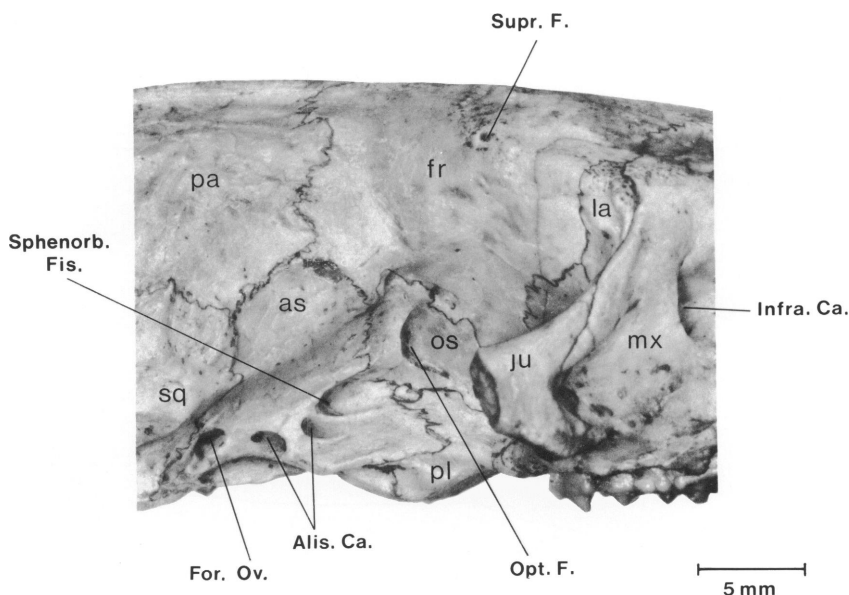
FIG. 12. Lateral view of right orbital wall of SDSM 332 of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

specialization. The orientation of the recess differs, however, between the two groups. This is due to the differences in expansion of the maxilla in the orbital wall for leptictids and "true" insectivorans.

The expanded orbital process of the palatine in *Leptictis* is, as discussed above, a probable primitive therian character. The outlines of this bone in the Oligocene taxa are somewhat like those in didelphids, tupaiids, and macroscelidids but the palatine shows more constriction in the region of the sphenopalatine foramen, due to the encroachment of the maxilla and orbitosphenoid on its anterior and posterior boundaries, respectively. Sutures within the orbital wall are obscured early in the cranial development of soricoids, chiropterans, talpids, and many other Recent and fossil mammals. Perhaps this early closure of sutures is also characteristic of the Cretaceous *Asioryctes*.

LACRIMAL
(figs. 1–3, 5, 8–12)

This bone is well preserved in *Leptictis*, and some of its features are discernible as well in *Palaeictops* (AMNH 96250). The lacrimal has no facial process. Instead its leading edge is a suture that continues dorsomedially from the tip of the dorsal process of the jugal on the antorbital rim. In lateral view, the lacrimal appears as a small triangular surface marked by a number of tiny pits and a prominent rounded tubercle (figs. 1–3). In posterior view the orbital face of the lacrimal is well exposed as a rectangular bone with a large, single, circular lacrimal foramen. Two small pits for the inferior oblique muscles lie near the maxillary-lacrimal suture just above the posterior opening of the infraorbital canal (figs. 9, 11). The orbital face of the lacrimal contacts the jugal, maxilla, palatine, and frontal. This description applies to *Palaeictops* except that the lacrimal foramen is somewhat larger, the lacrimal tubercle is weaker (or damaged in preservation?), and the sutures of the lacrimal are ill-defined.

The confinement of the lacrimal in leptictids to the orbit and the antorbital rim was noted by Butler (1956), who saw a similarity with "primitive erinaceids." It is uncertain whether this condition is more primitive than that wherein the lacrimal has a large facial process (Novacek, 1980). This latter condition is found in tupaiines (but not in *Ptilocercus*), *Rhynchocyon*, plesiadapids, and didelphids and was considered as a primitive
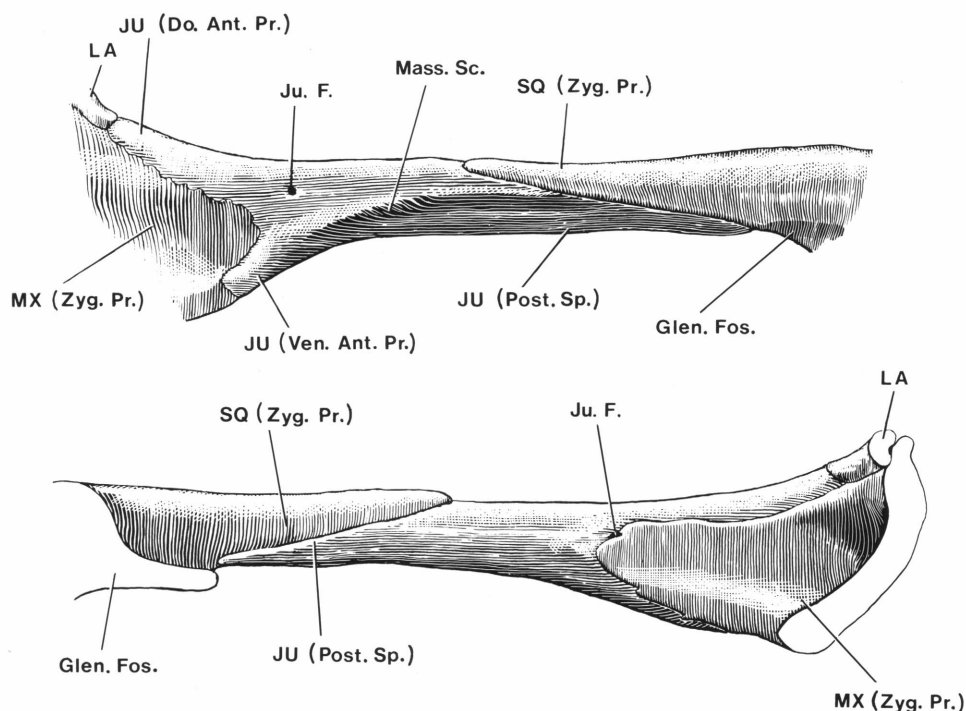
FIG. 13. (Above) lateral view, and (below) medial view of zygoma of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

eutherian trait by Williston (1925) and Salomon (1930). Muller (1934) doubted this interpretation, and Gregory (1920) noted that the pars facialis might be secondarily enlarged by elongation of the snout (e.g., *Orycteropus, Megalohyrax*) and development of horns (bovids). If the loss of the facial process is derived, this loss is shared by leptictids, lipotyphlan insectivorans, ptilocercines, lagomorphs, most rodents, and dermopterans. Hence this widely distributed trait is ambiguous as evidence for relationships among the basic eutherian lineages.

Overall morphology of the lacrimal does, however, compare favorably between leptictids and erinaceids. In both groups there is a prominent lacrimal tubercle, the pits for the inferior oblique muscle are well defined, and the lacrimal foramen is large and confined to the orbit (this feature may be secondary for hedgehogs—in erinaceines the lacrimal foramen is situated on the antorbital rim). The lacrimal tubercle is not developed in like manner in nonerinaceid insectivorans, tu-

paiids, macroscelidids, and other groups (table 3).

JUGAL
(figs. 1–3, 5, 6, 13)

The jugal in leptictids is always a large element, although its size varies with the relative proportions of the zygomatic arch. Details of the jugal are best seen in *Leptictis*. Anteriorly, the jugal is strongly furcate, with the dorsal process somewhat longer than the ventral process (figs. 1, 2, 13). There is a small jugal foramen just anterior and slightly dorsal to an elongate, blunt ridge for the masseter muscle. The posterior spine of the jugal is well marked by a diagonal suture with the zygomatic process of the squamosal. The suture runs obliquely from the dorsal edge of the midzygomatic arch to the ventral edge of the zygomatic arch near the anterolateral corner of the glenoid fossa. Thus, the jugal occupies more than two-thirds of the free span of the zygoma. In some Oligocene species, the jugal shows similar relationships, although it is

greatly expanded dorsoventrally due to the robust size of the zygoma. In *Palaeictops,* the jugal is not well preserved but its form seems similar to that in *Leptictis.*

It is generally agreed that a large jugal is a primitive therian trait, retained in didelphids, leptictids, rodents, lagomorphs, dermopterans, tupaiids, primitive primates, macroscelidids, but reduced in lipotyphlan insectivorans (Butler, 1956; Novacek, 1980). This feature does not simply correlate with the reduction or loss of the zygomatic arch seen in soricomorphs; even insectivorans (e.g., *Echinosorex*) with a well-developed zygoma show a relatively small jugal element (Butler, 1956; McDowell, 1958; Novacek, 1980).

FRONTAL
(figs. 1–3, 6, 10, 12)

The frontal occupies most of the skull roof in the orbital region. In dorsal view it is expanded anteriorly, where it meets the lacrimal and is constricted posteriorly, at a point just forward of the frontal-parietal suture (figs. 2, 6). In *Leptictis* the paired supratemporal crests extend forward about one-half the length of the frontal where they merge with the swellings on the frontal above the anterior orbit. The supratemporal crests in *Leptictis* are separated by a wide, sagittal trough that extends forward beyond the crests, but gradually shallows and terminates at the nasal-frontal suture. The trough is divided by a thin metopic suture (figs. 2, 6). In *Palaeictops bicuspis* there is a low, single sagittal crest that extends forward to a point opposite the interorbital constriction (fig. 3). From here, the crest diverges for a short distance as a V-shaped pair of faint ridges. Unfortunately, damage obscures the parietal-frontal suture.

In leptictids there is no well-developed supraorbital crest, shelf, or process of the frontal, only a blunt ridge that forms the lateral edge of a weak roof over the anterior orbital wall (figs. 6, 10, 12). One or two foramina lie slightly dorsal to the posterior end of the supraorbital ridge (figs. 10, 12).

The orbital exposure of the frontal is most clearly seen in *Leptictis* (e.g., SDSM 332). The bone extends nearly halfway down the midorbital wall. With a sinuous, irregular suture, the frontal contacts (running from an-

terior to posterior boundaries) the lacrimal, palatine, orbitosphenoid, alisphenoid, and parietal. A distinct, rounded foramen (probably for the ophthalmic nasociliary nerve) lies adjacent to the frontal-orbitosphenoid suture dorsal and slightly anterior to the optic foramen (figs. 10–12). More dorsal and slightly posterior to the anterior (ophthalmic) foramen is a slightly larger, semicircular, and anteroventrally oriented foramen for the ethmoid artery and vein. This opening marks the dorsal apex of the orbitosphenoid, whose suture defines the ventral border of the foramen. It lies just anterior to, but does not contact, the vertically oriented frontal-alisphenoid suture.

The inner surface of the frontal forms the roof of the nasal chamber, the posterior superior recess, and the anterior cerebrum. Most of the latter structure is, however, roofed by the parietal. In some specimens (e.g., *Leptictis dakotensis,* F:AM 108794) the scrolls of the turbinals can be seen through the translucent bone of the frontal. Internal features are most easily observed in sectioned and dissected skulls and from surface features of endocranial casts. These are described in the sections on the nasal cavity and the brain.

The description above is partially discrepant with Butler's (1956) account of the orbit in *Leptictis.* Contrary to Butler's (ibid., p. 459) observation, the expansion of the frontal and palatine completely excludes—rather than merely reduces—contact between orbitosphenoid and maxilla, and the frontal does not meet the squamosal to the exclusion of alisphenoid-parietal contact. Butler ascribed the presence of a frontal-squamosal bridge to individual variation, but this feature is absent in every well-preserved specimen available to me. I suspect the condition Butler described is an artifact of preservation.

The above-noted characteristics of the leptictid frontal can hardly be called specialized. The postorbital constriction marking the approximate anterior boundary of the cerebral hemispheres occurs only slightly anterior to the frontal-parietal suture. Thus, leptictids resemble didelphids, creodonts, and insectivorans in showing only a small forward expansion of the cerebrum (Butler, 1956, pp. 467–469). In all these taxa, the frontal largely covers the olfactory capsule. In macrosceli-

dids, dermopterans, most primates, and tupaiids the cerebrum is expanded considerably and the olfactory capsule is shifted forward.

Leptictids also lack a well-developed supraorbital crest or process, a feature that seems to develop independently in several eutherian lineages (Novacek, 1980).

The degree of exposure of the frontal in the orbital wall is obviously related to the development of the more ventral orbital elements. Leptictids have a much broader frontal-alisphenoid contact than do solenodontids, tupaiids, macroscelidids, and erinaceids. In some of these groups, the alisphenoid is virtually excluded from contact with the frontal by the enlarged orbitosphenoid (table 3).

PARIETAL
(figs. 1–3, 6, 10, 29)

The parietal is most notable for the presence of paired supratemporal crests in Oligocene leptictids. In these forms, and, to a lesser extent *Palaeictops,* there is marked ornamentation of the parietal for the attachment of the temporalis muscles. The outer wall of the parietal is distinctly convex, reflecting the bilateral expansion of the cerebral hemispheres. In *Palaeictops* this curvature (and, by inference, expansion of the cerebrum) is less pronounced. Anteriorly, the parietal is in broad contact with the frontal and alisphenoid; ventrally, the squamosal; and posteriorly, the supraoccipital. The supraoccipital actually produces a dorsal process that forms the well-developed lambdoidal cornice. The posterior parietal-supraoccipital relationship is not clearly preserved in *Palaeictops.*

The variation in form of supratemporal crests is useful in distinguishing different leptictids. As discussed above, early forms (*Palaeictops*) have a simple, single, sagittal crest. This feature is commonly distributed within therians and is a primitive condition for the family. In *Leptictis* the crests are doubled, parasagittal, and separated by a rather deep trough. The crests are parallel and normally show only slight curvature (figs. 2, 6). In a few *Leptictis* skulls where the braincase seems slightly expanded (SDSM 332), the crests are more widely separated and show a definite bilateral curvature that vaguely approaches a lyrate pattern. Plausibly, this more open pattern of the crests is the result of an ontogeny related to expansion and curvature of parietal.

PRESPHENOID
(figs. 2, 5, 14–16)

This element is shown clearly only in *Leptictis.* Ventrally, the presphenoid is exposed as a splint of bone in the roof of the deep cavum defined laterally by the paired entopterygoid crests of the pterygoid (figs. 5, 14). Along the midline of the presphenoid there is a well-developed vertical keel (fig. 14). The presphenoid extends forward between the paired palatines to penetrate the posterior incisure of the vomer, although these contacts are poorly defined in all fossil skulls.

Dorsally, (in the cranial vault), the presphenoid is indistinguishable from the orbitosphenoid and forms with that bone the large saddle-shaped element in the anterior floor of the cerebral cavity (figs. 15, 16).

ORBITOSPHENOID
(figs. 10–12, 15, 16)

In lateral view, the orbitosphenoid is a rather large, roughly rectangular element of the orbital wall (figs. 10, 12). Dorsally, it has broad contact with the frontal; anteriorly, with the palatine and the posterior rim of the sphenopalatine foramen; ventrally, with the palatine and alisphenoid; and posteriorly, with the alisphenoid. The optic foramen is an elongate, vertical, slitlike, semicurved, forwardly directed opening situated near the posterior edge of the orbitosphenoid. The sphenorbital fissure is located primarily within the alisphenoid (see below) with only a dorsal ridge extending into the orbitosphenoid. There is a shallow depression for the levator palpebrae superioris muscle directly above the optic foramen. The suboptic foramen is not present in the orbitosphenoid, but probably opens into the medial wall of the sphenorbital fissure (see discussion of alisphenoid).

As noted above, the intracranial exposure of the orbitosphenoid is fused with the pre-
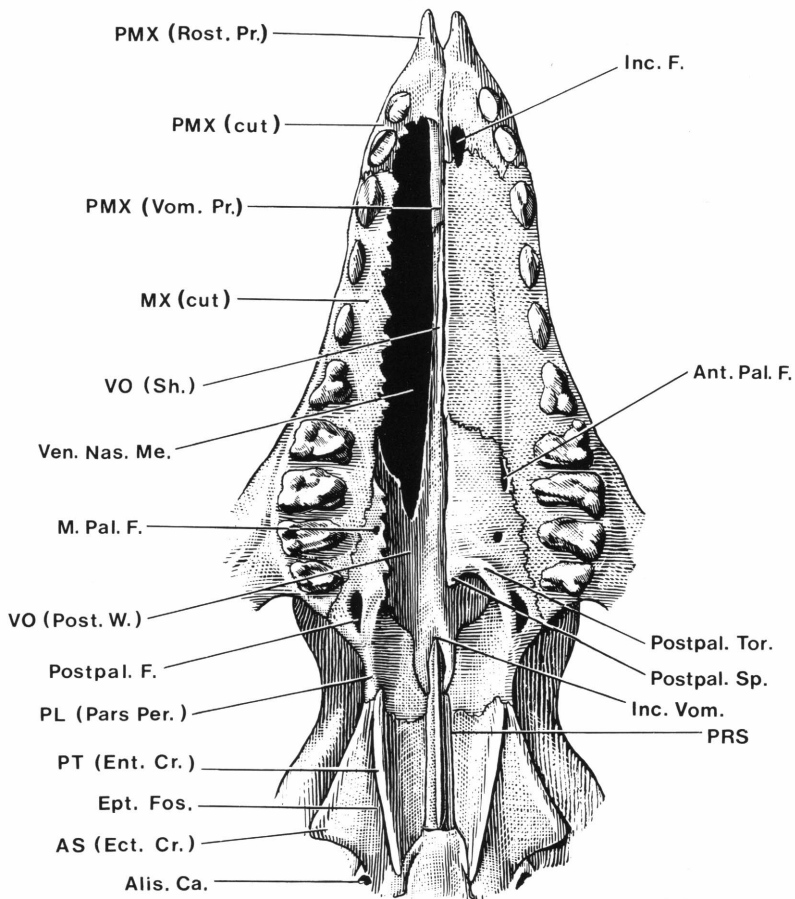
Fig. 14. Ventral view of palate and midcranium of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

sphenoid to form a large saddle-shaped element bounded anteriorly by the ventral edge of the cribriform plate and bordered posteriorly by the crescentic ledge over the sphenorbital fissure (figs. 15, 16). In dorsal view, the paired optic foramina are extended posteriorly as elongate troughs for the optic nerves. The presphenoid forms the rounded septum between these tracts.

The orbitosphenoid in leptictids is externally overlapped by the anterior expansion of the alisphenoid. This can be seen when one compares the greater internal exposure of the orbitosphenoid with its less extensive exposure on the lateral orbital wall (cf. figs. 10 and 15).

The optic foramen in leptictids is rather large, indicating the eye was well developed and perhaps slightly larger than that in erinaceids and *Didelphis*. This condition seems primitive, whereas either marked enlargement (macroscelidids, primates) or marked reduction (soricomorphs) represents divergently specialized conditions.

Other primitive features of the orbitosphenoid include the absence of a suboptic foramen anterior to the sphenorbital fissure (Butler, 1956, p. 473) and the low position of the element in the orbital wall. However, the forward expansion of the orbitosphenoid—with the effect of crowding the palatine—departs somewhat from what might be expected in the primitive condition for therians. The latter state is exemplified by *Pe-*
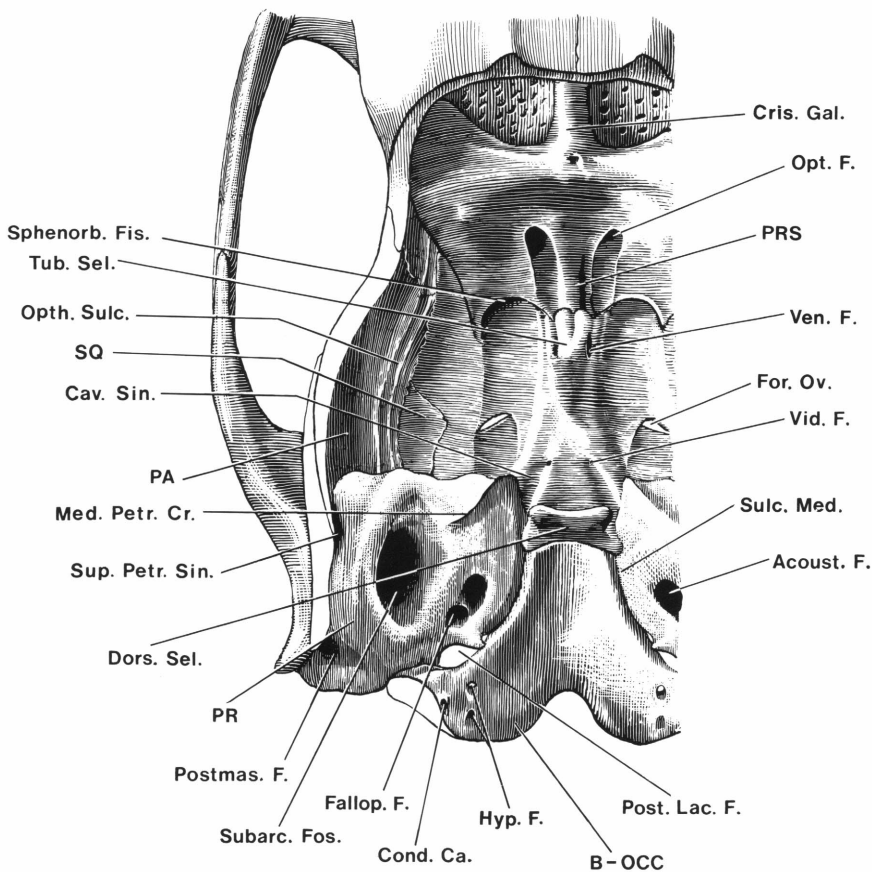
FIG. 15.　Dorsal view of intracranial vault of *Leptictis dakotensis*. Roof of skull "removed" to show intracranial features. For abbreviations see pp. 5–7.

trodromus, where the orbital palatine process is large, the alisphenoid small, and the exposure of the element posterior to the optic foramen is greater than that anterior to the foramen. It is acknowledged that these relationships are easily influenced by differential growth of the cerebral and olfactory lobes. Their significance in phylogenetic applications is uncertain.

ALISPHENOID
(figs. 2, 5, 10, 12, 14, 15, 20, 26)

The leptictid alisphenoid is, as in other mammals, a complex element that contributes to several major regions of the skull. It has a large orbital exposure and extensive contact with the frontal (anterodorsally), or-

bitosphenoid (anteriorly), and palatine (anteroventrally). It forms the sloping posterior wall of the orbitotemporal fossa where it contacts the parietal (posterodorsally) and squamosal (posteriorly). It is essentially fused with the pterygoids, which lie at its medioventral border. It has a ventrally and posteriorly directed process that merges with the basisphenoid and contributes to the concave anterior roof of the tympanic cavity. It forms much of the floor and lower walls of the cerebral cavity, where its various openings, pits, and ridges indicate the location of features of the base of the brain, cranial nerves, and blood vessels.

The alisphenoid in leptictids is not strongly inflated laterally as it is in certain groups (primates, rodents, lagomorphs) where the skull
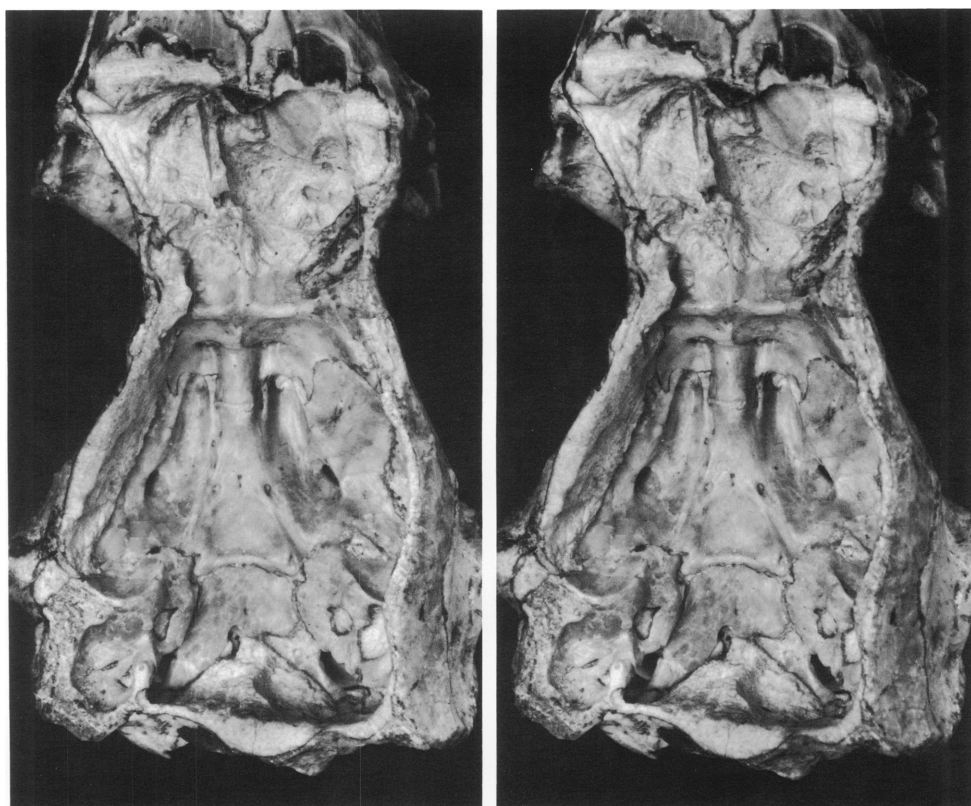
FIG. 16. Stereophotographs of intracranial vault of AMNH 38919, *Leptictis dakotensis*. Skull roof dissected. Features are identified in figure 15. For scale, see figure 2.

develops around an enlarged cerebrum. Hence, leptictids, like other primitive therians, retain a temporal fossa that extends posteriorly beyond the orbit.

The contact between the alisphenoid and the palatine, frontal, and orbitosphenoid has been described above. The shape of the alisphenoid in this region is complex. Its upper moiety is defined by a broadly curved suture, while its anteroventral aspect is a narrow, horizontal process that intrudes into the ventral palatine. The orbitosphenoid has a small process marked by an irregular suture that invades the alisphenoid in the region of the sphenorbital fissure, and thus forms part of the roof and medial wall of this fissure. As noted above, the alisphenoid broadly contacts the frontal. Contra Butler (1956, fig. 7) it is not tapered dorsally by the anterior expansion of the squamosal.

Several foramina pierce the orbital-temporal process of the alisphenoid (figs. 10, 12). Most anterior is the large, semicircular, forwardly directed sphenorbital fissure (equals sphenorbital foramen of Butler, 1956; foramen lacerum anterius of McDowell, 1958; and sphenoidal fissure of Wahlert, 1974). This opening usually conveys the oculomotor (III), trochlear (IV), and abducens (VI) nerves and the ophthalmic division and part of the maxillary division of the trigeminal (V) nerve. The foramen rotundum (for the passage of the remainder of the maxillary division of the trigeminal and a transverse vein) is not distinguishable. As noted above, the suboptic foramen does not open anterior to the sphenorbital fissure within the orbitosphenoid proper. Butler (1956, p. 459) described a skull of *Leptictis* in which the suboptic foramen opened into the medial wall of the sphenor-

bital fissure. It is probable, then, that the sub-optic foramen is bounded by the appendage of the orbitosphenoid forming the medial wall and roof of the sphenorbital fissure (Butler, ibid.).

Posterior and slightly ventral to the sphen-orbital fissure is the anterior opening of the alisphenoid canal for the passage of the internal maxillary artery and vein (fig. 26). The canal is quite short (figs. 10, 12); its lateral wall is a very narrow bridge of bone strongly emarginated in a biconcave fashion by its anterior and posterior openings. At the posterior extremity of the depression for the posterior opening of the alisphenoid canal, is a small, circular, laterally directed foramen. This is, for lack of a better term, a foramen subovale. It may have transmitted a vein connecting the two internal maxillary veins or a branch of the artery of the pterygoid canal. The foramen ovale is large, elliptical, laterally facing, and positioned well posterior to the alisphenoid canal (fig. 10). This foramen normally transmits the mandibular branch of the trigeminal (V) nerve (fig. 26), although given the lack of adjacent foramina it may have also served as the common opening for the masseteric and buccinator divisions of the maxillary nerve. The alisphenoid foramina are not distinctly preserved in *Palaeictops.*

At the base of its orbital exposure, the alisphenoid has a prominent, triangular ecto-pterygoid crest for the attachment of the external pterygoid muscles. In ventral view, these crests slope dorsomedially to form the lateral walls of the ectopterygoid fossae—the site of origin of the internal pterygoid muscles. The suture between the pterygoid and alisphenoid may lie at the apex of this cleft, but the two bones are, for all appearances, fused as one element in this region. Posteriorly, the ectopterygoid fossa broadens into a cupola positioned just medial to the foramen ovale (fig. 19). The posterior rim of this depression is partly formed by the leading edge of the tympanic cavity (fig. 2).

As noted above, the alisphenoid contributes to the tympanic region, but the extent of its contribution is uncertain. This is due to its broad fusion medially with the basisphenoid, which also must form part of the anterior roof of the auditory cavity. More recognizable is the boundary between the alisphenoid and the squamosal in this region, which appears to be just medial to or within a deep, elongate, vertically oriented trough in the anterolateral wall of the tympanic cavity (fig. 20). This trough, the Glaserian fissure, conveys the chorda tympani (fig. 26), a nerve that runs from the facial nerve through the middle ear cavity to the malleus (McDowell, 1958, p. 122). The chorda tympani joins the lingual nerve (of the mandibular ramus of the trigeminal) for the anterior taste buds of the tongue. There is clearly no notch or groove on the ventral surface of the tegman tympani for passage of the inferior ramus of the stapedial artery. (See descriptions of squamosal and petromastoid below.)

The dorsal intracranial surface of the alisphenoid is marked by a distinct horizontally trending (ophthalmic) groove partly shared with the frontal above (fig. 15). More ventrally, in the base of the cranial cavity, the alisphenoid and basisphenoid are broadly fused. Anteriorly, the large, slitlike sphen-orbital fissure continues posteriorly as a broad depression that flanks the tuberculum sellae. This depression posteriorly extends beyond the foramen ovale and represents the fossa for the trigeminal nerve and Gasserian ganglion (fig. 15). Medial to the Gasserian fossa is a raised area which likely represents the intracranial exposure of the basisphenoid (described below).

The important features of the leptictid alisphenoid (excluding its tympanic features) are: (1) the broad, dorsal expansion of the alisphenoid in the orbital wall, (2) the apparent confluence of the suboptic foramen and the foramen rotundum with the sphenorbital fissure, (3) the presence of a short alisphenoid canal, (4) the lack of foramina adjacent to the foramen ovale for masseteric and buccinator nerves; (5) the presence of a deep Gasserian fossa, (6) the distinct ectopterygoid crest. It seems that most of these traits are expected in primitive therians (Novacek, 1980), although the dorsal expansion of the alisphenoid is, as noted above, somewhat anomalous. Moreover, the ectopterygoid crests represent a plausible specialization common to leptictids, erinaceids, macroscelidids, bats, tupaiids, dermopterans, and primates, but lacking in tenrecids, soricoids, chrysochlor-

ids, as well as *Didelphis* and creodonts (But-
ler, 1956, p. 472). This crest increases the
area of origin of the ventral head of the ex-
ternal pterygoid muscle.

The alisphenoid is an important element
in the sidewall of the braincase, highlighted
in many discussions of mammalian system-
atics and comparative anatomy. There is,
however, some confusion regarding the ho-
mologies of the alisphenoid and adjacent ele-
ments in higher groups of mammals. The
standard view (Kermack, 1963; Kermack and
Kielan-Jaworowska, 1971) attributes the de-
rived condition to monotremes (and possibly
multituberculates), wherein the sidewall of
the braincase is formed primarily by an an-
terior lamina that is continuous with the peri-
otic; the sidewall contributions of the ali-
sphenoid and squamosal are insignificant. By
contrast, therians are said to show a large
sidewall contribution by the ascending pro-
cess of the alisphenoid, a smaller contribu-
tion by the squamosal, and a trivial contri-
bution by the posteriorly positioned periotic.
Reference markers for these relationships are
the foramina for the second and third branch-
es of the trigeminal nerve. These are located
within the ascending process of the alisphe-
noid in therians, but are represented by
notches in the ventral edge of the anterior
lamina of the "periotic" in monotremes.

As one might anticipate, the description of
a lamina possibly continuous with either the
periotic or alisphenoid leads to ambiguities.
Thus, Presley and Steel (1976) and Presley
(1981) provided ontogenetic evidence that the
same element, a membrane bone replacing
the spheno-obturator membrane, forms the
sidewall of the braincase in both monotremes
and therians. Differences between these
groups pertain only to later stages: the mem-
brane bone fuses with the periotic in mono-
tremes, whereas this element fuses with the
ventral alisphenoid in therians. Kemp (1983)
further trivialized this difference by claiming
that monotremes and therians differed only
in the sequence of fusion of this membrane
with adjacent elements. Accordingly, the
monotreme and therian conditions are clear-
ly homologous (Patterson, 1980; Kemp,
1983). The morganucodontid braincase wall
appears to be a mosaic of the monotreme and
therian conditions (Kermack, 1963). The

periotic (anterior lamina?) is well developed,
but so is the ascending process (?) of the ali-
sphenoid. For this reason, Kemp (1983) re-
gards the morganucodontid condition as a
plesiomorphic one, from which derive the
therian and monotreme states. Moreover, in
a review of the ontogeny of the braincase wall
in various mammals, Maier (MS and personal
commun.) argued for the homology of the
therapsid epipterygoid and the mammalian
alisphenoid, with *Morganucodon* represent-
ing an intermediate stage in the transfor-
mation. Maier (ibid.) also found the devel-
opment of the epipterygoid and alisphenoid
so intimately related that there is no strong
reason for Presley and Steel's (1976) distinc-
tion between an anterior ascending process
(being homologous to the epipterygoid) and
a posterior lamina ascendens (corresponding
to the alisphenoid).

PTERYGOID
(figs. 2, 5, 14, 19)

The pterygoid is best preserved in *Leptictis*
where its entopterygoid crests are observed
as a pair of rounded, vertical keels extending
from the posterior palatine process to a point
opposite the posterior opening of the alisphe-
noid canal. These crests are intact in only a
few specimens. The pterygoid region in *Pa-
laeictops* is damaged but both entopterygoid
and ectopterygoid flanges similar to those in
the Oligocene forms are present.

As noted above, the pterygoid is fused with
its adjacent elements, the presphenoid, ali-
sphenoid, and basisphenoid, and its bound-
aries are difficult to determine. It doubtless
forms the lateral roof of the interpterygoid
fossa, where its boundaries are marked by a
pair of elongate pharyngeal grooves that run
along the internal base of the entopterygoid
crest (fig. 2). The pharyngeal grooves convey
the pharyngeal nerve, artery and vein be-
tween the tuba auditiva and the sphenopala-
tine ganglion (fig. 26).

The entopterygoid crests form the medial
walls for the ectopterygoid fossa. These
depressions are the site of origin for the in-
ternal pterygoid muscle. The triangular fossa
extending from the back of the entopterygoid
crest to the anteromedial rim of the tympanic
cavity (figs. 2, 19) is probably the area of

junction between the pterygoid and alisphenoid.

The dorsal (intracranial) surface of the pterygoid is obscured by broad expansion and fusion of the basisphenoid and alisphenoid.

The design of the ectopterygoid fossa is such that the internal pterygoid muscles are confined to the space defined by the pterygoid crests. This condition, also seen in erinaceids and *Solenodon,* is not present in macroscelidids, tupaiids, or primates. In the latter three taxa the internal pterygoid migrates forward and far dorsal to attach to the palatine in front of the optic foramen (Butler, 1956, fig. 7). It seems plausible that the leptictid-lipotyphlan condition is derived, but relevant distributional information on the attachments of the internal pterygoid muscles is very poor.

BASISPHENOID
(figs. 2, 5, 15, 16, 18, 19, 24)

The basisphenoid is broadly fused with the pterygoid and alisphenoid and basioccipital. Ventrally, its most obvious feature is a somewhat trapezoidal platform wedged between the more anterior presphenoid and more posterior basioccipitals. There is a slight sculpturing on its ventral surface (figs. 2, 19) indicating pharyngeal grooves and depressions for the recti capiti muscles that continue posteriorly on the surface of the basioccipital. The lateral extension of the basisphenoid probably includes a contribution to the anterolateral tympanic cavity, although this would be excluded from the middle ear proper by the medial border of the bulla. The development of the basisphenoid in this region is, however, obscured by its extensive fusion with the alisphenoid.

The intracranial exposure of the basisphenoid is the elongate, raised sella turcica (for the pituitary gland) in the middle region of the cranial floor. The tuberculum sellae consist of a rounded pair of ridges that extends forward from the sella turcica to an obscured junction with the presphenoid. Flanking the tuberculum sellae are a pair of small foramina (fig. 15), presumably for small veins draining the internal spaces of the presphenoid and basisphenoid.

Posterior to the tuberculum sellae the elongate hypophyseal fossa extends to the back

of the basisphenoid. Its posterior limit is marked by a prominent, semivertical dorsum sellae, whose dorsal end is expanded into a rounded posterior clinoid process (figs. 15, 18, 24). Bilateral to the hypophyseal fossa are a pair of shallow elongate sulci for the cavernous sinus (fig. 15). These lead posteriorly to an anterior carotid foramen between the petromastoid and the basisphenoid that probably served as the common pathway for the inferior petrosal vein and the promontory branch of the internal carotid artery (see description below). There is a small foramen near the anterior end of the sulcus for the cavernous sinus. This probably served as the drainage exit for the vascular net within the basisphenoid. There is no evidence of an anterior clinoid process or a suboptic foramen on the intracranial surface of the basisphenoid.

McDowell (1958, p. 204) noted that leptictids were unlike basic lipotyphlans and like tupaiids in having a prominent dorsum sellae. His discussion, however, implies that the dorsum sellae is simply a primitive trait, and that the Lipotyphla are definable, in part, by the loss of this structure. The ventral surface of the leptictid basisphenoid also differs somewhat from lipotyphlans. In the latter, this element is usually a less elevated surface and pharyngeal sculpturing is very faint or absent. Erinaceines show the interesting secondary development of a very deep basisphenoid pit.

SQUAMOSAL
(figs. 1, 2, 13, 15, 17, 18,
20, 22, 24–28)

The squamosal is a large element that joins the parietal dorsally, the alisphenoid ventrally and anteriorly, the jugal at the leading edge of the posterior zygomatic process, and the petromastoid ventromedially and posteriorly. These relationships are well defined by sutures only in *Leptictis.* The irregular parietal-squamosal suture extends horizontally from the triple junction of the squamosal, alisphenoid, and parietal to the lambdoidal crest. The suture (as shown in ANSP 11042) actually turns the corner of this crest to contact the occipital exposure of the mastoid. Below the parietal-squamosal suture and
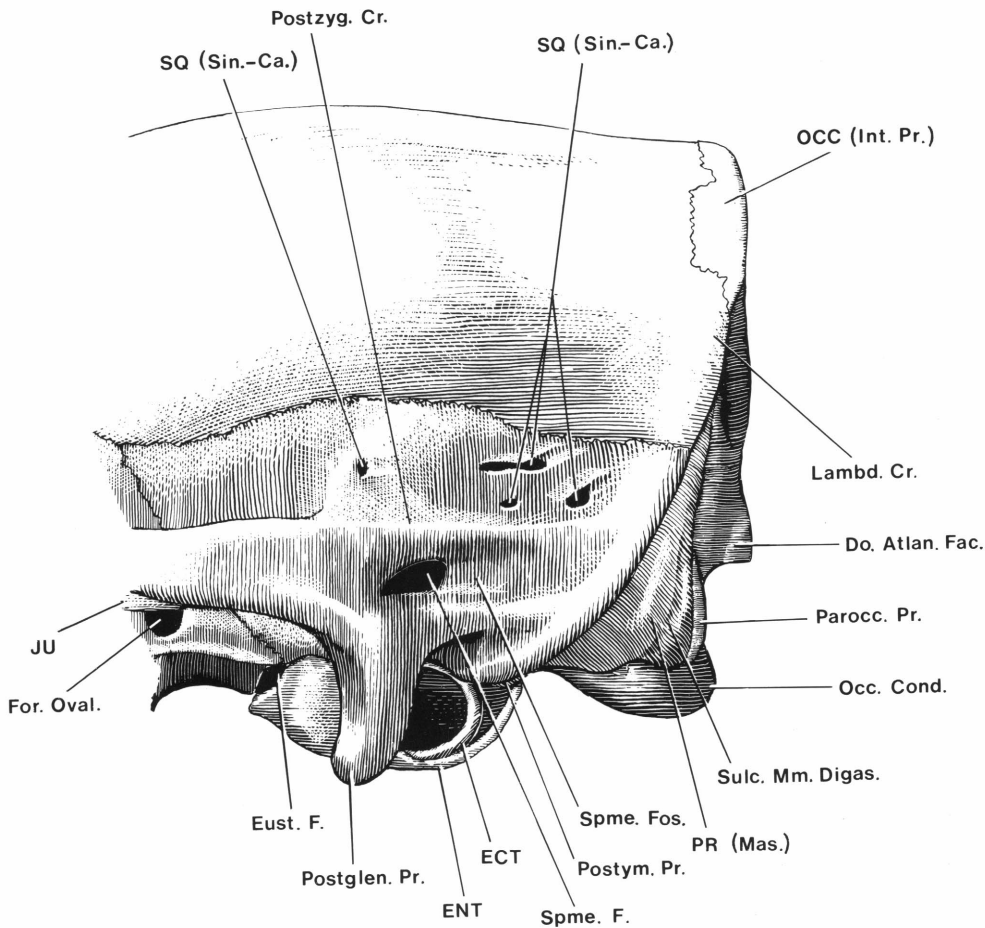
FIG. 17. Lateral view of left temporal region in *Leptictis dakotensis*. For abbreviations see pp. 5–7.

above and slightly posterior to the zygomatic process of the squamosal, are two or three small foramina that open into shallow surface grooves. These canals appear to converge with an intracranial squamosal sinus that connects with a large intracranial canal for the superior petrosal sinus (figs. 17, 18, 24, 28).

Below the squamosal sinus-canals is a longitudinal crest that marks the dorsal border of the root of the zygomatic process. This crest extends forward to a point where the zygomatic sweeps abruptly outward to form the posterior section of the zygomatic arch. The anterodorsal surface of the zygomatic process is a shallow concavity with a tiny foramen that most likely joins the squamosal sinus. The squamosal contribution to the zy-

gomatic arch is an anteriorly tapered process that, in lateral view, overlaps the jugal for some distance (figs. 1, 2, 13). In ventral view, the glenoid fossa is a large, shallow depression, slightly more transverse than anteroposteriorly elongate. The postglenoid process is well developed and forms a wall to most of the posterior border of the glenoid fossa. The jaw articulation and its functional implications have been discussed above.

In lateral view, a large, circular suprameatal foramen (subsquamosal foramen in Butler, 1956, fig. 4) pierces the posterior surface of the zygomatic process just above the external auditory meatus (fig. 17). This foramen probably carried a (suprameatal) vein that joined the superior petrosal sinus and exter-
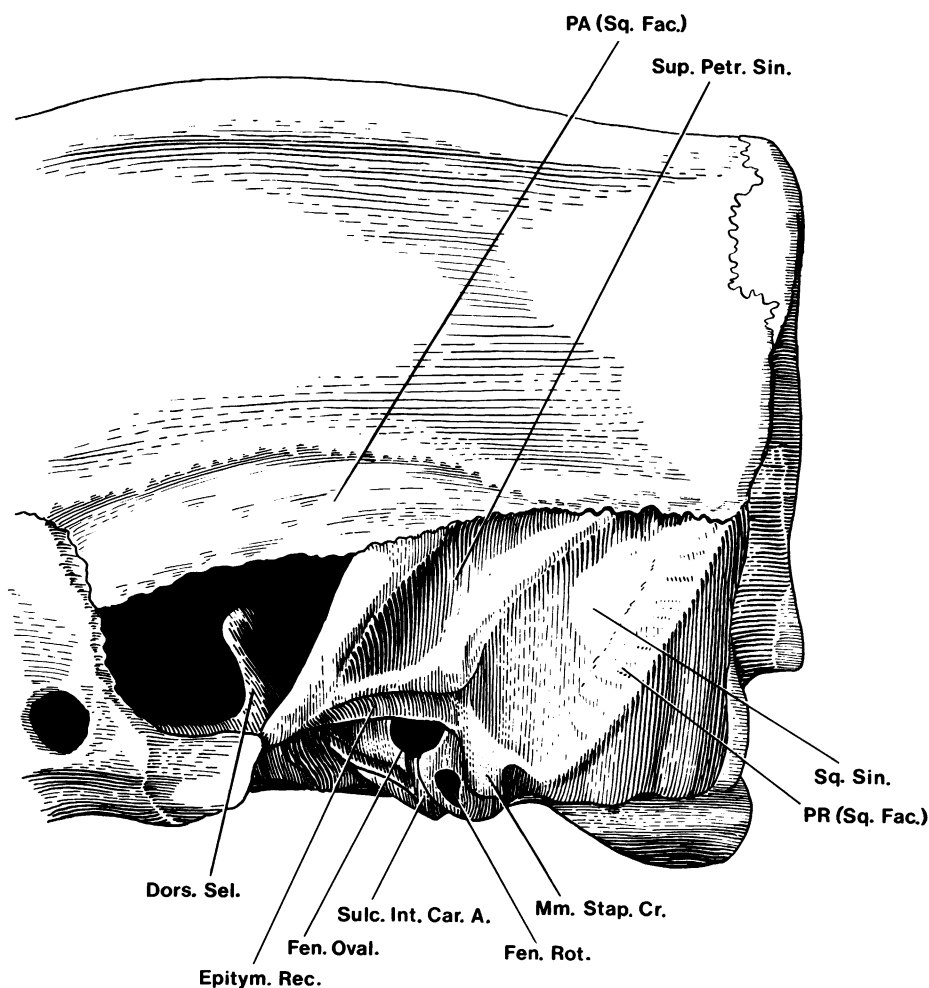
Fig. 18.   Lateral view of left temporal region in *Leptictis dakotensis*. Squamosal partly removed to show squamosal sinuses. For abbreviations see pp. 5–7.

nal jugular vein (fig. 28). The junction of canals for these three vessels can be clearly seen in cross section (AMNH 3944, fig. 24). In *Leptictis* the suprameatal foramen opens into a well-excavated fossa, but this fossa is weak or absent in other leptictids.

In ventral view, the limits of the squamosal are difficult to discern. The squamosal-alisphenoid suture appears to run over the preotic crest on the leading edge of the tympanic cavity (fig. 22). The suture then courses over the roof of the tympanic cavity, just medial to, or within, the Glaserian fissure. Because this fissure is lateral in position, most of the anterior tympanic cavity is contributed

by the alisphenoid (see above); the squamosal forms only the lateral wall of the tympanic cavity, into which opens the epitympanic recess.

A large, circular postglenoid foramen is situated just medial and very slightly posterior to the postglenoid process. This foramen is sometimes continuous ventrally with a faint trough running down the medial face of the postglenoid process. The postglenoid foramen is the opening through which the external jugular vein connects with the superior petrosal sinus (figs. 26, 28).

The meatal surface of the squamosal is smooth, and in lateral outline forms a shal-

low, ventrally concave curve (figs. 17, 20) well below the level of the roof of the tympanic cavity. Its posterior boundary is marked by a prominent post-tympanic process that also forms the ridge anterior to the squamosal-mastoid suture.

The intracranial surface of the squamosal (observed only in *Leptictis*) forms, with the parietal, an expansive concavity for the cerebrum. The most prominent feature on this surface is a shallow groove that arcs upward and continues forward nearly parallel to the parietal-squamosal suture positioned just above it (fig. 15). This groove probably carried the superior ramus of the stapedial artery and (more anteriorly) the ophthalmic artery (fig. 27).

The squamosal is poorly preserved in *Palaeictops,* but a few features can be discriminated. The postglenoid foramen lies posterior, rather than medial, to the postglenoid process in *Palaeictops*. The suprameatal foramen is present in *P. bicuspis,* but it does not lie within a suprameatal fossa. The meatal surface of the squamosal is narrower than in the Oligocene taxa; it forms only a bridge of bone lateral to the deeply excavated epitympanic recess. The Glaserian fissure for the chorda tympani and a post-tympanic process are similar to those features in *Leptictis*. The postglenoid process in *Palaeictops* may be smaller than in later forms, although in the glenoid region all skulls of this genus are badly damaged.

The salient features of the squamosal are: (1) the presence of one or more squamosal sinus-canals, (2) the anterior extension of the squamosal in the zygomatic arch so that this element broadly overlaps the more ventral, posteriorly projecting jugal, (3) a large, shallow, and somewhat transversely oriented glenoid fossa, (4) the prominent postglenoid process, (5) the presence of a suprameatal foramen, (6) a distinct, elongate Glaserian fissure for the chorda tympani, (7) the deep epitympanic recess, (8) the large, posteromedially positioned postglenoid foramen, (9) a meatal arch of the squamosal ventral to the level of the roof of the tympanic cavity, and (10) a prominent post-tympanic process.

Many of these squamosal characters (e.g., 2, 3, 4, 8, 10) are undoubtedly primitive for therians (Butler, 1956; Novacek, 1980) and

therefore fail to provide clues to the affinities of leptictids. A few characters are either of ambiguous polarity or are probably derived, and warrant some comment. One condition of interest is the presence of the squamosal sinus-canals. Although their function is uncertain, these canals may have served as the drainage route for enlarged pinnae (McDowell, personal commun.). A single squamosal sinus-foramen is present in didelphids. Erinaceids have from one to three of these canals in a position very similar to that in *Leptictis*. In *Solenodon* and tenrecids there is usually a single opening above the posterior ridge defining the root of the zygomatic process. The canals are variably present in tupaiids and megachiropterans, but absent in macroscelidids and dermopterans. In primitive rodents (e.g., *Paramys*) there is a pair of canals (temporal foramina of Wahlert, 1974) between the squamosal and the zygomatic process. The distribution of this trait in these and other mammals suggests that the presence of at least one squamosal sinus-canal is primitive. However, the number and position of the canals (e.g., as in rodents) may indicate a special relationship. In this regard, the condition shared by *Leptictis* and erinaceids seems more specialized but cannot be regarded as morphotypical for leptictids, as other leptictids may show the condition present in didelphids and nonerinaceid insectivorans.

The suprameatal foramen occurs to a limited extent in eutherians, but the feature is present in some didelphids. In the latter group the foramen usually faces more posteriorly because of the more abrupt, lateral flairing of the zygomatic process. A large suprameatal foramen is not present in erinaceids, although there are sometimes one or two tiny openings in the expected location. The foramen is typically absent in most other insectivorans, macroscelidids, dermopterans, tupaiids, chiropterans, and primates. In lagomorphs and rodents there is a foramen in the suprameatal position, but this is apparently the postglenoid foramen shifted dorsally and posteriorly with the drastic refashioning of the jaw articulation (Wahlert, 1974). Thus, there are two alternatives with no clear means of resolution: either the suprameatal foramen is a derived trait of leptictids independently ac-

quired in didelphid marsupials, or the trait is primitive for therians and lost in many lineages. Butler (1956) seemed to favor the latter interpretation.

An interesting feature of the squamosal contribution to the leptictid auditory region is the deep, vertically oriented Glaserian fissure. This groove appears early in ontogeny as the aperture for Meckel's cartilage, which eventually disappears and is replaced by the chorda tympani and, in some cases, the ramus inferior of the stapedial artery (Klaauw, 1931, p. 164). The presence of a Glaserian fissure is, based on ontogenetic and distributional evidence, a primitive therian condition. However, the deep troughlike appearance of this groove in *Leptictis* is more reminiscent of the condition in lipotyphlans than in most tupaiids, macroscelidians, didelphid marsupials, and many other mammalian groups (table 3). (In the tupaiid *Ptilocercus,* the troughlike Glaserian fissure is uniquely narrow and arises in the anterior wall of the epitympanic recess.) The narrowness of this fissure in leptictids indicates that if the inferior ramus of the stapedial artery followed this pathway (as it does in erinaceids and other insectivorans), it was an extremely small vessel. There is evidence, however, to indicate that this branch entered the cerebral cavity via a small foramen posterior to the Glaserian fissure (Novacek, 1980, and fig. 26 herein). The exclusion of the inferior ramus of the stapedial from the Glaserian fissure is probably a derived eutherian character (see remarks below under Petromastoid).

The epitympanic recess is typically present in eutherians, but its size and position varies among different groups. The development of this fossa correlates with another squamosal character noted above, namely the presence of a meatal arch of the squamosal ventral to the level of the tympanic roof. This arch forms the floor and part of the lateral wall of the epitympanic recess in leptictids, erinaceids, and a variety of other taxa. However, didelphids typically show the squamosal-meatal arch only slightly depressed below the level of the tympanic chamber. As a result, the epitympanic recess in didelphids is a shallow basin bordered laterally by a narrow cleft. This may reflect the primitive mammalian condition in which the epitympanic recess is

very poorly excavated, as in *Ornithorhynchus* (the recess is also small in *Tachyglossus,* but is often confused with the larger tympanic recess; see comments in Klaauw, 1931, p. 73).

The epitympanic recess lodges the incudomalleolar articulation, so its development reflects the size of these ossicles. For example, the recess is very large in *Chrysochloris,* a burrowing form with large, loosely articulated ossicles suited to low-frequency impedance matching (Fleischer, 1973). The recess is also very deep in Sirenia, *Herpestes, Felis, Canis, Orycteropus,* some rodents (*Rhizomys*), lagomorphs, *Equus,* and *Bradypus.* In some of these cases (e.g., *Orycteropus, Bradypus*) the epitympanic recess and epitympanic sinus form a single large cavity (Klaauw, 1931).

In living mammals the membranous lateral wall of the epitympanic recess is dorsal to the level of the tympanic membrane (pars tensa) and so is formed by the membrana Shrapnelli (preferable to the term pars flaccida—see Bondy, 1907, p. 399). The composition of the bony lateral wall of this recess varies notably in mammals. In leptictids, *Tachyglossus,* didelphids, *Sus, Procavia,* cervids, tragulids, and most insectivorans the lateral wall is formed primarily by the squamosal. This appears to be the primitive condition, as contributions to this wall by other elements seem to be a function of one of the following modifications (see Kampen, 1905; Bondy, 1907; Klaauw, 1931): (1) bony fusion of a dorsally closed ectotympanic (i.e., ring-shaped rather than horseshoe-shaped) with the tegmen tympani of petrosal (some rodents, some lagomorphs, viverrids); (2) broad fusion of the periotic with the squamosal in early stages of ontogeny (some primates); (3) development of an elongate ectotympanic tube for the external auditory meatus that also serves as part of the lateral wall of the epitympanic recess (perissodactyls, some lagomorphs, macroscelideans, dermopterans, tupaiids); (4) forward expansion of the mastoid process of the petrosal (erinaceines, but not other erinaceids); (5) incomplete development of the bony lateral wall so that the wall is partly formed with a membrane distinct from the membrana Shrapnelli (*Tachyglossus, Sorex,* Chiroptera). The last condition may indeed represent a primitive one in
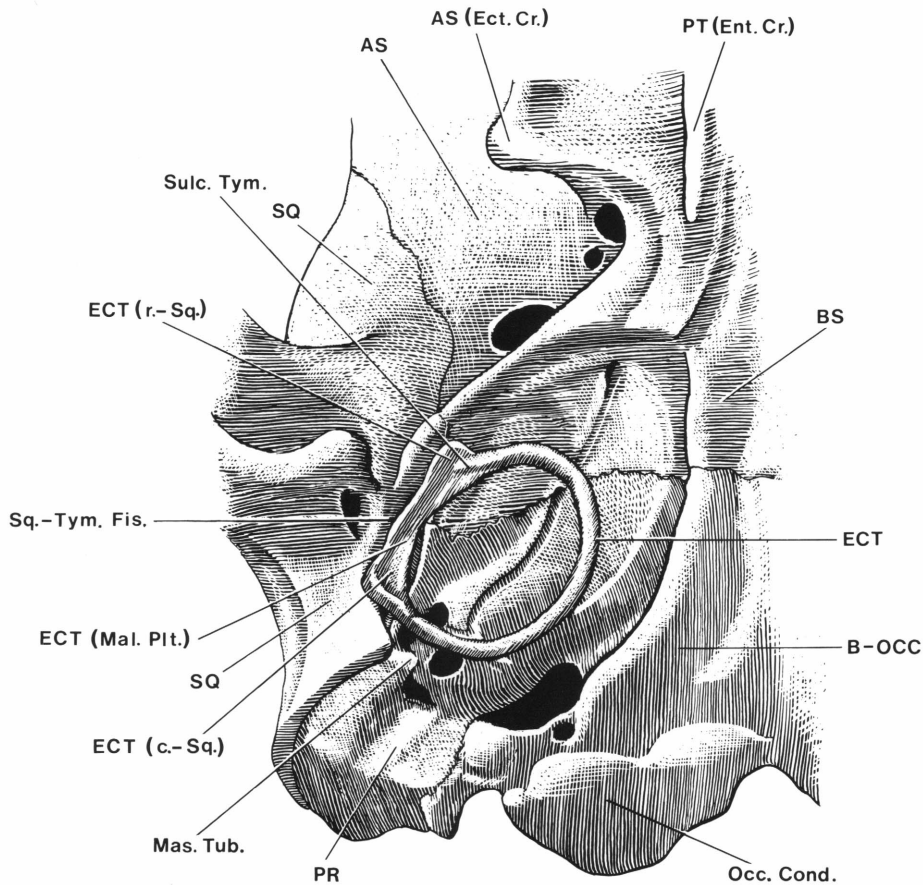
FIG. 19.   Ventral view of right tympanic region of *Leptictis dakotensis*. Bulla removed to show ectotympanic ring. For abbreviations see pp. 5–7.

cases where the bony portion of the wall is formed by the squamosal (e.g., *Tachyglossus,* but not necessarily *Sorex* or Chiroptera). It should be noted that the above conditions are not exclusive of each other; in some instances the architecture of the epitympanic recess is a function of ectotympanic expansion of the external meatal tube and lateral growth of the petrosal (e.g., lagomorphs).

ECTOTYMPANIC
(figs. 19–21)

The ectotympanic is preserved only in specimens of *Leptictis.* This element is annular, rather than horseshoe-shaped; its anterior and posterior crura are in broad dorsal contact. Dorsally, the ectotympanic is flattened into a mallear plate (figs. 19–21). The

rostral end of this plate is marked by a distinct triangular crest (figs. 19, 20) that abuts against the preotic crest of the squamosal. The gap above the mallear plate and ventral to the medial surface of the meatal trough of the squamosal presumably conveyed a portion of the chorda tympani and the inferior ramus of the stapedial artery (see descriptions of petromastoid below, squamosal, above). An elongate groove of the dorsolateral surface of the ectotympanic probably contacted the processus folii of the malleus. Interestingly, no leptictids preserve the malleus or other ear ossicles. It seems likely, therefore, that the malleus was not broadly fused with the dorsal ectotympanic, as it is in many mammals. The remainder (more ventral aspect) of the ectotympanic is simple and cy-

lindrical with a faint groove for contact with the tympanic membrane. The ectotympanic ring is ellipsoidal in outline. Its ventromedial part is concealed by the entotympanic bulla (see below), which forms the floor of the tympanic region. The extent to which the bulla covers the ectotympanic is not clear because these elements have been shifted from their original positions during preservation. Likewise, the angle of inclination of the ectotympanic ring is not certain. As in many mammals, the ring is inclined so that its dorsal (mallear) part is more lateral than its ventral part. The angle between the oblique dorso-ventral plane of the horizontal plane of the skull lies anywhere between 50 and 35°.

Numerous studies support the notion that a simple ring-shaped or horseshoe-shaped, strongly inclined ectotympanic is a primitive therian trait (Gregory, 1910; Klaauw, 1931; Archibald, 1977; Kielan-Jaworowska et al., 1979; Novacek, 1977b, 1980). During ontogeny the ectotympanic has been shown to migrate from a more horizontal to a more vertical orientation (see Klaauw, 1931; Hunt, 1974; Novacek, 1977b). This shift is often accompanied by expansion of the ectotympanic into a meatal tube or a medial contribution to the auditory bulla. In some adult mammals, however, the horizontal orientation of the ring is maintained with the effect that the tympanic membrane actually represents a partial floor of the tympanic cavity. The fact that this condition is present in monotremes, soricomorphs, and a number of early eutherians has led to the claim that the basic ontogeny and phylogenetic transformation of the ectotympanic are equated (Archibald, 1977; Novacek, 1977b).

MacPhee (1981) cautioned, however, that this equation is by no means secure. He points out that the "embryonic" annular ectotympanic in adult lemurs and tree shrews is the product of cessation of growth around the time of birth, and that this ontogeny is rare and perhaps anomalous for modern mammals. MacPhee (1981, p. 252) advocated some degree of expansion of the ectotympanic as the normal transformation, but suggested that this expansion is not substantial. From this, it is unclear how much a departure from the simple annular or semiannular morphology is to be deemed primitive. One may infer that this slight expansion does not resemble the broad bullar or meatal flanges of the ectotympanic seen in many mammals (see Klaauw, 1931; Novacek, 1977b, table 2). Hence, the transformation of the ectotympanic in its simplest terms, seems unaffected by Mac-Phee's (1981) concerns. The adult condition for primitive therians plausibly more closely resembles the common embryonic condition, whereas marked expansion of the ectotympanic and its more vertical orientation, represents more derived conditions. It should be emphasized that these modifications are diverse and possibly independently acquired in a variety of mammalian lineages (Novacek, 1980).

The dorsal closure of the ectotympanic in *Leptictis* is of interest because in several insectivoran groups (soricids, tenrecomorphs, solenodontids) the crura of this element are separated by a slight gap. The significance of this comparison is unclear. The differences, for example, between the dorsally open ectotympanic of certain tenrecids (see McDowell, 1958, fig. 37) and the complete ring in *Leptictis* are minor. Perhaps the slight expansion represented by the mallear plate in the latter (fig. 19) fulfills MacPhee's (1981) expectation for the primitive eutherian condition. It seems more likely, however, that the dorsal fusion of the anterior and posterior crura is more derived than the horseshoe-shaped ectotympanic.

ENTOTYMPANIC BULLA
(figs. 5, 20, 21)

In *Leptictis* the entotympanic forms a somewhat inflated bulla that covers most of the tympanic cavity. The medial flange of the bulla is a vertical wall that contacts a blunt, rugose ridge on the promontorium of the petromastoid. Laterally, the bulla forms a curved flange that conceals at least the ventromedial aspect of the ectotympanic ring. The anteromedial corner of the bulla is expanded into a process with a concave lateral surface (fig. 20). This anterior bullar process undoubtedly functioned with the hamular process of the pterygoid as a cradle for the eustachian tube. The bulla covers ventrally the promontorium and much of the tympanic ring, tegmen tympani, and facial canal. However, the stylo-

mastoid foramen and internal edge of the meatal surface of the squamosal and the dorsal (mallear) plate of the ectotympanic are not concealed by the lateral moiety of the bulla.

One of the most interesting discrepancies in earlier studies of *Leptictis* concerns the auditory bulla. Butler (1956) described the bulla in *Leptictis* as an outgrowth of the tympanic process of the petrosal. McDowell (1958), however, described the bulla in this form as an entotympanic, a separate ossification in mammals without a homologue in the reptilian skull (Klaauw, 1931). As noted above, there is no evidence of a continuous surface between the petrosal and the bulla. Instead, a suture contact is indicated, and in specimens where the bulla is absent a roughened ridge along the medial border of the promontorium and tympanic cavity (fig. 23) marks its contact with this separate bullar element. Hence, this element is, as McDowell maintained, an entotympanic bulla.

None of the skulls have an ossified bulla preserved that covers the entire tympanic chamber. In some specimens (CMNH 14, MCZ 19678) an ectotympanic ring is only partly enclosed by the bulla. The ring is also inclined at a low angle to the horizontal plane of the basicranium (see above). At least two explanations for this condition seem possible. Either the bony bulla is fully preserved and is actually a reduced element only partially covering the chamber, or the lateral portion of the bulla has been fragmented and removed from the specimens during burial and preservation. The absence of evidence for breakage along the lateral margin of a well-preserved bulla in SDSM 3644 favors the first alternative. The bulla in leptictids might therefore be interpreted as an incipient structure similar to that in some didelphine marsupials, tenrecids, and edentates, although the bony elements comprising the bulla in these taxa differ.

Both rostral and caudal entotympanics have been identified by Klaauw (1931) in bats, hyraxes, dermopterans, edentates, and macroscelidids, and by Hunt (1974) in some carnivores. There is no evidence for the distinction of these elements in leptictids. Unfortunately, none of the subadult skulls (with deciduous teeth), where identification

of separate ossifications holds greater possibilities, were preserved with attached ossified bullae. However, the well-developed anterior bullar process described above may represent the rostral entotympanic, since the precursor cartilage for this element normally forms as an embryonic support to the eustachian tube.

Like many other fossil mammals, leptictids were originally thought to lack an ossified bulla. Matthew (1899), in fact, recognized a separate species, *Ictops bullatus,* because the type and only referred specimen was unique in having a small bony capsule. As I have noted above and elsewhere (Novacek, 1977a, 1977b), the ossified bulla is typical of *Leptictis* species; its absence in skulls is attributable to the comparatively "loose" attachment of the entotympanic to the basicranium, and its subsequent loss during fossilization. I was able to find an osseous bulla in only 5 out of 66 well-preserved skulls of *Leptictis,* but its former presence in many of these skulls was clearly indicated by ankylosed sutures. Absence of an ossified bulla in fossils can be misleading as evidence for the condition in the once-living form.

The significance of the entotympanic and other bullar elements was reviewed in Klaauw (1931), Novacek (1977b), and MacPhee (1981). Based on these studies, the following scheme is favored. (1) The primitive condition in eutherians was probably one similar to that in monotremes, where the bulla is absent and the ectotympanic is inclined at a very low angle to the horizontal plane of the basicranium, nearly contacting the medial wall of the tympanic cavity. (2) The widespread distribution of entotympanic among mammals indicates that it was an early feature of eutherians; but its probable absence in the marsupial morphotype (MacPhee, 1981) suggests that it was absent in the common ancestor of metatherians and eutherians. (3) The partial bulla in leptictids represents an early stage in the derivation of a large bulla from the monotremelike condition. This more conservative condition is also present in some primitive didelphine marsupials and edentates. [In the Cretaceous forms *Asioryctes* and *Kennalestes,* the slightly expanded ectotympanic forms a partial covering of the tympanic region. Kielan-Jaworowska (1969, 1975) did not identify an entotympanic in-
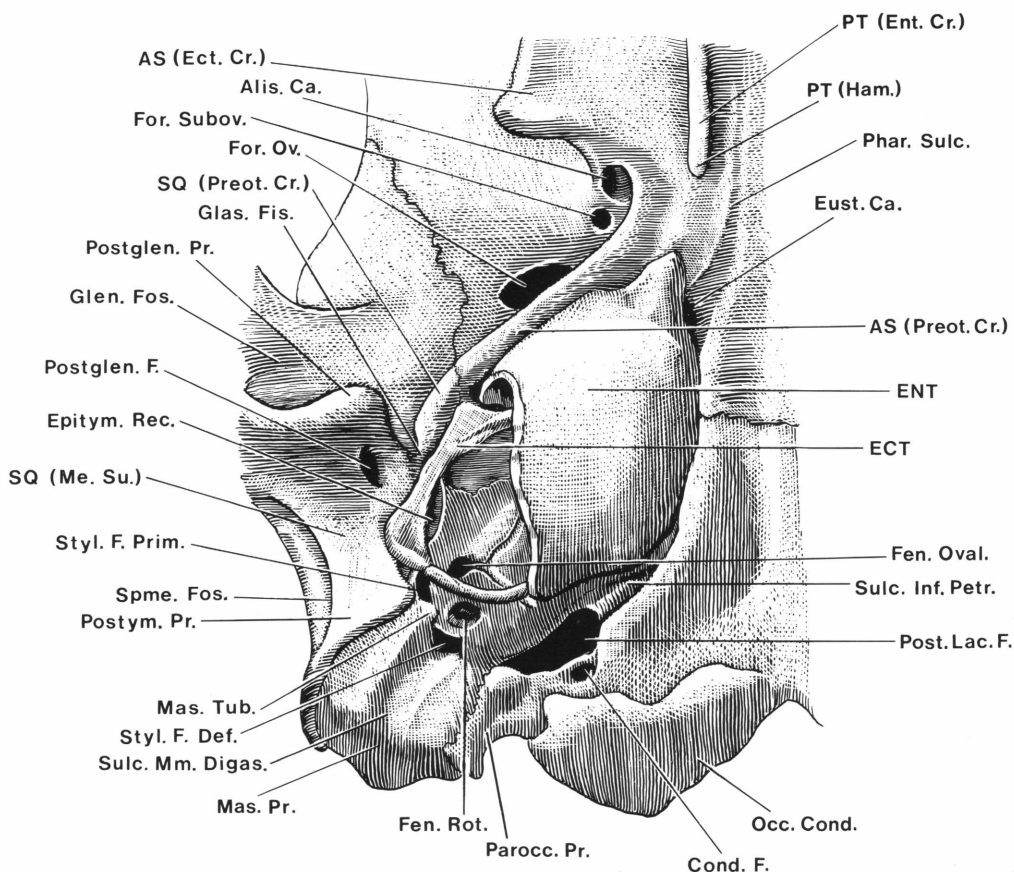
FIG. 20. Ventral view of right tympanic region of *Leptictis dakotensis*. Bulla partly dissected to reveal lateral tympanic region. For abbreviations see pp. 5–7.

corporated in this element.] (4) The petrosal bulla of primates, the ectotympanic bulla of rodents, rabbits, and other eutherian orders, the composite bulla of macroscelidids, the cartilaginous bulla of some carnivores and bats, and the basisphenoid-petrosal bulla of erinaceid and tenrecid insectivorans all represent derived eutherian conditions. In many cases derivation of bullar types is unclear; the transition involving the wholesale replacement of the entotympanic cartilage by bone of another element (such as the petrosal, see McDowell, 1958) has not been substantiated.

PETROMASTOID
(figs. 15, 16, 19–28)

The petromastoid is a complex bone that represents the major element of the tympanic region. It comprises the bony labyrinth and surrounding promontorium cochleae, the semicircular canals, part of the anterior and lateral roof of the tympanic cavity, and the mastoid process and its structures. In addition, the petromastoid serves as a passageway for a number of important cranial nerves, arteries, and veins. The morphology of this element varies little within leptictids, although there are minor differences between *Palaeictops* and the Oligocene species.

From a ventral aspect, the petromastoid is dominated by a large, fusiform promontorium (figs. 22, 23). The promontorium is broadest in its posterior region and tapers toward the anteromedial corner of the tympanic cavity. Its ventral surface is slightly rounded, but is interrupted by a few prominent features. A crescentic ridge for contact
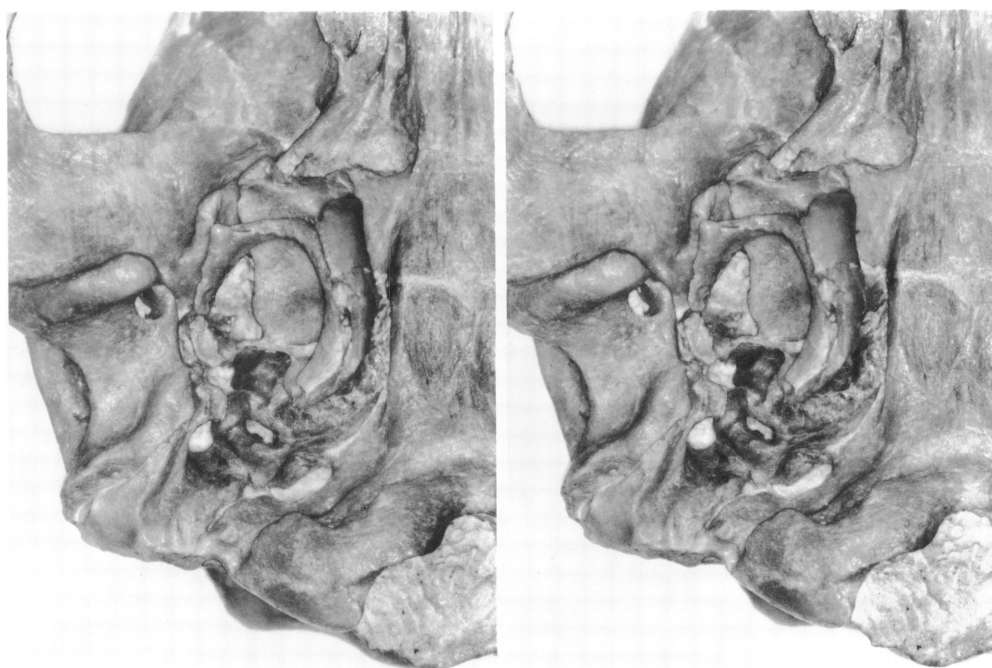
FIG. 21. Stereophotographs of ventral view of right tympanic region of MCZ 19678, *Leptictis dakotensis.* Bulla shifted from natural position. Features are identified in figure 20. For scale, see figure 2.

with entotympanic arcs along the posterior and medial border of the promontorium (figs. 22, 23). This petrosal ridge, which has a distinctly roughened ventral surface, begins below the fenestra rotunda and extends to the anteromedial corner of the promontorium.

In addition to the petrosal ridge, there is a branching pattern of sulci on the promontorium. These are presumably for the internal carotid artery system and possibly small accessory nerves. A large common sulcus (for the internal carotid) courses anterolaterally from the posterior terminus of the median petrosal ridge and borders ventrally the fenestra rotunda. After a short distance, this sulcus branches into a dorsally trending groove for the stapedial artery, and a forwardly directed sulcus for the promontory artery (figs. 22, 23, 26). The stapedial groove meets the fenestra ovalis; hence, the stapedial artery passed through the crura of the stapes. Dorsal and lateral to this point, the pathway of the stapedial artery is more difficult to follow. There is a small foramen located at the posterior edge of the epitympanic recess, above the lip of the meatal roof of the squa-

mosal. This foramen probably served as the exit for the superior ramus of the stapedial artery, a vessel whose pathway leads forward to join the ophthalmic artery (fig. 27). The inferior ramus of the stapedial probably exited the tympanic cavity in a small foramen at the forward apex of facial canal, a point just anterior and lateral to the fenestra ovalis. There is no evidence to indicate that the inferior ramus was conveyed below or on the roof of the tympanic cavity or within the Glaserian fissure (see squamosal, above).

The pathway for the promontory artery is more clearly indicated. The sulcus for this vessel courses anteromedial for the length of the promontorium and ends in a small anterior carotid foramen (fig. 22) located in the suture separating the petromastoid from the sphenoid (basisphenoid and alisphenoid). The fenestra rotunda (fenestra cochlea) is well exposed in ventral view. It faces posteriorly and slightly laterally. A well-developed dorsal rim of the promontorium overhangs the antrum of the fenestra rotunda.

Lateral and adjacent to the fenestra rotunda is a deep pit whose boundaries are formed
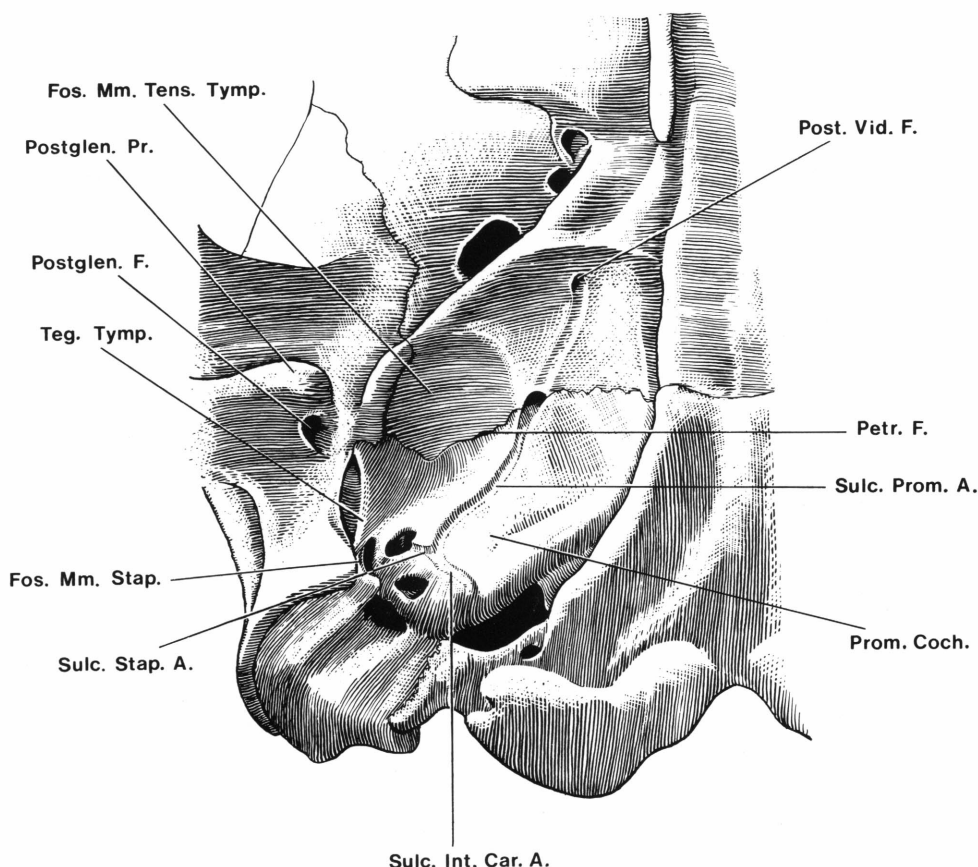
FIG. 22. Ventral view of right tympanic region of *Leptictis dakotensis*. Bulla and ectotympanic ring removed. For abbreviations see pp. 5–7.

by the bridge of bone connecting the promontorium with the mastoid region of the petrosal and a prominent mastoid tubercle (figs. 20, 22, 23, 25). This fossa is the foramen stylomastoideum definitivum for the exit of the facial nerve. It is continuous anteriorly with the facial canal, which is partly concealed from ventral view by the mastoid tubercle. The concave area of the mastoid posterior to the stylomastoid foramen probably represents the area of origin of the stapedius muscles (fig. 26). There is no well-defined fossa muscularis minor for this muscle.

As noted above, the stylomastoid foramen is delimited medially by a prominent petromastoid bridge. This osseous link separates the stylomastoid foramen from the large, ellipsoidal posterior lacerate foramen. However, there is no prominent crest of the petromastoid in this region, which, in many

mammals either contacts an osseous bulla or forms a lip that conceals all or part of the fenestra cochlea from ventral view.

The mastoid process posterolateral to the stylomastoid foramen is a distinctive, spatulate element in ventral view wedged between the dorsal meatal roof of the squamosal anteriorly and the paroccipital process of the basioccipital posteriorly. The mastoid process has a well-developed groove for the digastric muscle that runs diagonally for most of its ventral exposure (figs. 20, 21, 23).

The posterior lacerate foramen occupies much of the area between the posteromedial edge of the petromastoid and the basioccipital. There is no separate jugular foramen, so the posterior lacerate foramen probably conveyed the internal jugular vein as well as cranial nerves IX, X, and XI (figs. 26, 28). At the anteromedial corner of this foramen is a
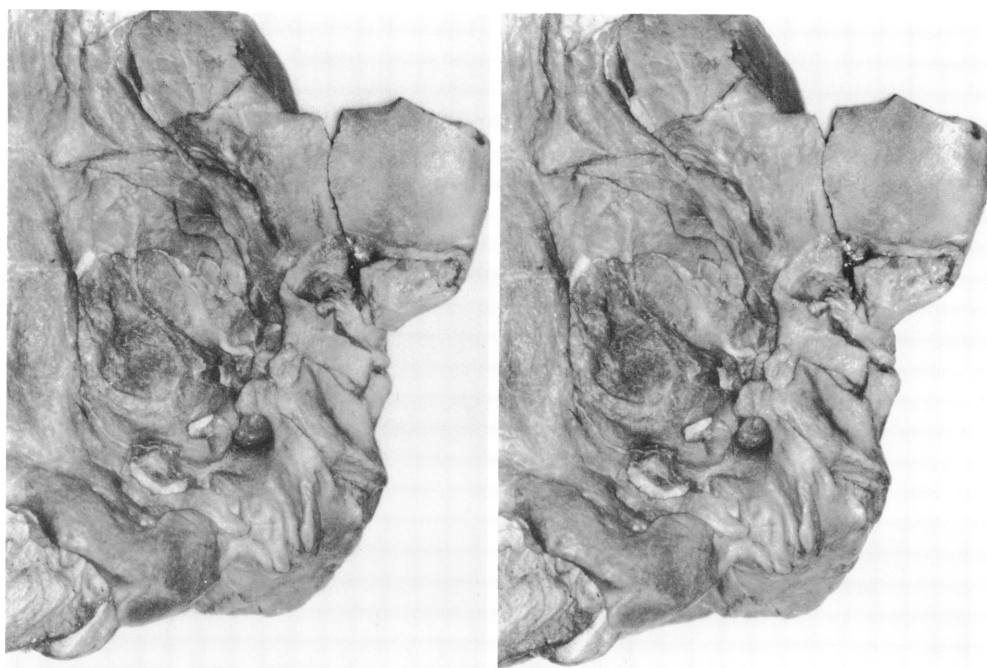
Fig. 23. Stereophotographs of ventral views of left tympanic region; MCZ 19678, *Leptictis dakotensis.* (Bulla and ectotympanic not preserved.) Features are identified in figure 22. For scale, see figure 2.

narrow, shallow trough (fig. 20) that curves around the posteromedial edge of the promontorium, becomes increasingly narrow anteriorly, and burrows between the petrosal and basioccipital. This sulcus probably served as the exit for the inferior petrosal sinus (figs. 26, 28, and comments below).

On the lateral side of the promontorium is a well-developed mastoid tubercle with a faint, rounded fossa on its ventral surface. There is no evidence that this tubercle supported part of the malleolar plate of the ectotympanic. In all specimens where it is preserved, the ectotympanic is lodged well anterior and ventral to the mastoid tubercle (figs. 20, 21). Alternatively, this process may be partly composed of the tympanohyal, the most cranial ossification of the hyoid apparatus. The tympanohyal often fuses with the petrosal in late developmental stages (De-Beer, 1937; MacPhee, 1981).

As noted above, the epitympanic recess is a distinct but areally confined fossa partly covered ventrally by the meatal roof of the squamosal. The internal boundary of the fossa is formed by a ridge that also marks the

lateral rim of the facial canal. Where the ectotympanic is preserved, this region of the tympanic roof is ventrally hidden by the malleolar plate.

A very faint depression on the tympanic eminence of the basisphenoid trends anteromedially from the most anterior corner of the promontorium (fig. 20). This groove probably marks the pathway of the eustachian canal. The canal is better defined with the bulla in correct position, which clearly shows that the rostral bullar process forms a ventral cradle to the eustachian tube (see fig. 20, and comments above). It is noteworthy that the bulla contacts the petrosal lateral to the eustachian canal. Hence, part of the tympanic roof formed by the basisphenoid is isolated from the remainder of the tympanic cavity by the median wall of the bulla.

The intracranial (dorsal) surface of the petromastoid marks the area of the cranial vault that lodges the cerebellum. A prominent feature of this surface is an extremely deep and large subarcuate fossa (figs. 15, 16, 25). The other major depression, the internal acoustic meatus, lies medial and slightly anterior to

the subarcuate fossa. The meatus contains within it a medial acoustic (cochlear) foramen for the auditory (VIII) nerve and a more posterolateral Fallopian foramen for the pas-

sage of the facial (VII) nerve. The two foramina are of oval outline and are similar in size. The Fallopian foramen can be traced to the opening at the apex of the facial canal on the
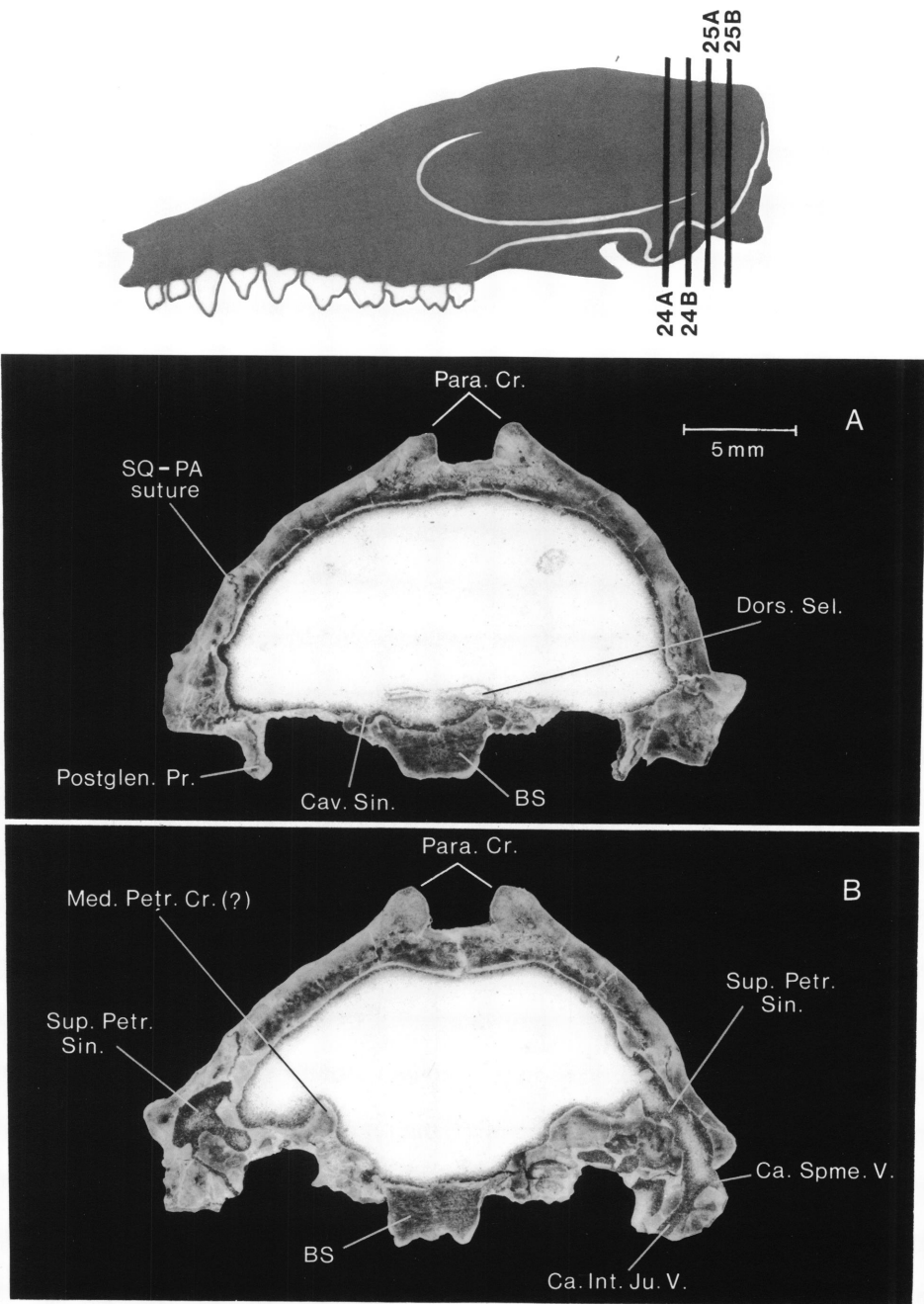
FIG. 24. Cross sections of basicranium of AMNH 3944, *Leptictis dakotensis*. Silhouette of lateral skull. Figure indicates location of sections. For abbreviations see pp. 5–7.

ventral surface of the petrosal. Normally, the intermedius branch of the facial nerve (fig. 26) continues anteriorly through a facial canal within the tegmen tympani and exits through a very small hiatus Fallopii at the anterior border of the petrosal (Cifelli, 1982, p. 801). This was the likely course of the intermedius branch in *Leptictis,* but the hiatus Fallopii is not clearly seen on the broken leading edge of isolated petrosals. Part of the facial canal may be indicated by a narrow ridge lying just lateral and anterior to the Fallopian foramen.

The aquaeductus cochleae is a very small,

circular foramen in the anterior wall of the posterior lacerate foramen. It is better exposed dorsally than ventrally, but is difficult to discern from any view. The aquaeductus cochleae is the exit for veins that drain the cochlea and run posteriorly to connect with the jugular vein.

Running anteriorly from the posterior lacerate foramen is a shallow sulcus medialis. This sulcus, which curves on the intracranial surface of the petrosal roughly parallel to the lateral edge of the basioccipital, probably conveyed the inferior petrosal sinus. It is doubtful that this sulcus also carried a third
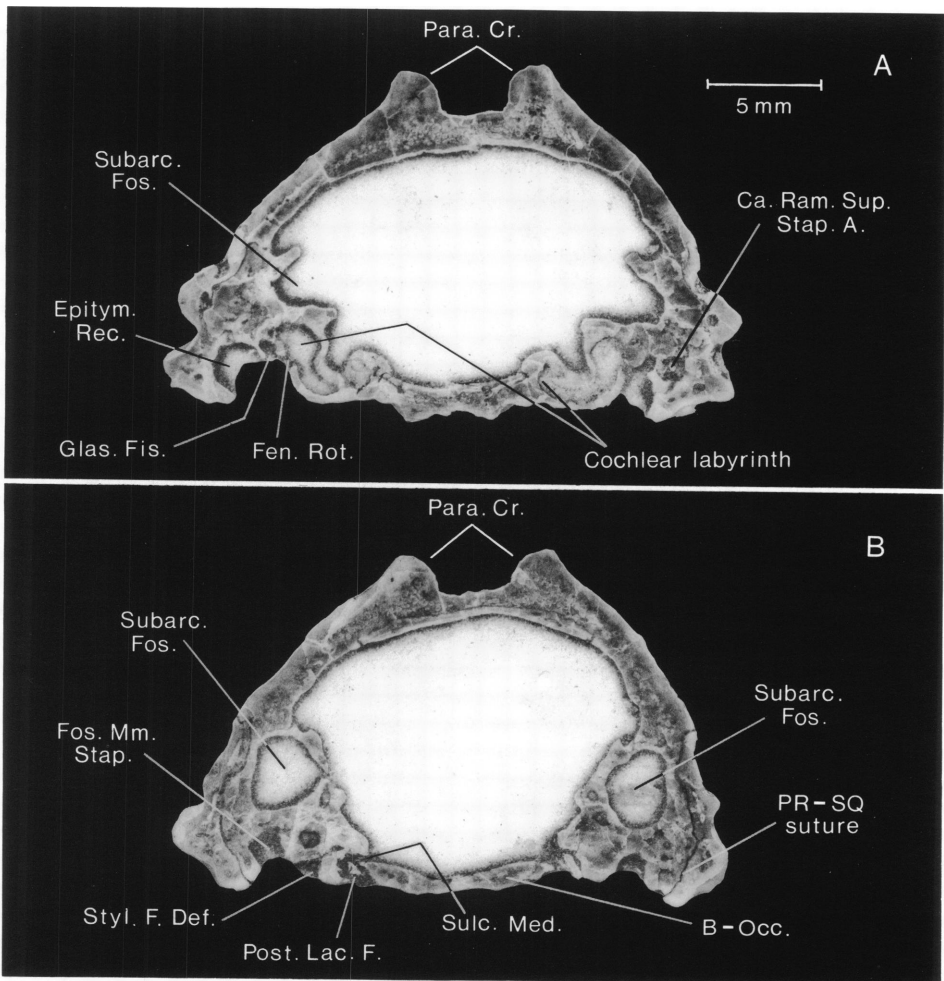

FIG. 25.   Cross sections of basicranium of AMNH 3944, *Leptictis dakotensis.* Location of sections indicated in figure 24. For abbreviations see pp. 5–7.

(medial) branch of the internal carotid artery (see Novacek, 1980; MacPhee, 1981; Cifelli, 1982; Wible, 1983; and remarks below).

The internal cast of petrosal preserved with a braincast (F:AM 96730) shows that the cochlea had nearly three full turns (fig. 30).

From the above description it is clear that the petromastoid contains many features of comparative interest. These include: (1) a distinct medial petrosal crest for contact with the entotympanic bulla; (2) ventrally open sulci for the promontory and stapedial branches of the internal carotid artery; (3) an exit foramen for the superior ramus of the stapedial artery; (4) the probable exit from the tympanic cavity of the inferior ramus of the stapedial, posteriorly positioned at the apex of the facial canal; (5) the ventral exposure of the posterolaterally facing fenestra rotunda; (6) the presence of a well-demarcated stylomastoid foramen definitivum; (7) the clear separation of the stylomastoid foramen from the posterior lacerate foramen by a petromastoid bridge; (8) a large mastoid process of the petrosal with a deep groove for the digastric muscle; (9) the lack of a jugular foramen separate from a posterior lacerate foramen; (10) a sulcus medialis for the drainage of the inferior petrosal sinus; (11) a well-developed mastoid tubercle that probably incorporates a fused tympanohyal; (12) a ridge on the facial canal marking the medial boundary of a small epitympanic recess; (13) a shallow eustachian canal; (14) isolation of the basisphenoid portion of the tympanic roof by the medial wall of the osseous bulla; (15) a very deep subarcuate fossa; (16) a large internal acoustic meatus located directly medial to the subarcuate fossa; (17) a very small aquaeductus cochleae in the anterior wall of the posterior lacerate foramen.

A considerable literature is devoted to comparative description of the mammalian petromastoid and its associated soft structures. Papers particularly relevant to this study include Kampen (1905), Klaauw (1931), Butler (1956), McDowell (1958), MacIntyre (1972), Szalay (1975), Novacek (1977b, 1980), Archibald (1977), MacPhee (1979, 1981), Cartmill and MacPhee (1980), Cifelli (1982), and Wible (1983). From such work it is apparent that several of the above-noted features (2, 3, 5, 6, 9, 10, 12, 13, 16, 17) are either primitive eutherian traits or are derived traits shared by a large number of lineages.

Noteworthy among features of this category are the sulci for the promontory and stapedial branches of the carotid artery. According to current consensus, Matthew (1909) was wrong in proposing that the primitive eutherian morphotype had three branches of the internal carotid artery. Matthew's (1909) reconstruction of a primitive carnivoran pattern allows a medial internal carotid artery between the promontorium and the basisphenoid in addition to the promontory and stapedial branches of the lateral internal carotid artery. However, no living mammal shows the presence of all three branches (Presley, 1979). It is probable that the primitive internal carotid was represented by a medial vessel excluded from the tympanic cavity by either the fibrous membrane of the tympanic floor, or, in cases where the membrane is replaced, the osseous bulla (Wible, 1983). This condition is present in marsupials and monotremes. However, in adult eutherians where the median artery is present, it seems to develop within the fibrous membrane and is either fully enclosed within the median bullar wall (rodents, edentates) or excluded from the tympanic cavity by the less completely developed bulla. Wible (1983) therefore argued that the Mesozoic eutherians Kennalestes and Asioryctes, which show only a median sulcus, developed the median internal carotid in a eutherian rather than marsupial-monotreme fashion. The differences between the two developmental pathways are, however, so subtle that they can hardly be discriminated in abullate fossil skulls. Wible's (1983) interesting hypothesis awaits more decisive evidence.

The great majority of eutherian orders resemble Leptictis in having a more lateral promontory branch of the internal carotid rather than a branch located medial to the tympanic region. Nevertheless, the outgroup condition and the ontogenetic argument (Presley, 1979) suggest that this lateral pattern is not necessarily primitive for eutherians. Developmental evidence suggests that the promontory artery represents the lateral migration of the internal carotid from the medial position (Presley, 1979). Hence, the
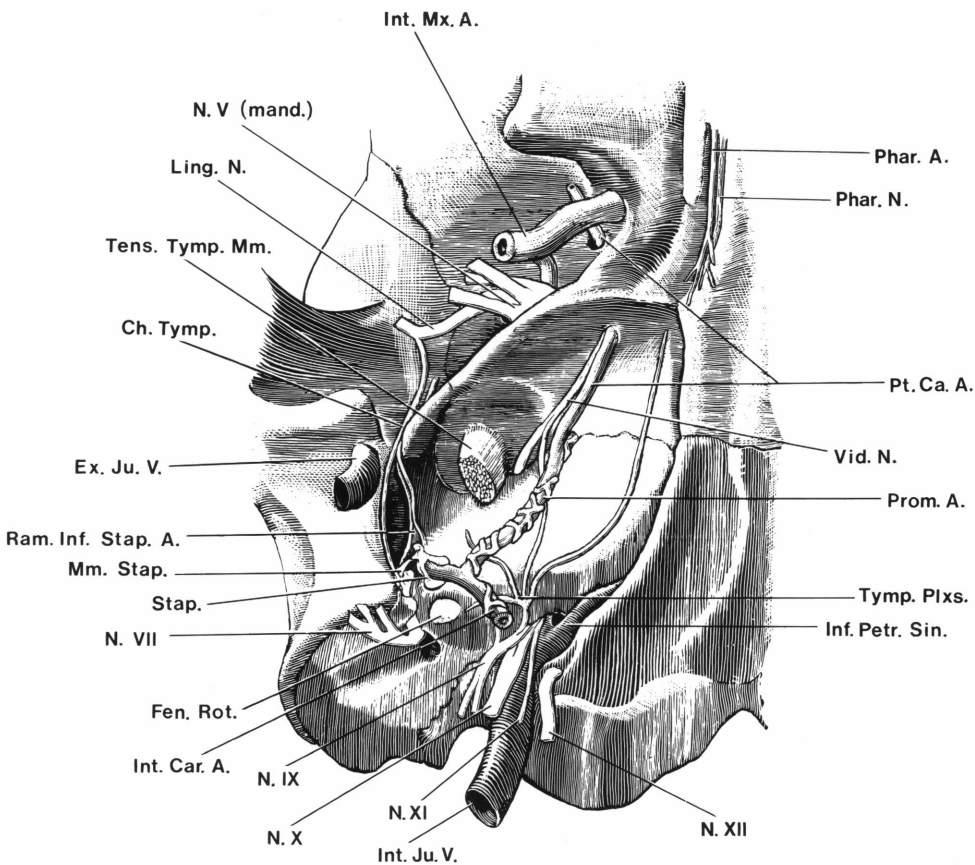
FIG. 26.   Ventral view of right tympanic region of *Leptictis dakotensis* with blood vessels and nerves reconstructed. For abbreviations see pp. 5–7.

current terminology actually represents only two branches of the internal carotid: (1) the stapedial artery and (2) either a promontory artery or a medial internal carotid artery, depending on its lateral or medial position, respectively. In many taxa, the promontory and stapedial arteries are completely enclosed by the formation of bony tubes rather than sulci.

A feature of the carotid circulation that in leptictids seems specialized is the more posterior exit of the inferior ramus of the stapedial from the tympanic cavity. The distribution of this feature is limited (Novacek, 1980), and contrasts with the usual condition, wherein the inferior ramus is conveyed along the tympanic roof in a broad Glaserian fissure (or a separate fissure) and exits through this cleft in the preotic crest. The leptictid

pattern thus represents a clear, and possibly derived, departure from the basic insectivoran condition. The superior ramus of the stapedial in leptictids exits from the otic cavity in its usual position—a foramen behind the epitympanic recess.

Another petromastoid feature of interest is the extremely deep subarcuate fossa. In comparisons of several mammal taxa, Cifelli (1982) found the extensive excavation of the fossa in leptictids to be unique, although its distribution among all Recent mammal orders had not been clarified. The subarcuate fossa contains the flocculus of the cerebellum and its size doubtless relates to the development of that part of the brain. Comparisons of this feature among a large set of mammal groups (table 3) suggests that the presence

FIG. 27. Dorsal oblique view of reconstructed pattern of arterial circulation in basicranial-temporal region of *Leptictis dakotensis*. Only major vessels are shown. For abbreviations see pp. 5–7.

of the deep subarcuate is primitive for therians while a shallow, faint subarcuate depression may be derived. The extreme excavation of this fossa exemplified by leptictids and dermopterans could, however, also be a more derived condition.

Features of the leptictid petromastoid that are also present only in lipotyphlans and a few other taxa (table 3) are the presence of a well-developed medial petrosal crest on the promontorium, and a large mastoid tubercle that nearly contacts the lateral edge of the promontorium. These are likely eutherian specializations and, in combination with several other traits, they suggest a close relationship between leptictids and lipotyphlan insectivorans (see comments below).

OCCIPITALS
(figs. 2, 5, 6, 20, 26, 29)

In all leptictids, the supra-, ex-, and basioccipitals are broadly or partially fused and these elements can be considered together. The supraoccipital occupies most of the dorsal region of the back of the skull; it is crowded ventrally by the well-developed occipital exposure of the mastoid process. There is rarely a clear separation of the exoccipital and the supraoccipital, although the boundary between the two elements is probably along a line that bridges the mastoid-supraoccipital suture with the foramen magnum. A small mastoid foramen (for a vein draining the nuchal muscles and joining the internal jugular vein) lies in or adjacent to the mastoid-supraoccipital suture. In *Leptictis*, the parietal bone extends around the corner of the lambdoidal crest to form a triangular-shaped process that nearly touches the mastoid foramen (fig. 29). This region is damaged in known material of *Palaeictops*.

In species of *Leptictis*, the supraoccipital has a small, roughly triangular process on the roof of the skull (fig. 6). *Palaeictops* shows a dorsal exposure of the supraoccipital similar to but weaker than that in *Leptictis*.
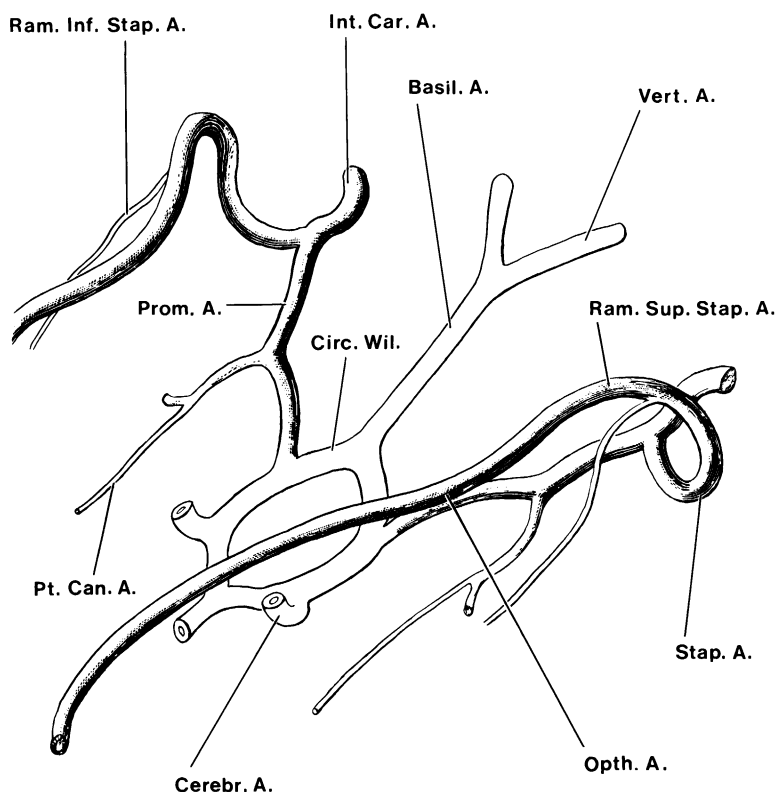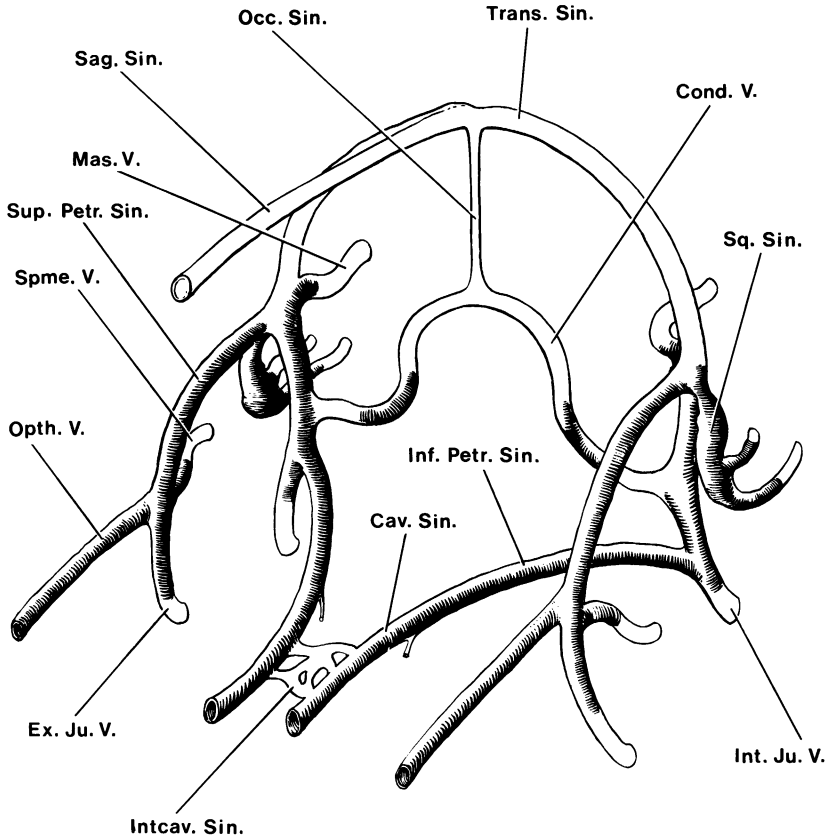
FIG. 28. Dorsal oblique view of reconstructed pattern of venous circulation in basicranial-temporal region of *Leptictis dakotensis*. Only major vessels are shown. For abbreviations see pp. 5–7.

The occiput does not bulge in a posterior direction and is hidden in dorsal view by the supraoccipital lambdoidal crest.

In its occipital exposure, the supraoccipital of *Leptictis* has a prominent vertical median crest (figs. 2, 29). The crest is absent in *Palaeictops*. In *Leptictis* there are shallow pits, ridges, and scars for the nuchal muscles flanking the median crest. Preservation of these pits in *Palaeictops* is pitiful.

The exoccipital is, as noted above, poorly differentiated from the supra- and basioccipital. It is, however, well demarcated by an irregular suture from the occipital eminence of the petromastoid. In *Leptictis* the petromastoid is broader, the exoccipital more confined. The dorsal atlantal facet at the edge of the foramen magnum is rounded and prominent. The paroccipital process is very weak, being slightly demarcated by shallow troughs separating it from the occipital condyles and the post-tympanic process formed by the

junction of the squamosal and mastoid process (see above). The conditions for these features are not clear in any species of *Palaeictops*.

The foramen magnum in leptictid species faces directly posteriorly. In *Leptictis,* the foramen is vaguely pentagonal (although its ventral edge shows the biconcave curvature effected by the ventral border of the occipital condyles). The dorsal rim of the foramen is strongly convex and extends well above the occipital condyles (fig. 29). In no leptictid is there a large occipital foramen between the medial rim of the dorsal lobe of the condyle and the ascending edge of the foramen magnum.

The dorsal lobe of the occipital condyles is ventrally confined; it does not reach a point opposite the upper margin of the foramen magnum. The lobe has a strong convex curvature in all leptictids but its outline varies. The upper part of the lobe is helical in *Lep-*
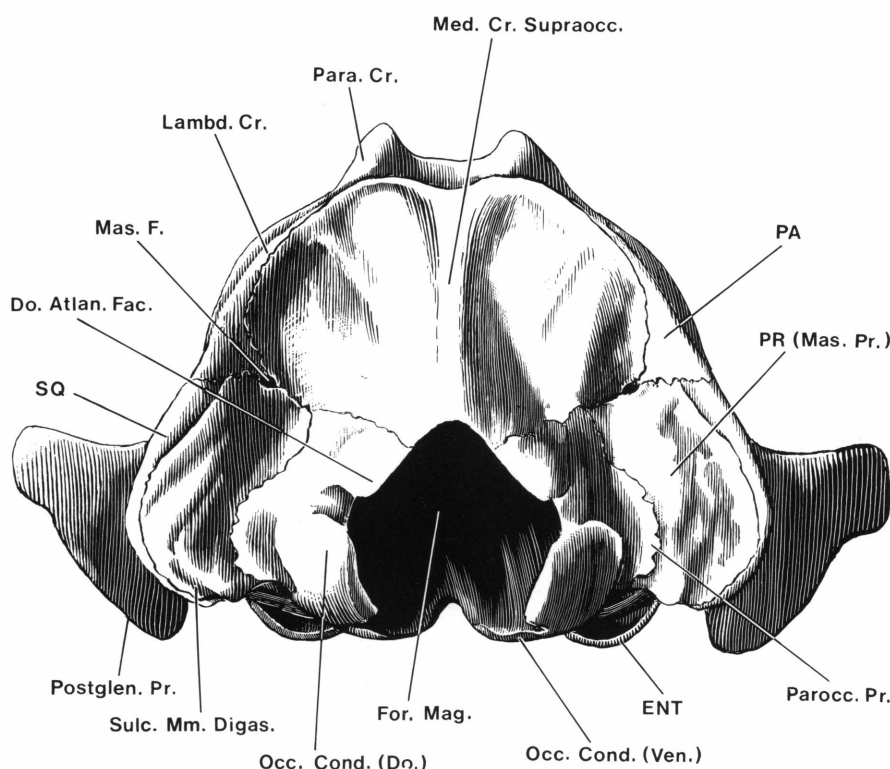
FIG. 29.   Posterior view of occipital region of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

tictis, but more cylindrical in *Palaeictops* because its outer margin shows a strong medial curvature. The functional implications of this variation are not clear. It seems likely, though, that the snout-upward movement of the head was more restricted in *Palaeictops.*

The basioccipital consists of the ventral lobes of the occipital condyles, the shallow fossa between the condyle and the low paroccipital process and the posterior lacerate foramen, and the trapezoidal process articulating anteriorly with the basisphenoid. The broad fusion in leptictids of this element with adjacent bones is expected; the basioccipital in mammals is usually distinct only in late embryos and neonates.

The ventral lobes of the condyles show a marked sinusoidal curvature along their lateral margins, due to their strong medially directed curvature at the posterior edge of the skull and opposite the hypoglossal foramen (figs. 2, 5, 20). There is a well defined, but shallow, trough between the condyle and the small, blunt paroccipital process. There is only a single large hypoglossal foramen located approximately midway between the condyle and the posterior notch for the jugular foramen. The anterior moiety of the basioccipital shows very shallow fossae for the rectus capti muscles, located bilateral to a weak median crest. These are continuous with the more anterior troughs and crest on the basisphenoid. The division between the basioccipital and basisphenoid is obscured, but a faint suture in some specimens (e.g., *Leptictis dakotensis,* MCZ 19678, AMNH 38919) indicates that these elements are separated along a transverse line opposite the anterior corner of the promontorium cochleae (figs. 22, 23). The above-described conditions for the basioccipital are shared by *Leptictis* and *Palaeictops.*

The intracranial surface of the occipitals (observed only in *Leptictis*) shows a large posterior exit for the condyloid canal in the median surface of the dorsal occipital condyle.

Features of the occipitals noted above are: (1) a well-developed occipital process of the

mastoid, (2) a small parietal exposure on the occipital surface, (3) a single large mastoid foramen, (4) the extension of the supraoccipital on the dorsal roof of the skull, (5) a well-developed lamboidal crest that conceals the occiput from dorsal view, (6) a rounded or flattened dorsal atlantal facet, (7) a very weak paroccipital process, (8) a posteriorly facing, elliptical, or pentagonal foramen magnum, (9) the dorsal lobes of the occipital condyles not extending to the upper margin of the foramen magnum, (10) the sinusoidal curvature of the ventral lobes of the occipital condyle, (11) a single hypoglossal foramen, (12) the anterior border of the basioccipital opposite the anteromedial corner of the promontorium cochleae, (13) a large posterior exit for the condyloid canal in the antrum of the foramen magnum.

Characters 1, 3, 4, 5, 6, 8, 11, 12, and 13 are widely distributed among marsupials and eutherians (table 3) and are probably primitive eutherian traits. The pentagonal or key-hole-shaped foramen magnum in *Leptictis* and *Erinaceus* is an interesting similarity, but it appears to be a secondary trait in both Leptictidae and Erinaceidae. Other members of these groups show the typical ellipsoidal-shaped foramen magnum.

The remaining occipital features, if not derived, show enough variation within therians to deserve comment. The lack of a well-developed paroccipital process (not homologous with the process of the same name of the reptilian opisthotic, see McDowell, 1958, p. 126) in leptictids is a departure from the condition typical of didelphids, erinaceids, tenrecids, lagomorphs, rodents, creodonts, carnivorans, artiodactyls, and perissodactyls. The process is, however, weak or absent in *Solenodon,* dermopterans, tupaiids, and macroscelidids. It is difficult to attribute correlative factors to this pattern of variation. Usually the process is weak where the hypoglossal fossa of the basioccipital is crowded by the large mastoid process and the ventral occipital condyle. However, the correlation is not without exceptions; *Solenodon* shows a basioccipital of comparable width along the posterior skull margin to that of *Tenrec,* yet only the latter has a prominent paroccipital process. It is likely that the lack of the paroccipital process is a derived eutherian fea-

ture, but the loss of this process occurred more than once in the above-listed groups, depending on the hypothesis of relationships chosen.

The extension of the parietal as a small element in the occiput is likewise a rare condition in therians. Unfortunately, this condition is most clearly evident only in *Leptictis.* Skulls of *Palaeictops* vaguely show this trait, and another distinctive character of the Leptictidae is potentially available. For the present, the condition distinguishes the Oligocene species.

The ventral confinement of the occipital condyles relative to the foramen magnum is a departure from the common condition in didelphids, dermopterans, macroscelideans, many tenrecids, galericine erinaceids, rodents, and megachiropterans. The condition is, however, largely a function of allometric relationships involving the size of the spinal cord and foramen magnum. It therefore varies considerably within the above groups. Also variable is the S-shaped curvature of the ventral condyles. This character, while present in all leptictids where the skull is known, is shared by insectivorans (e.g., *Solenodon, Echinosorex, Tenrec*) and macroscelideans, but is rarely found as a primitive condition for other mammalian groups.

BRAIN
(fig. 30)

Complete endocranial casts of leptictids are known only for *Leptictis dakotensis.* Early considerations of *Leptictis* (Leidy, 1869a; Moodie, 1922; Scott and Jepsen, 1936) are discrepant in respect to details of the cerebrum, but their general conclusions correspond—the *Leptictis* brain bears a strong resemblance to that in erinaceid insectivores. Moodie (1922) further noted features (neopallial development, lower position of the rhinal fissure) which he believed indicated a more advanced condition than in the hedgehog brain. He concluded (1922, p. 369), "The Insectivora, as indicated by *Ictops,* have retrograded in cerebral structure, as they have in other ways. This is shown by the fact that the Oligocene forms had a much more expansive neopallium than modern forms, as the European hedgehog. There has been no

advance in cerebral complexity in this group since Oligocene times."

Szalay (1969, p. 293), in making comparisons of the endocasts in microsyopids with leptictids and other eutherians, remarked that the specimens Moodie studied did not show crucial details of the midbrain and cerebellum. In his examination of better-preserved endocasts, Szalay noted that *Leptictis,* like *Microsyops,* has a higher neocortex than cerebellum, and, contra Moodie's (1922) illustrations, the midbrain is broadly exposed.

Well-preserved endocranial casts of *Leptictis dakotensis* from the Frick Collection at the American Museum of Natural History allow a detailed account (Novacek, 1982a) that addresses the above-noted discrepancies. The salient points of this study are the following: In *Leptictis* the olfactory bulbs are prominent but of intermediate size when compared with some eutherian groups. They are notably smaller (relative to the cerebrum) than in *Tenrec ecaudatus, Erinaceus europeus, Setifer*; are comparable in size to *Solenodon*; and are relatively much larger than in tupaiids, talpids, macroscelidids, soricids, microsyopids, plesiadapids, and notharctine and more advanced primates. Large olfactory lobes are regarded as a primitive eutherian condition but their extremely large size in some insectivorans could be a derived trait correlated with highly developed olfactory abilities.

The dorsal external surface of the neopallium shows a neocortical sulcus (see detailed description in Novacek, 1982a). The rhinal fissure is extensive, running from the midbrain and roughly following the curvature of the lateral margin of the cerebrum just ventral to the cast of a large blood vessel. As Moodie (1922) claimed, this fissure is quite low in position and thus the neopallium is larger than in hedgehogs (*Erinaceus*). Moodie (1922, p. 349) also described a "slight depression which runs transversely across the anterior end of the cerebrum and doubtless represents an orbital sulcus (S. orb.)." What he identified as the orbital sulcus, as indicted from his description and illustration, might be a depression confluent with the rhinal fissure, as there is no evidence of anterior bifurcation of the rhinal fissure. However, this small sulcus is not clearly continuous with

the rhinal fissure and is here recognized as a small, anterior neocortical sulcus.

The sagittal sinus clearly separates the two cerebral hemispheres. A prominent cast of a blood vessel is present on the lateral side of the cerebrum below the rhinal fissure. This may represent a large lateral venous sinus but the identity of the vessel is not clear (Szalay, 1969). The base of the cerebrum in some specimens preserves casts of the foramina that show the positions of the ophthalmic and trigeminal nerves. The trigeminal nerve stalks were large and closely positioned to each other. The pons is an elevated bulb nearly situated between the stalks of the mandibular branch of the trigeminal. The pyriform lobes are large, but smaller than in some living insectivores, and do not protrude strongly ventrad.

Among lissencephalic mammals, the relative size of the neopallium in leptictids is exceeded in talpids, tupaiids, and macroscelidids (fig. 2 in Novacek, 1982a). Certain insectivorans show a relatively smaller neopallium (*Tenrec, Echinosorex, Solenodon*). The neopallium is small in microsyopids but faint lateral and suprasylvian sulci were identified by Szalay (1969). However, only one neocortical sulcus was identified by Radinsky (1977). Neocortical sulci are present, though sometimes weakly developed, in *Microsyops,* in early Tertiary perissodactyls and carnivores (Edinger, 1964), and notharctid primates (Radinsky, 1970). A familiar interpretation of this information (Sanides, 1970, pp. 153–158) is that the evolution of the mammalian cerebrum reflects three integrally related trends; namely, increase in size of the neopallium, downward migration of the rhinal fissure, and increased gyrification. The pyriform (olfactory) lobe in *Leptictis* is smaller than that in some insectivorans and might be interpreted as a derived condition. However, the olfactory development of erinaceids is correlated with a large pyriform lobe, and these conditions could possibly be specialized for insectivorans.

Casts of *Leptictis* do not show divisions between the corpora quadrigemina from a dorsal aspect, but there is a prominent V-shaped confluens sinum. There is also a wide transverse sinus on the lateral side of the brain between the cerebrum and the cer-
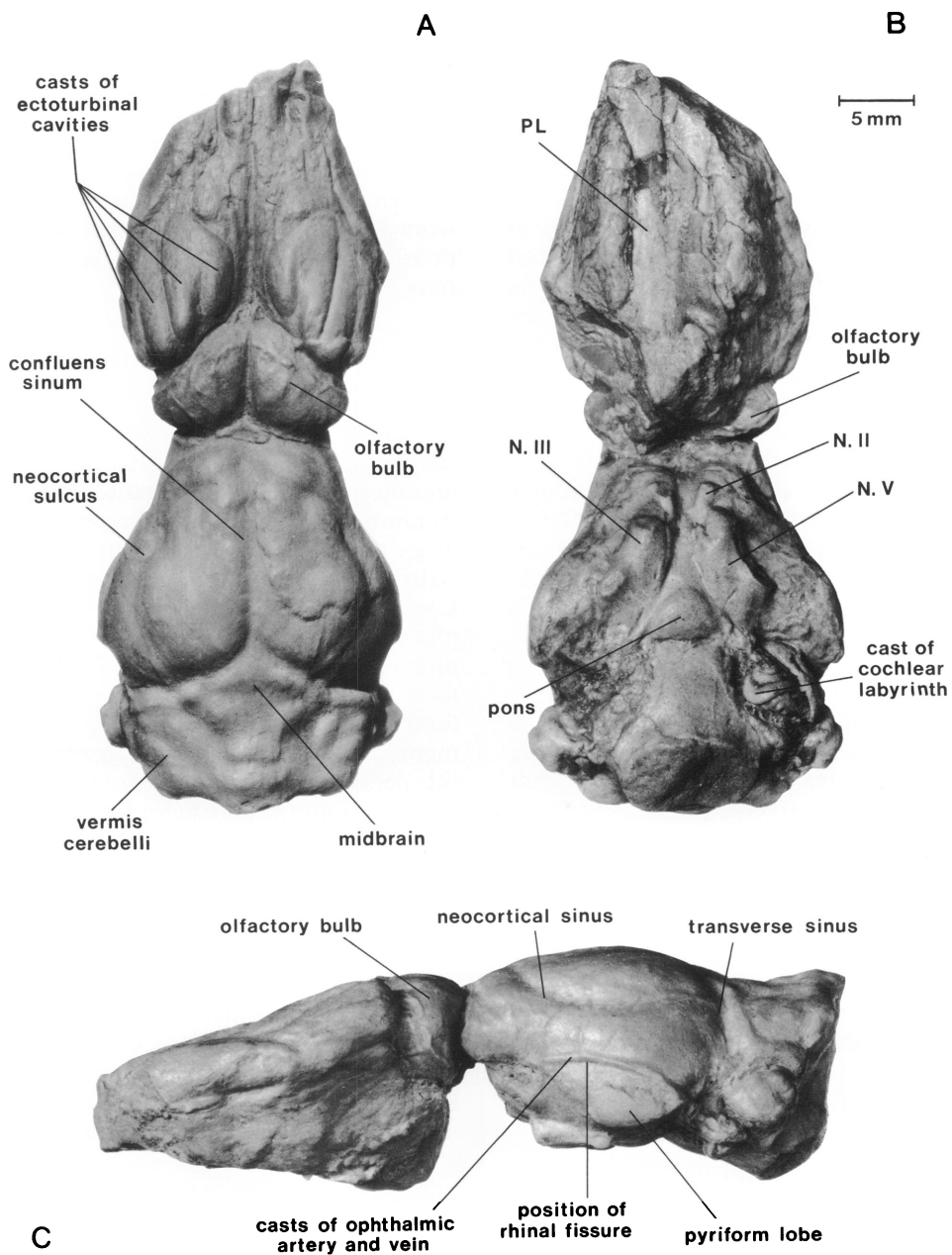
FIG. 30. (A) Dorsal, (B) ventral, and (C) left lateral views of F:AM 96730, endocast of *Leptictis dakotensis*. For abbreviations see pp. 5–7.

ebellum. Contra Szalay (1969), there is no indication of the exposure of the midbrain in *Leptictis* (see Novacek, 1982a). Exposure of the midbrain has been cited as a primitive eutherian trait (Edinger, 1964; Szalay, 1969). In this respect, the *Leptictis* brain seems somewhat more advanced than the brain in *Tenrec, Setifer, Elephantulus, Solenodon,* and *Talpa,* but resembles closely the condition in *Echinosorex,* and is more primitive than the brain in tupaiids and primates.

In *Leptictis,* there is evidence of extensive

formation of cerebellum sulci. The top of the cerebellum exceeds the height of the neopallium, a condition which Szalay (1969, p. 292) suggested is derived for eutherians. Alternatively, cerebellar height would be lower than a large neopallium in animals with more specialized brains.

A braincast (without olfactory bulbs) of *Leptictis dakotensis* (F:AM 96727) displaced approximately 5 cc of water. This result was also obtained by Moodie (1922, p. 372) for another specimen. The volume of water displaced by the olfactory bulbs from F:AM 96727 was approximately 1 cc. It is of interest to determine the brain size: body size relationship of these animals. The average body weight of *Leptictis dakotensis* is obviously impossible to establish with certainty, but can be crudely estimated through several means, discussed at length in Novacek (1982a). These techniques yield encephalization quotients (EQs) ranging between 0.70 and 0.54 (with olfactory bulbs) or 0.58 and 0.45 (without olfactory bulbs). This range is bracketed by body size estimates that vary between 600 and 900 g (table 1 in Novacek, 1982a). These results are of interest because they suggest that *Leptictis* had a larger EQ than most "basal insectivorans" (sensu Bauchot and Stephan, 1966). Furthermore, EQ estimates are not significantly lower than those in some early primates (see data in Radinsky, 1977; Jerison, 1979). It should be cautioned that these results might merely support the notion that *Leptictis* is a very specialized member of its family with a somewhat enlarged brain. There is no evidence of relative brain size in earlier (Paleocene and Eocene) leptictids.

LEPTICTID AFFINITIES

The central hypothesis of this section is that leptictids should once again be returned to the Insectivora. The data recruited for this argument are derived cranial traits shared by lipotyphlans and leptictids as ascertained from the foregoing comparative study (see table 3). Features of the leptictid postcranial skeleton have also been compared with a variety of mammals (Novacek, 1980). Sampling of these features is neither as comprehensive nor as well founded in studies of development and form. However, certain postcranial features are well known from distributional information and are highly relevant to the central hypothesis and its alternatives. Such postcranial information is cited in this discussion. In this context, it is unfortunate that the mammalian tarsus, which is currently the focus of much comparative work (e.g., Szalay, 1977; Cifelli, 1983) is so poorly described in lipotyphlan insectivorans.

LEPTICTIDS AND EUTHERIAN MONOPHYLY

Eutheria are most effectively defined by the geometry of the reproductive system, the presence of the chorioallantoic placenta, the trophoblast, and aspects of reproductive biology (e.g., prolonged gestation) correlated with these structures (Lillegraven, 1969; Luckett, 1977; Novacek, 1982b). This emphasis on "soft evidence" poses an obvious problem for the allocation of fossils alleged to be eutherians, particularly in cases where fossils lack overwhelming evidence for their membership *within* Recent groups. Leptictids certainly fit this incognito category, and the presumption that these forms are eutherian mammals warrants comment. At least six dental and cranioskeletal characters support the eutherian relationships of leptictids. These are:

1. The maxilla and frontal are in broad contact with the nasal-facial region. In primitive marsupials this contact is narrow because the posterior nasals are broadly inflated and the lacrimal has a strong facial process. Leptictids actually show a stronger departure from this "marsupial" condition than do many placentals (table 3; comments below).

2. There are sulci for both promontory and stapedial branches of the internal carotid artery. The basic condition within marsupials is the emphasis of an internal carotid branch that lies medial to the promontorium cochleae and the auditory bulla (Wible, 1983; comments above). Some eutherians (e.g., edentates, rodents) may retain this condition.

3. The auditory bulla is formed by an entotympanic. There is no evidence of such an element in marsupials (MacPhee, 1981, contra Novacek, 1977b and earlier work). It is likely that the entotympanic is unique to some

eutherians but not necessarily primitive for this group.

4. The pelvic girdle lacks prepubic bones (Novacek, 1980, fig. 14).

5. The upper molars have relatively narrow stylar shelves. In early marsupials and a variety of Mesozoic mammals of "therian grade" the stylar shelves are much broader (Kielan-Jaworowska et al., 1979).

6. The astragalus has a trochlea with distinct lateral and medial crests and has a constricted neck between the trochlea and the distal head. The leptictid tarsus clearly has a eutherian stamp and shows strong resemblances to certain members of this infraclass (Szalay, 1977; Novacek, 1980; comments below).

In addition, there are several features of the leptictid cranium shared only with lipotyphlan insectivores and a few other mammals (table 3; comments below). None of these features seems primitive for marsupials.

I resist including in this list the lack of a medial inflection of the angular process of the jaw. In marsupials the angular process is inflected but this is also true of the Late Cretaceous *Gypsonictops,* a possible near relative of leptictids. Certain other Cretaceous eutherians (see Kielan-Jaworowska et al., 1979) probably retained this more general condition.

Note that none of the conditions listed is common to all eutherians except perhaps the molar morphology and the absence of prepubic bones. The conditions listed may be specializations arising *within* Eutheria, but they compel one to infer that more definitive "soft" eutherian characters were present in leptictids.

LEPTICTIDS AS INSECTIVORANS

The earliest theories on leptictid affinities are generally in keeping with Leidy's (1868) claim of their close relationship to erinaceid insectivores. Gill (1872) showed greater caution by retaining leptictids as Insectivora incertae sedis without implicating them as particularly close relatives to any of the families he included within that order. It is in Gregory's (1910) "Orders of Mammals" that a definite allocation of leptictids to Erinaceoidea appears and, doubtless, his interpreta-

tions strongly influenced many subsequent workers. Despite the remarkable depth and scope of Gregory's study, his evidence for lumping leptictids and erinaceids in the Erinaceoidea was not explicitly stated. Obviously he regarded leptictids as the more primitive and possibly ancestral members of the superfamily, although a sister group relationship is suggested in figure 31, p. 467, of his monograph. However, he cited no obvious shared specializations separating erinaceoids from other insectivores, even though he recognized this group as diverging from the basic placental stock later than tenrecids, soricids, talpids, and chrysochlorids. Instead, Gregory stated (p. 262) that review of leptictid characters "confirms the lowly position of that family and its ancestral relation to the Erinaceidae." Gregory regarded such leptictid characters as a long slender muzzle, small upper canines, slender mandible, large jugal, unfenestrated palate, small auditory cavity, and distinct postglenoid process as evidence that *Leptictis* (=*Ictops*) "approached backward" toward the stem of the "Zalambdodonta," his grouping for tenrecs, *Solenodon,* "potamogalids," and chrysochlorids.

If allocation of the Leptictidae to the Erinaceoidea seems uncertain, one might still consider their inclusion within the Insectivora. Gregory's concept of this order was restricted to Haeckel's Lipotyphla and an unnamed suborder to include the problematic hyopsodontids. Importantly, he departed from the views of many earlier and subsequent workers in excluding Haeckel's menotyphlan tupaiids and macroscelidids. The unity of the Insectivora, namely the linking of Erinaceoidea, "Zalambdodonta," and Soricomorpha was based on several characters of the soft anatomy and ear region (see Gregory, 1910, p. 266) either absent or unknown in leptictids. Thus the Insectivora as diagnosed by Gregory makes little provision for the inclusion of the latter family.

The problem became clearly evident with Butler's (1956) study of the skull of *Leptictis* (=*Ictops*). Noting that leptictids shared many primitive characters in common with basic insectivoran stocks, Butler remarked on the paucity of derived similarities with erinaceids; he identified only four: (1) the intraorbital lacrimal foramen, (2) the extensive or-

bital wing of the maxilla which meets the frontal, (3) the confinement of the palatine bone to the floor of the orbit, and (4) the presence of an ectopterygoid process. These characters alone seem hardly adequate, as Butler emphasized, in demonstrating a close erinaceid-leptictid affinity. None of them exclude sufficiently other lipotyphlans, macroscelidids, tupaiids, and dermopterans. Accordingly, Butler recognized the Leptictoidea as a distinct superfamily of lipotyphlans, regarding it as independently derived from an ancestral group of Cretaceous insectivores. In a more recent review, Butler (1972) removed leptictids from the Lipotyphla entirely, claiming the characters of the ear region and orbital wall argue against a close association with the order. This conclusion mirrored the arguments of McDowell (1958).

One problem with these earlier studies is the limited range of comparisons. Thus, a broader sampling of taxa may demonstrate that the characters held in common between leptictids and lipotyphlans are sufficiently restricted in distribution to offer evidence of relationships. Comparisons of skull features among the major groups of Recent mammals (table 3) suggest that several characters support a close affinity between leptictids and insectivores. These are:

1. There is a broad contact between the maxilla and frontal in the facial region. This contact is extensive because there is no marked expansion of the posterior nasals or the facial process of the lacrimal. A narrower maxilla-frontal contact, present in didelphids, *Asioryctes, Kennalestes,* tupaiids, edentates, carnivores, and macroscelideans (table 3, character 6a) is probably primitive for eutherians. The geometry of the sutures in this region of the skull is strikingly similar in leptictids and lipotyphlans, a resemblance not clearly found in other mammal groups.

2. The infraorbital canal is moderately short, with the anterior opening slightly forward of the antorbital rim of the zygoma and the posterior opening of the cleft between the root of the zygoma and the anterior apex of the orbital wall. This condition is found at least in chiropterans and proboscideans. In rodents and lagomorphs the canal is extremely short, resembling a simple foramen in the anterior zygoma (the infraorbital canal seems to be secondarily elongated in certain rodent groups; see Wahlert, 1974). A long infraorbital canal is common to many mammals (table 3, character 14a), including *Asioryctes, Kennalestes,* and *Barunlestes.*

3. The maxilla intrudes into the orbit and nearly touches the frontal. As noted above, this is an interesting feature of some uncertain significance as evidence for relationships. Assuming that the poor exposure of the maxilla in the orbit is a primitive trait (Butler, 1956; Novacek, 1980), the leptictid condition approaches, but does not match, the condition in lipotyphlans. In the latter, the maxilla is extensive enough in the orbit to contact the frontal and prevent contact between the lacrimal and palatine. The "leptictid-like" maxilla is also found in lagomorphs, perissodactyls, and sirenians. The more extensive maxilla is, in addition to lipotyphlans, also found in rodents, proboscideans, some edentates, and hyracoids. However, the geometry of the anterior orbital mosaic is not strongly similar between these latter groups and lipotyphlans. The conditions of the orbital mosaic are poorly preserved in *Asioryctes* and other Cretaceous eutherians.

4. There is a large common recess for the separate sphenopalatine and dorsal palatine foramina. This is a trait rarely found in eutherians. It occurs only in leptictids, lipotyphlans, some carnivores, and tubulidentates. In most mammals the foramina are widely separated and not bounded by a common recess (table 3, character 20a). Rarely, the foramina unite as a common opening or the dorsal palatine foramen is absent (table 3, character 20c).

5. The lacrimal is confined to the orbit or the antorbital rim; it lacks a strong facial process. This trait relates to condition 1. It is also found in macroscelidids, rodents, lagomorphs, and hyracoids (table 3, character 22b). Most workers agree that the strong lacrimal facial process, as shown in didelphids, tupaiids, *Asioryctes, Kennalestes,* and many other groups, is a more primitive condition (see comments above, and Novacek, 1980).

6. A well-defined Glaserian fissure in the lateral roof and anterior wall of the tympanic cavity. Although the ontogenetic appearance of a fissure for the chorda tympani is a prim-

itive therian condition (comments above), the fissure is rarely indicated in adults as a distinct trough or cleft in the osseous wall of the tympanic cavity. A comparable fissure is found in hyracoids and tubulidentates (table 3, character 42b). In some tupaiids the Glaserian fissure is an extremely narrow cleft that arises deep within the epitympanic recess. The fissure is somewhat narrower in leptictids than in lipotyphlans. This is probably because, in the former, it did not convey the inferior ramus of the stapedial artery.

7. A well-developed petrosal crest on the medial promontorium. This crest either forms a roughened suture with the entotympanic (as in leptictids), or remains unattached to the bulla (as in soricids, *Solenodon,* and *Nesophontes*), or forms an extensive wing that contributes to the bulla (as in erinaceids and tenrecids). The petrosal crest also occurs in macroscelidids, tupaiids, dermopterans, and some primates and rodents (table 3, character 50b). By itself, then, the character does not represent strong evidence of leptictid-lipotyphlan ties.

8. A large, ossified mastoid tubercle that incorporates the tympanohyal, has a distinct, ventral depression and is well directed medially, nearly contacting the promontorium. Although the mastoid tubercle is present in many mammals, it usually does not show all the above-noted traits. A tubercle of similar form is, however, known in tubulidentates and some chiropterans (table 3, character 58b). Distributions plotted for the tympanohyal by Novacek (1980) actually show the variable occurrence of bridges of the petromastoid that isolate the stylomastoid foramen from the tympanic chamber (see also Butler, 1956). These structures do not resemble the mastoid tubercle in leptictids and lipotyphlans, nor do they necessarily incorporate the tympanohyal, the most cranial element of the hyoid bar (Klaauw, 1931). In pholidotans, the large petromastoid bridge fuses with the promontorium and ventrally seals off the facial canal (table 3, character 58c).

9. The anterior border of the ventral occipital condyle shows a strong sigmoid curvature. This condition, which appears also in some macroscelideans, fossil primates, and carnivores might be recognized as primitive.

However, the lack of the trait in most marsupials and eutherians suggests otherwise (table 3, character 69a).

The above-listed features move one to consider the close leptictid-lipotyphlan relationship as a serious possibility for higher eutherian classification. The arguments I anticipate against this claim are that none of the characters (except perhaps item 1) are unique to these taxa, that some traits (for example, items 1 and 5) are closely correlated, and that there are apparent derived resemblances between either leptictids or lipotyphlans and other groups. The first two arguments probably apply to virtually any proposal for a superordinal category of mammals based on cranioskeletal evidence. The third argument is weakened by the result that the most efficient summary of the cranial evidence favors the leptictid-lipotyphlan grouping over alternatives (figs. 31–33).

Leptictids are decidedly more specialized than (morphotypical) lipotyphlan insectivorans in having, among other things:

1. A deep antorbital fossa for snout muscles (but shallower in *Palaeictops*).

2. An alisphenoid canal separated by bone from the Gasserian fossa (following McDowell, 1958).

3. A small ossified (entotympanic) bulla (I concur with Gregory, 1910, that the sphenoid-petrosal bulla in certain lipotyphlan insectivorans is a secondary feature for the group).

4. A posterior exit of the inferior ramus of the stapedial artery from the tympanic cavity.

5. A swollen manubrial element with an enlarged ventral keel (may not be present in primitive leptictids).

6. A large number of postcranial features (closely appressed cervical vertebrae, pelvic structure and orientation, limb elongation, astragalocalcaneal morphology) which suggests a specialized mode of locomotion (see Novacek, 1980 and comments below).

Traditionally, leptictids have been associated with insectivores because of their close similarities to erinaceomorphs in cheek tooth morphology. What little is known about early eutherian dental evolution suggests that most of these resemblances involve primitive features (see comparisons above). Leptictids

seem more specialized than erinaceomorphs in showing late retention of deciduous premolars, in having molariform last permanent premolars, and other features noted in the above discussion of dentitions. However, the question to consider is whether these derived cranioskeletal and dental features that distinguish leptictids from lipotyphlans actually point to stronger relations of either group with other taxa. Such alternative relationships are considered below.

TUPAIIDS, MACROSCELIDIDS

The old concept of a menotyphlan grouping for tupaiids and macroscelidids has been abandoned in most current systematic treatments (Patterson, 1965; Butler, 1972; McKenna, 1975; Szalay, 1977; Novacek, 1980, 1982b). A few remarks on the Menotyphla in the context of this discussion seem warranted because leptictids have been variously cited as ancestral, collateral, or somewhere intermediate to tree shrews and elephant shrews. Gregory (1910, p. 262) stated that "*Ictops*" was probably ancestral to menotyphlans due to its possession of such primitive characters (ibid., p. 272) as an elongate muzzle, a moderate postorbital constriction, a "rounded" braincase, divided parasagittal crests, a stout, slender zygomatic, and a distinct postglenoid. Obviously, these characters by themselves hardly indicate special relationship with either tupaiids or macroscelidids. Also, they do not account for the subsequently discovered morphological diversity within Lepticidae (for example, parasagittal crests are only present in Oligocene leptictids). In a more recent argument for the validity of the Menotyphla, Butler (1956, p. 476) cited 16 skull features in common between macroscelidids and tupaiids. Of these characters, many are also present in dermopterans and primates, five are certainly primitive for Eutheria, at least two are of dubious polarity, and six are shared with leptictids. Butler rightly emphasized the problems of using these as defining characteristics, and he later (1972) distinguished elephant shrews and tree shrews as separate and not closely related mammalian orders, Macroscelidea and Scandentia, respectively. This view agrees with Patterson's (1965) emphasis on the isolated

position of the elephant shrews and his critical analysis of the "Menotyphla" (see also Novacek, 1984).

The leptictid involvement in the menotyphlan problem was bolstered by McDowell's (1958 and unpublished) studies. McDowell (1958, p. 204) concluded that leptictids were closely related to tupaiids and, more distantly, to macroscelidids and extinct zalambdalestids. He emphasized similarities that include (1) large entotympanic element in the bulla; (2) an annular ectotympanic; (3) a distinct facial wing of the lacrimal; (4) a large jugal; (5) a palatine with an orbital wing which contacts the lacrimal; (6) a true postglenoid process; (7) the lack of a bony canal for the inferior ramus of the stapedial artery; (8) an alisphenoid canal separated by bone from the Gasserian fossa; (9) strong dorsum sellae with clinoid processes; (10) a strong pubic symphysis; and (11) astragalar trochlea which curves over the proximal surface of the body of the astragalus. Based on the above comparative studies, I deem 7 (items 2, 4, 5, 6, 7, 9, 10) of these 11 characters to be primitive and character 3 to be inaccurate: the facial wing of the lacrimal in leptictids (where known) is markedly reduced compared with tupaiids. Only three characters (1, 8, 11) seem relatively derived and, of these, items 1 and 11 are widely distributed among mammalian taxa. Recognition of a leptictid-"menotyphlan" connection seems poorly substantiated by the above-cited features.

Even with leptictids excluded, the "Menotyphla" cannot be salvaged. The derived characters commonly cited to link tupaiids and macroscelidids include specializations of the brain, orbital wall, and auditory region (see Novacek, 1980, fig. 24). Most of these features apparently correlate with cerebral development and are found in many mammals. It should be emphasized, however, that the brain structure in macroscelidids and tupaiids is notably contrasting. Le Gros Clark (1933, p. 1004) remarked, ". . . it would be difficult to conceive two mammalian brains which are more fundamentally different and divergent in their structure than those of *Macroscelides* and *Tupaia*." Although this phenetic divergence fails to refute the menotyphlan concept, it clearly demonstrates that little beyond the vague attribute "enlarged

cerebrum" supports a relationship between elephant shrews and tree shrews. Patterson (1965) asserted that shared-derived similarities of the orbital wall between macroscelidids and tupaiids are merely the result of parallel needs for increased housing of enlarged, but dissimilar, brains. His remarks imply independent evolution of derived osteological similarities between the two taxa. This suspicion is supported by the strong linkage between macroscelidids and a lagomorph–rodent clade by several shared-derived traits.

To sum, few osteological specializations link tupaiids, macroscelidids, and leptictids and, contrary to the opinions of many early workers, there seems little evidence in support of a close affinity between these taxa.

"ARCHONTA"

McKenna (1975) and Szalay (1977) advocated a return to the concept of Archonta (sans macroscelidids) espoused by Gregory (1910). This mammalian super group would thus comprise tupaiids (Scandentia), Primates, Dermoptera, and Chiroptera. Szalay (1977) commented extensively on the evidence for unity of the Archonta, emphasizing the pedal similarity shared by *Ptilocercus,* Paleocene primates, and dermopterans (and possibly the enigmatic Mixodectidae). He enumerated the tarsal features linking these groups, but provided no characterization of Chiroptera. His interpretation met opposition in the opinions of Jenkins (1974) and Kay and Cartmill (1974), who have emphasized that tupaiids and early primates merely show a mode of scansorial-terrestrial locomotion harking back to the primitive eutherian condition. Perhaps, as Szalay (1977) suggested, tupaiids and primates share some derived features in pedal morphology, but a more diverse sampling of cranioskeletal features (Novacek, 1980) led me to question the validity of the larger group, Archonta. Szalay's interesting argument that the glissant dermopteran, and volant chiropteran roles resulted from arboreal adaptation like those of primates and tupaiids, requires more detailed comparisons of limb osteology in archontans with that of other eutherians. This aspect of the skeleton is so much more intensively studied in primates than in most

other mammalian groups that it defies an objective basis for comparison. As noted elsewhere (Novacek, 1980, fig. 26) the archontan grouping is not enhanced by the inclusion of leptictids.

ANAGALIDS

The curious anagalids, known only from the Early Tertiary of Mongolia and China, have been scrutinized in several studies of early eutherian interrelationships. Simpson (1931) originally described *Anagale gobiensis,* represented by an exquisitely preserved skull and jaws, and partial skeleton from the Shara Murun Valley, Inner Mongolia. Following detailed comparisons with other mammalian groups, Simpson (ibid.) made the interesting suggestion that anagalids were closely related to tupaiids and provided the first indisputable evidence of tupaioids in the Early Tertiary record. For support of his theory, Simpson cited several similarities between tupaiids and anagalids, including (1) a long infraorbital canal, (2) large orbits, (3) lacrimals with a facial exposure, (4) prominent jugal, (5) entotympanic bulla, (6) simple, ring-shaped ectotympanic, (7) large cerebral hemispheres, (8) cranial foramina "*Tupaia*-like," (9) separate tibia and fibula, (10) presence of a superior astragalar foramen, and (11) short metatarsals. It should be clear at this point that many of these features (1, 2, 4, 6, 9, 10, 11) are probably primitive eutherian characters and thus fail to ally anagalids with any mammals. Simpson (1931) excluded anagalids from close relationship with leptictids because the latter showed basically "erinaceid features" (occipital-mastoid exposure, short lacrimal expansion, "false" bulla, distally fused tibia-fibula) and "peculiar characters" (molariform last premolars, intraorbital lacrimal foramen, and squamosal foramen).

Evans (1942), following a detailed study of the osteology in macroscelidids, concluded that anagalids were intermediate between African elephant shrews and tupaiids. McKenna (1963) went further in removing anagalids from near relationships with tupaiids, noting differences in bullar structures, specializations in the anagalid feet (fissured unguals), and characters enumerated by Evans

(1942). More recently, McKenna (1975, p. 35) maintained that anagalids represent early Asian Macroscelidea "that have not yet fused the tibia-fibula or yet strongly reduced or lost M_3^3." Szalay (1977) has endorsed this view in a general way by advocating the close relationship between anagalids, macroscelidids, zalambdalestids, eurymylids, pseudictopids, and lagomorphs without attempting further resolution among these groups.

Central to the question of anagalid affinities is whether the known skull and postcranial characters allow adequate comparisons with other eutherians. It should be noted that details of the auditory region, except for structures of the bulla, are not presently available (at least as recorded from published studies) for anagalids. Likewise, many elements of the skeleton have been incompletely described. (*Anagale* is presently undergoing further preparation and will be the subject of a study by McKenna and Bleefeld.) For the present, consideration of the anagalid material as described by Simpson (1931), Evans (1942), and other workers must suffice.

McKenna (1975) interpreted Evans's (1942) study as documentation for a close relationship between macroscelidids and anagalids. However, it is important to note two shortcomings of Evans's analysis: he did not attempt to distinguish specializations from primitive eutherian characters in the majority of comparisons, and he cited features in the specialized *Rhynchocyon* as representative of the typical condition in Macroscelididae. Rather, analysis should reflect the distinction between primitive and derived characters, and detailed observations of macroscelidine skeletal material, particularly that of *Petrodromus*, a genus Evans (1942, p. 101) regarded as "the most primitive member of the family."

Such comparisons show that anagalids are linked with macroscelidids by several common traits, including: (1) a weak postorbital constriction, (2) a supraorbital shelf, (3) a postorbital process on the frontal, (4) a very large optic foramen, (5) an inclined anterior border of the coronoid process, (6) the great reduction or absence of the postglenoid process, (7) a relatively high jaw condyle, (8) moderately large incisive foramina, (9) moderately long postmeatal distance, (10) an ec-

totympanic element in the bulla, (11) the lateral expansion of the ectotympanic into a meatal tube, (12) nearly continuous sustentacular and naviculoastragalar facets, (13) the posterior restriction of the astragalar trochlea, (14) flattened and reduced distal astragalar facets, and (15) the small size of the ectal facet.

While these traits clearly exclude leptictids from close association with anagalids-macroscelidids, they are especially characteristic as well of lagomorphs and rodents (e.g., items 1, 2, 4, 5, 6, 7, 8, 9, 10, 11). In fact, this similarity is enhanced by other available information on the skull of *Anagale* (Novacek, 1985, fig. 5). Pending further study, anagalids at least must be considered as an additional member in a superclade joining macroscelidids, lagomorphs, and rodents (McKenna, 1975; Novacek, 1982b, 1985). In particular, McKenna's (1975) grouping of anagalids with macroscelidids is certainly supported by this review.

As one might anticipate, leptictids present a weaker alternative as an anagalid relative than the above-discussed candidates. Leptictid similarities to either anagalids (emargination of posterior palate between M³s) or macroscelidids (deep antorbital depression, lacrimal foramen in orbit, lack of superior astragalar foramen) are overshadowed by the list of potential synapomorphies for these latter groups. Moreover, leptictids do not approach macroscelidids and anagalids in the latters' special similarity with lagomorphs and rodents (Novacek, 1985, fig. 5).

LAGOMORPHS, ZALAMBDALESTIDS, PSEUDICTOPIDS

McKenna (1975) has recently argued for the close relationship of lagomorphs, zalambdalestids, and pseudictopids based on specializations of the jaw, wear pattern of crown, the pattern of tooth replacement, and foot structure. His views were generally supported by Szalay (1977) who did not venture a hypothesis for the sequence of splitting for these taxa. The controversial Eurymylidae, an extinct Asian family, has also been recognized as an early lagomorph group (Wood, 1942; Van Valen, 1964). However, Sych (1971) argued for the remote separation of

eurymylids from a basic eutherian stock and erected the new order Mixodontia for eurymylids to indicate their distinction. Other workers have noted the morphologic diversity of eurymylids, recognizing a basic split between "true" eurymylids and mimotonids that relates these groups to rodents and lagomorphs, respectively (McKenna, 1975; personal commun., Li and Ting, 1985). Referable skull and postcranial material is incompletely studied and eurymylids will not be considered here further.

Zalambdalestids and, to a lesser extent, pseudictopids, are much better known from osteological evidence and their possible relationships to lagomorphs are worth examining. In this regard, McKenna (1975, pp. 34–35) stated, "A *Zalambdalestes*-like animal, possibly still with tibia and fibula unfused, could have given rise to later lagomorphs by loss of I^1 I_2 I_3 C_1^1 dP_1^1 and P_2 to yield dental formula I_1 I^2 P^2 P_4^4 P_5^5 M_1^1 M_2^2 M_3^3 from which both ochotonids and leporids could be derived." McKenna's hypothesis suggests a more remote time of divergence for pseudictopids and, in this way, contradicts an earlier view expressed by Van Valen (1965) which is based primarily on evidence from crown morphology of the cheek teeth. Different lines of evidence are discussed by Van Valen (1965), Kielan-Jaworowska (1969, 1975, 1979), Sulimski (1969), Szalay and McKenna (1971), McKenna (1975), and Szalay (1977). While zalambdalestids, including *Zalambdalestes* Gregory and Simpson, 1926, and *Barunlestes* Kielan-Jaworowska, 1975, seem closer to the lagomorph condition in snout characters, diastema (Van Valen, 1965), fused tibia-fibula, and elongate metatarsals (Kielan-Jaworowska, 1975), most skull and teeth characters are conservative, and indicate no special relationship with lagomorphs. Pseudictopids, on the other hand, show definitely derived resemblances in the wear pattern of molars and in cheek tooth crown morphology, but the referable skeletal elements available are primitive except for tarsal features, some of which also characterize anagalids, macroscelideans, and more advanced leptictids in addition to lagomorphs (tarsal features of *Pseudictops* are under examination by Ann Bleefeld). Additional postcranial elements in zalambdalestids led Kielan-Jaworowska

(1979) to reject a close affinity between this group and lagomorphs.

Whatever the relationships of these taxa, it is clear that leptictids have, at most, a very remote connection to lagomorphs and their possible fossil relatives. Among Recent groups, lagomorphs seem most closely related to rodents (Gregory, 1910; Novacek, 1982b, 1985; Li and Ting, 1985; and remarks below), an idea also endorsed by McKenna (personal commun.), but later withdrawn by him (McKenna, 1975).

KENNALESTES, GYPSONICTOPS

Primitive morphology and great antiquity have doubtless contributed to the "ancestral" reputation of *Kennalestes*. Kielan-Jaworowska (1969) first described this animal from cranial and dental material discovered in Upper Cretaceous localities (Djadokhta Formation) of Bayn Dzak, Mongolia. She referred the genus with query to a broadly defined superfamily Leptictoidea, a group also comprising zalambdalestids. *Kennalestes* was differentiated from leptictids by its possession of nonmolariform posterior premolars and posteriorly expanded nasals which contact the lacrimals. This latter feature, probably a primitive eutherian character, was also cited as common to *Zalambdalestes* and other Bayn Dzak eutherians. Kielan-Jaworowska (ibid.) further noted that *Kennalestes* differs from *Gypsonictops* in its possession of premolariform premolars and wider stylar shelves on upper molars. These differences imply presence of more primitive eutherian dental characters in *Kennalestes*. As McKenna (1975) claimed, *Kennalestes* is like *Gypsonictops* and unlike leptictids in having a fifth (deciduous?) lower premolar at the P_3 locus. In addition, certain dental differences between *Kennalestes* and primitive leptictids clearly show that leptictids are derived over *Kennalestes* (table 2, characters 3, 4, 6, 8, 11, 12, 13, 15, 16, 17, 18, 20, 21, 29).

Although this result emphasizes the primitive nature of *Kennalestes,* it is not very helpful for understanding the affinities of this animal. Possible indications of synapomorphy between leptictids, *Gypsonictops,* and *Kennalestes* would lend support to McKenna's (1975) contention, based principally

on his hypothesis of dental replacement, that *Kennalestes* represents the most primitive member of the Ernotheria, a super group also comprising leptictids, macroscelidids, anagalids, lagomorphs, zalambdalestids, and pseudictopids. A survey based on Kielan-Jaworowska's (1969, 1977) descriptions reveals few, if any, possible shared-derived characters. As in leptictids, there is only a single large lacrimal foramen opening within the orbit, a character that may be derived over the primitive eutherian condition. However, *Kennalestes* is distinctly more primitive than leptictids in having a large facial exposure of the lacrimal. Kielan-Jaworowska (1969) suggested the possibility of an expanded orbital wing of the maxilla contacting the frontal, but could not claim this as certain due to poor preservation in the orbital region. The only derived dental feature of any significance in *Kennalestes* would be the development of a last upper premolar with a molarlike outline, lingual cingula, and conules, but this tooth does not nearly approach the molariform condition in leptictids and *Gypsonictops*. In short, presently there seems little basis for a close relationship between *Kennalestes* and the latter taxa that would exclude other eutherian groups. A similar argument pertains to the older Mongolian genera "*Prokennalestes*" and "*Prozalambdalestes*" (see Kielan-Jaworowska et al., 1979).

PROCERBERUS, CIMOLESTES, AND ASIORYCTES

The dental distinction between "palaeoryctoids," leptictids, and *Gypsonictops* has been discussed at length by various authors (Van Valen, 1967; Lillegraven, 1969; Clemens, 1973; Butler, 1972). The evidence clearly points to a very early divergence between palaeoryctoids on one hand, and *Gypsonictops* and leptictids on the other. The former group is characterized by many primitive features not common to the latter (high piercing cusps, transverse upper molars, lack or poor development of hypocones, weakly developed cingula, wide stylar shelves, emphasis of labial prevallum and postvallum shear, etc.). Thus the unity of palaeoryctoids on dental evidence is questionable and there is reason to suspect that some of the phenetically similar

members relate to widely divergent groups of mammals (for example, see Lillegraven, 1969; McKenna, 1975).

Amplifying the case for remote differentiation of palaeoryctoids is the discovery of *Asioryctes* (Kielan-Jaworowska, 1975) from Barun Goyot Late Cretaceous faunas of Nemegt Basin, Mongolia. This genus may be either an early palaeoryctid or soricoid lipotyphlan. In addition, Kielan-Jaworowska (1977) cited several primitive postcranial features (lack of a transverse foramen in the atlas, a suture between axial and atlantal parts of the second cervical vertebra, three bones in the proximal row of the carpus, centrals and praepollex present, partial superposition of astragalus on the calcaneus, lack of a definite astragalar tibia-trochlea, and the presence of an astragalar-cuboid contact) that suggest that *Asioryctes* represents a very archaic group of therian mammals.

In several respects, *Procerberus* straddles the dental boundary between leptictids and "palaeoryctoids." Sloan and Van Valen (1965) originally classified this animal as an early leptictid. However, Lillegraven (1969) made detailed cross comparisons between *Gypsonictops, Leptictis, Procerberus,* and *Cimolestes* and presented a strong argument for reference of *Procerberus* to the "Palaeoryctidae" (sensu lato). The major resemblance of the last genus to *Gypsonictops* and early leptictids is the development of three distinct trigonid cusps and a well-developed talonid with two or three cuspules in the last lower premolar of some specimens. Also, the last upper premolar has a small but distinct metacone and the stylar shelves of the upper molars are narrow. Despite these resemblances, Lillegraven (1969, p. 68) noted several features that align *Procerberus* with *Cimolestes*: in the last lower premolar the protoconid is laterally compressed; an anterior cingulum is absent, the metaconid is much smaller than the protoconid, and there is a distinct posterior ridge on the protoconid; the upper molars lack or irregularly develop lingual cingula, have more lingually positioned conules and a sharper metacrista on M^{1-2}, and show a greater emphasis in "carnassial style" shearing function.

From these comparisons it is evident that *Procerberus* is unlike leptictids and is similar

to palaeoryctids mainly in the retention of primitive eutherian dental features. However, a few resemblances such as wear features and shearing surfaces might be specializations shared with leptictids. The dental evidence merely suggests that *Procerberus* is either a (1) bona fide member of the "Palaeoryctidae" representing a lineage long divergent from *Gypsonictops* and leptictids and closely related to *Cimolestes*; (2) a very primitive member of the leptictid clade that has developed only a few of the derived features characteristic of teeth in undoubted members of this group; or (3) a third major lineage of uncertain relationship with leptictimorphs and palaeoryctoids. Based on the present information, there is no clear choice among these alternatives.

While these early taxa are reasonably well represented by dentitions, evidence from other systems is usually either poor or absent. There are few known skeletons (e.g., *Asioryctes*) and these specimens generally show primitive eutherian characters (Kielan-Jaworowska et al., 1979). Contributing a different perspective on the biology and systematics of these groups is a study by Szalay and Decker (1974). These authors associated isolated tarsal elements with *Procerberus* and *Cimolestes,* claiming that the astragalus and calcaneum in the two genera are virtually identical, differing only in relative size. If Szalay and Decker are correct in their association, it is clear that *Procerberus* and *Cimolestes* share several derived tarsal characters in common with leptictids. Szalay (1977) has recently applied this interpretation in his establishment of the order Leptictimorpha to include *Cimolestes* and *Procerberus* as well as *Gypsonictops* and leptictids. Confounding this hypothesis is the lack of firm evidence for association of the isolated tarsals with dentitions of *Cimolestes* and *Procerberus,* the lack of firm evidence for the monophyly of *Cimolestes,* and the possibility (sensu McDowell, 1958, p. 180) that certain early "palaeoryctoids" might have special affinity with *Apternodus* or other lipotyphlans.

"ERNOTHERES" AND "PREPTOTHERES"

The above considerations have significant bearing on more broadly conceived theories of eutherian relations. McKenna (1975) proposed that there are three major clades of eutherian mammals. The first, represented by edentates, diverged shortly after the time of differentiation of eutherians from a common marsupial-placental stock. The subsequent separation of two other eutherian clades was also very remote (mid-Cretaceous or earlier?). According to McKenna (1975), a basic line of evidence for the latter dichotomy involved variation in mode of dental replacement. He postulated that one group, the Ernotheria (to include *Kennalestes, Asioryctes,* "palaeoryctines," *Gypsonictops,* leptictids, didymoconids, macroscelidids, anagalids, pseudictopids, zalambdalestids, eurymylids, ochotonids, and leporids) diverged from the primitive eutherian postcanine formula $dP^1_1\ P^2_2\ P^3_3\ P^4_4\ P^5_5\ M^1_1\ M^2_2\ M^3_3$, through loss of P^3_3, to arrive at the formula $dP^1_1\ P^2_2\ P^4_4\ P^5_5\ M^{1-3}_{1-3}$.

More complex dental modifications were suggested by McKenna for the other major clade, the Preptotheria (=Eutheria − [Edentates + Ernotheria], rodents were regarded by McKenna, 1975, as Eutheria incertae sedis). Preptotheres supposedly retained a deciduous last premolar (DP^5_5) but lost M^3_3 to arrive at their postcanine formula $dP^1_1\ P^2_2\ P^3_3\ P^4_4\ DP^5_5\ M^1_1\ M^2_2$. McKenna's suggestion was influenced by a supposed transitional (but ambiguous) condition in some deltatheridians, and the adjustments of dental formula necessary to explain the homology of an enlarged, trenchant upper premolar (traditionally designated P³ but designated as P⁴ by McKenna, 1975).

Although the loss of an anterior premolar such as P^3_3 in the evolution from the primitive eutherian five-premolar condition seems a likely event, McKenna's suggestion for the preptothere dental formula is problematic (see Hecht, 1976; Szalay, 1977). Derivation of such a formula involves at least two innovative steps; the loss of M^3_3 and retention of a deciduous P^5_5. Neither of these events has been clearly documented in mammalian evolution at the level McKenna postulated. Indeed, there may even be a question as to how the theory might be tested with paleontological data (Novacek, in press). Rather than consider such a problem further here, it seems worthwhile to scrutinize the Ernotheria-

Preptotheria dichotomy on the basis of other lines of morphological evidence. Such a procedure does not, of course, provide a direct test for McKenna's theory on trends in dental replacement, but is of interest to determine whether his hypothesis of relationships based on that theory is corroborated or falsified by independent characters.

The most obvious line of approach from the perspective of this study is to consider the supposed unity of the Ernotheria, since this group is alleged by McKenna to contain the leptictids. Can derived osteological characters, in addition to those cited by McKenna (1975), be identified which are common to the ernotherian clades, and which serve to separate Ernotheria from Preptotheria? Further, do such characters appear only rarely in other eutherian groups, allowing a minimal amount of independent events implicit in the model of relationships?

Szalay (1977) has already addressed these questions in a general way, and concluded, based on variation in tarsal structure, that the cause for ernotherian unity is not well served. He maintained that all members of the Ernotheria for which tarsal specimens are known possess a specialized astragalus and calcaneal structure, but that leptictids have diverged in a direction separately from that of other ernotheres in respect to specializations of these elements. Accordingly, Szalay (ibid.) grouped macroscelideans, anagalids, pseudictopids, and duplicidentates as the order Lagomorpha. Leptictids were dispatched to a separate group, the Leptictimorpha, for reasons discussed in foregoing sections. Though I agree with Szalay (1977) that fundamental differences exist in tarsal structure among these groups, I think that the picture revealed by calcaneal and (especially) astragalar morphology is more complex than his suggestion of a basic leptictimorph-"lagomorph" (sensu Szalay) dichotomy. For the "ernotheres" I would recognize at least three basic tarsal types (Novacek, 1980, fig. 19):

1. The "leptictid type." This astragalocalcaneal complex was characterized by Szalay (1977). It shows some features (highly convex naviculoastragalar facet) that suggest free movement of the lower ankle joint, in combination with specialized features suggesting extreme adaptations to dorsiplantar flexion (strong curvature and extensive surface of the trochlea, reduction or loss of calcaneum fibular facet, loss of the superior astragalar foramen), and lateral stability (enlarged lateral trochlear crest) during movement of the foot.

2. The "lagomorph type." The salient features of this arrangement involve, as Szalay (1977) stated, specializations for restriction in fore and aft mechanics in the upper ankle, lower ankle, and midtarsal joints. The superior astragalar foramen persists even in probable cursors like Pseudictops and Anagale. The trochlea is elongated, extending to the neck anteriorly but very restricted posteriorly. The naviculoastragalar and spring ligament facets are flattened distally and thus do not allow for a full arc of movement of the lower ankle joint. The calcaneoastragalar facet is more strongly concave than in leptictids, but faces mainly posteriorly; the astragalar neck (particularly in ochotonids and leporids) is elongate; the sustentacular facet and distal astragalar facets are nearly confluent; and the astragalocalcaneal facet is reduced but its orientation varies (nearly horizontal to long axis of calcaneum in some lagomorphs but acute to nearly parallel in Pseudictops). It should be pointed out that some diversity in structure exists among the type 2 astragali in lagomorphs, anagalids, and pseudictopids.

3. The "macroscelidid type." This complex, while showing tendencies toward both type 1 or type 2 tarsals, does not fit well into either category. Like the latter, the distal astragalar facets are reduced, the astragalocalcaneal facets are absent, and the curvature of the trochlea is more limited posteriorly. Like the former, there is no superior astragalar foramen, the trochlea is broad and lower, the calcaneoastragalar facet faces laterally and posteriorly, the trochlear lateral crest is more pronounced than in type 2, and the sustentacular and distal astragalar facets are slightly separated by a shallow groove. Most interestingly, macroscelidids have several unique features not found in either types 1 or 2: the dorsal outline of the astragalar trochlea has a distinct convexity medial to the fibular crest; a very extensive and deep depression is located immediately below the trochlea on the anterior surface of the astragalus, the astragalar neck is extremely short, the cuboid facet on the calcaneum is strongly convex; there is no peroneal tubercle; and the sustentacular

groove on the calcaneum for the flexor fibularis is extremely deep and broad. This characterization is based primarily on observations of *Petrodromus*. Proximal tarsal structure in elephant shrews is diverse (Evans, 1942) but it is likely that the macroscelidine construction of a type near *Petrodromus* was primitive for the family. The macroscelidid pattern seems to suggest a broad arc of dorsiplantar flexion and greater lateral stability as in type 1, along with a limitation of lower ankle joint movement common to type 2.

Thus, the tarsal diversity within the Ernotheria suggests a threefold division of tarsal types, namely (1) leptictids; (2) a broad "lagomorphlike" group comprising leporids, ochotonids, pseudictopids, and (with weaker tarsal resemblance) anagalids; and (3) macroscelidids. All of these groups have derived tarsal characters which correlate well with their (cursorial) locomotion but the diversity described does not comprise homologous evidence for the monophyly of the Ernotheria.

"Ernotheres" remain problematic, even when one considers a broader suite of morphological evidence. The following are characters common to the groups included by McKenna (1975) in the Ernotheria.

1. A moderately large orbitosphenoid element; the polarity of this character is not certain (see discussion above on orbital wall). This bone is also large in some erinaceids.

2. There is some degree of maxillary fenestration, although this is not certain in the case of the zalambdalestids and anagalids. Fenestration is moderate in leptictids, but more pronounced in lagomorphs and macroscelidids.

3. The optic foramen is moderate to large in size, indicating a well-developed eye. The optic foramen was probably small in the most primitive insectivores, but it is large in many eutherians, including tupaiids and primates. The moderate size of this foramen is probably primitive for therians.

4. The suboptic foramen is absent or opens into the sphenorbital fissure. This condition, common to metatherians and many eutherians, is probably primitive.

5. The coronoid process is somewhat hooklike in lateral outline but of quite variable structure. This trait correlates with a shift in site of attachment for the temporalis and the convergence of its radiate fibers in tendon at a more limited point of insertion. In some leptictids the coronoid is more rounded and approaches the erinaceid condition. The coronoid is also hooklike in tupaiids.

6. The anterior border of the coronoid is somewhat inclined, but significantly more vertical in leptictids. The anterior border is also inclined in tupaiids.

7. A high jaw condyle has been cited as a derived character linking ernotheres (McKenna, 1975). However, the condyle is relatively much lower in leptictids and (to a lesser extent) zalambdalestids, approaching the insectivoran condition. The condyle is also high in the "nonernotheres" Dermoptera, Edentata, Pholidota, Tubulidentata, Hyracoidea, Artiodactyla, Perissodactyla, and Sirenia.

8. There is a distinct ectopterygoid process. This feature is also present in erinaceids, tupaiids, dermopterans, chiropterans, and euprimates.

9. The medial internal carotid artery is either small or absent. Even though such a condition is doubtless a eutherian specialization, it is common to many clades of the infraclass (see table 3, character 51b).

10. The brain to body size ratio measured by EQ (encephalization quotient) is greater than 50. Macroscelidids and lagomorphs have relatively larger brains than most insectivores (where low values for EQs are in the 24–30 range). Advanced leptictids also have large brains, but the primitive condition for the family is unknown. This feature may exclude zalambdalestids. Many other eutherians (for example, tupaiids) have comparatively high EQs.

11. The olfactory bulbs are moderate to small, a feature also common to tupaiids and primates, among others. Leptictids are the least specialized in this regard although the zalambdalestid, pseudictopid, and anagalid conditions are not clearly known.

12. There is either an ectotympanic or entotympanic or composite bulla, fully ossified in the adult. Insectivores may have primitively lacked a bony bulla, but most eutherians have a bulla of one kind or another (table 3, character 49). The possibility of independent evolution of similarly constructed

bullae in divergent clades seems strong (Novacek, 1977b).

13. Several features of the hindlimb and pelvis, when taken together, indicate specializations for cursorial adaptations. These include an acute iliosacral angle, anteriorly flaired iliac wings, a deep and elongate trochlea, a deep sulcus muscularis tibia, incipient to extensive fusion of the tibia and fibula; a pronounced tibial crest, crural index greater than 90, and intermembral index less than 75 (see Novacek, 1980). These features are best known in lagomorphs, leptictids, pseudictopids, and macroscelidids. Knowledge of anagalids and zalambdalestids is poor, although new information is expected. These traits suggest a derived character complex not approached in many other early differentiated eutherian groups. The hindlimb and pelvic bones for tenrecids, soricoids, erinaceoids, tupaiids, and early primates may show specializations in isolated features listed above, but on the whole, they are closer to the primitive eutherian condition. The possibility of independent evolution of hindlimb and pelvic specializations for several eutherian clades cannot be excluded, particularly because distribution of appendicular traits in mammals is so poorly known.

14. Various astragalar and calcaneal features suggest specializations in locomotory adaptations but, as discussed above, at least three different tarsal types cannot easily be united with a common homologous plan.

15. The major derived dental characters involve molarization of the posterior premolars, reduction of stylar shelves, and a decrease in sectorial-orthal shear in favor of transverse shearing, crushing, or grinding; and reduction in size and number of anterior premolars. Other dental characters cited by McKenna (1975, pp. 33–34) for ernotheres are, as he emphasized, diversely present in various clades. These include differential wear patterns, unilateral hypsodonty, prismatic crowns, enlarged anterior lower incisors, and the like.

From the above list it is obvious that there are major problems with the recognition of "Ernotheria." Many ernothere characters noted above are primitive. Nearly all of the shared-derived osteological characters are also present in many other eutherians. Character systems like the hindlimb and pelvic structure (13) could have evolved independently in several ernotherian lineages. Clearly needed in these cases are careful first-hand comparisons of such characters as femur trochlea structure and the development of pelvic spines for muscle insertions. Unfortunately, the preliminary comparisons made here do not fulfill this aim. To conclude, the above evidence fails to support the "Ernotheria." Alternatively, a concept of a superclade excluding leptictids but comprising the remaining Ernotheria (see Szalay, 1977) might be better founded if a close relationship between macroscelidids, rodents, lagomorphs, and putative fossil members (anagalids, pseudictopids, zalambdalestids, eurymylids, and didymoconids) can be demonstrated on the basis of more complete skeletal information.

Related to the ernothere problem is Szalay's (1977, 1985) claim that leptictids and rodents are closely related by functionally important basicranial and tarsal features. Szalay did not elaborate on the basicranial evidence but he did cite several derived tarsal features shared by these taxa. Elsewhere (Novacek, 1980) I have argued that these features are ambiguous because they are present in several eutherian groups, including macroscelideans, tupaiids, and certain primates (e.g., fibular facet weak or absent, superior astragalar foramen absent, lateral crest of astragalar trochlea prominent). Szalay (1985) recently cited another character linking rodents and leptictids — the strong tibial posterior process. However, this process is not so pronounced in all leptictids and the overall distribution of this trait within Eutheria is poorly known. At present, the special cranial similarity between lipotyphlans and leptictids and the variety of morphological evidence for an affinity among rodents, lagomorphs, and anagalids outweighs the support for a leptictid-rodent grouping.

OTHER GROUPS

Several eutherian taxa have been implicated as leptictid relatives, but have not been adequately examined here. The curious pantolestids (see Cook, 1954; Butler, 1972; Lillegraven, 1969; McDowell, 1958; Van Valen,

1967) have been allied with leptictids, but early pantolestids are known only from incomplete dentitions. The matter has been under study by McKenna (personal commun.) for some time. Taeniodonts (Patterson, 1949) have been allied closely with leptictids by Szalay (1977) but opposing views (Van Valen, 1966, 1967; Lillegraven, 1969) seem equally convincing. Microsyopids show some leptictid features in the skull (Szalay, 1969) but these are mainly a matter of symplesiomorphy. I see no strong reason to regard, *a la* Bown and Gingerich (1973), microsyopids as annectant taxa between "ancestral" leptictids and primates. Microsyopids simply share a large number of cranial plesiomorphies with leptictids and primates (see McKenna, 1966 for comparisons of basicranium; also Szalay, 1969). At present these groups are of moot importance in deciphering leptictid affinities.

EUTHERIAN CLASSIFICATION

From the foregoing it seems that several recent theories for higher eutherian classification fall short of providing well-defined, monophyletic clades. What patterns might be salvageable from the morphological evidence reviewed here? The least problematic groups are those supported by unique homologies. Strict rules that eliminate all other kinds of characters from consideration lead to very minor resolution of the eutherian "radiation" (fig. 31). However, this approach does identify several interesting groups: (1) proboscideans-sirenians, (2) 1 + hyracoideans, (3) 1 and 2 + perissodactyls, artiodactyls, and cetaceans, (4) rodents and lagomorphs, (5) lipotyphlan insectivores, (6) 5 + leptictids, (7) edentates and pholidotans. Easing the constraints to allow characters that show limited homoplasy preserves the above groups and identifies several additional higher-level clades (fig. 32). This picture is not much improved upon by considering a larger sampling of cranial data shown in table 3 and reviewed in this paper. The resultant pattern shows greater resolution (fig. 33) but the additional clades are only weakly supported by characters that appear to be highly homoplastic.

As noted above, hierarchical classifications based on reasonably compelling evidence for relationships are useful. A pattern of higher relationships for Eutheria, namely, one consistent with the solution shown in figure 32 (see also Appendix), seems amenable to a formal classification. The results of such an attempt are outlined in table 4. Similar proposals in recent years are not accompanied by sufficiently explicit characterizations. The aim of this arrangement, then, is to mirror the groupings that seem best supported by the morphological evidence reviewed here and elsewhere (Novacek, 1980, 1982b). In the interests of communication, the standard names of orders are maintained where possible. Names for superordinal categories are also largely derived from published names in well-known works (e.g., Linnaeus, 1758; Gregory, 1910; Simpson, 1945; McKenna, 1975), although here these names might denote groups of new rank or slightly different content. Ranks are established to reflect hierarchical branching, but ranks do not proliferate unless warranted by splitting sequences. For example, the remote divergence of edentates and pholidotes is represented by their grouping within the cohort Edentata, a category of rank equal to the cohort Epitheria, which unites all other Eutheria. However, the contents of Edentata comprise only Xenarthra and Pholidota; this does not require the subdivision of Edentata into superorders, grandorders, and mirorders. Again, in this arrangement, the standard eutherian orders constitute the reference level of the classification; ranks either group or subdivide from this level. A more detailed account of the classification follows.

CLASS MAMMALIA LINNAEUS, 1758

SUBCLASS THERIA PARKER AND HASWELL, 1897

INFRACLASS EUTHERIA GILL, 1872

DEFINING CHARACTERS: Precocious segregation and differentiation of embryonic trophoblast (Luckett, 1977); chorioallantoic placenta; prolonged intrauterine gestation; ureters that pass lateral to derivatives of Mullerian ducts; enlarged cerebral hemispheres; corpus callosum; relatively narrow stylar shelves on upper molars; epipubic bones absent.

COMMENTS: Strict adherence to this diagnosis would prevent the allocation of fossil

TABLE 3
Selected Cranial and Jaw Features of Leptictids and Other Mammalian Groups[a]

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
1. Nasals anteriorly projecting, not retracted	1a. As in L (Di, Sc, Ed, Ro, La, Ca, Ar, Pe, Eup)	1b. Nasals retracted to moderate degree (Ma, So, Te, Er, De, Ch, Ph, Tu, Hy) 1c. Nasals strongly retracted (Pr, Si, some Ce[c]) 1d. Nasals excluded from anterior rostrum by dorsal premaxilla (Mo, some Ce)
2. Nasal-frontal contact broad[d]	2a. As in L (Mo,[d] De, Di,[d] Tu, Hy, Ar, Pe)	2b. Nasal-frontal contact narrow (Ma, Sc, So, Te, Er, Ch, Ed, Ro, La, Ca, Ph, Pr, Ce, Si, Eup)
3. Small incisive foramina	3a. As in L (Di, Ma, Sc, So, Te, Er, Ed, Ca, Ph, Tu, Hy, Ar, Pe, Eup)	3b. Incisive foramina large, elongate, set posteriorly in palate (Ro, La) 3c. Foramina coalesce with modification of premaxilla (De, Ch, Si) 3d. Rostrum greatly modified, single large foramen or foramen absent (Mo, Pr, Ce[c])
4. Posterodorsal process of premaxilla not extending to frontals	4a. As in L (Mo, Di, Ma, Sc, So, Te, Er, Ed, Ca, Ph, Hy, Ar, Pe, Ce,[c] Eup)	4b. Process contacts frontal (Ro, La, Pr, Si) 4c. Process weak or absent, maxillary-premaxillary suture on lateral rostrum nearly vertical (De, Ch, Tu, some Ed)
5. Prominent crista galli of mesethmoid[e]	5a. Crista galli weak or absent (Mo, Di, Ma, Sc, Ar, Ce, R, So, Te, some Er, some Ch, La, some Ca, Ar, Ce, some Eup)	5b. As in L (some Di, De, some Er, some Ch, some Ed, some Ca, Tu, Hy?, Pr, Si, some Eup) 5c. Mesethmoid divided by prominent, rounded ridge (some Ed, Ph)
6. Broad contact of maxilla with frontal in facial region	6a. Contact narrow, confined by nasal and lacrimal (Mo, Di, Ma, Sc, De, Ch, Ed, Ca, Hy, Ar, Pe, Pr, Si, Eup)	6b. As in L (So, Te, Er) 6c. Contact narrow, confined by premaxilla and lacrimal (Ro, La) 6d. Contact very broad as antorbital rim is absent and lacrimal is shifted ventrally (Ph)
7. Two ectoturbinals	7a. As in L (Di, Te, Er, So)	7b. More than 2 ectoturbinals (Ar, Pe, Tu, some Ed) 7c. Reduction in number of ectoturbinals (some Eup)
8. Nasal-facial exposure of maxilla much greater than premaxilla	8a. As in L (Mo, Di, Ma, Sc, So, Te, Er, De, Ch, Ed, Ca, Ph, Tu, Ar, Pe, Pr, Eup)	8b. Nasal-facial exposure of maxilla and premaxilla nearly equal (Ro, La, Hy, Ce,[c] Si)
9. Lateral maxilla-jugal contact bifurcate	9a. Contact oblique, not bifurcate (Mo, Di, Ma, Sc, Ed, Ro, La, Tu, Hy, Pe, Pr, Ce, Si, Eup)	9b. As in L (Ch, Ca, Ar) 9c. Jugal small or absent (So, Er, Te, Ph) 9d. Contact shifted to face ventrally (De)

TABLE 3—(*Continued*)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
10. Infraorbital canal moderately short	10a. Canal long (Mo, Di, Ma, Sc, De, Ed?, Ca, Ph, Tu, Ar, Pe, Ce,[c] Eup)	10b. As in L (Er, Ch, Pr, So, Te) 10c. Canal extremely shortened to a large foramen in the anterior root of the zygoma (Ro, La, Si) 10d. Canal short but posterior exit well within orbital wall behind root of zygoma (Hy)
11. Infraorbital canal of large caliber	11a. As in L (Di, Ma, So, Te, Er, Ch, Ro, Ca, Tu, Ar, Pe, Pr)	11b. Canal narrow in diameter (Sc, De, Ed, La, Ph, Hy, Ce, Eup) 11c. Canal extremely broad in caliber (Si)
12. Deep antorbital fossa for nasolabial muscles	12a. Antorbital fossa shallow or indistinct (Mo, Di, Sc, So, Te, Er, De, Ch, Ed, Ro,[f] La, Ca, Ph, Tu, Hy, Ar, Pe, Ce,[c] Si, Eup)	12b. As in L or deeper (Ma, Pr, some Ed)
13. Maxilla with much more extensive palatal process than premaxilla	13a. As in L (Mo, Di, Ma, Sc, So, Te, Er, De, Ch, Ed, Ca, Ph, Tu, Hy, Ar, Pe, Pr, Ce,[c] Si, Eup)	13b. Premaxilla and maxilla of roughly equal exposure on palate (Ro, La)
14. Maxilla intrudes into orbital wall but does not contact frontal	14a. Maxilla excluded from orbital wall (Mo, Di, Ma, Sc, De?, Ch?, Ca, Ph?, Tu, Ar, Ce,[c] some Eup)	14b. As in L (La, Pe, Si) 14c. Maxilla with large orbital process, contacts frontal (So, Te, Er, Ro, Pr, Ed, Hy, some Eup)
15. Anterior and middle palatine foramina present	15a. As in L (Mo, Di, Ma, Sc, So, Te, Ro, La, Ca, Hy, Ar, Pe, Pr, Si, Eup)	15b. Foramina join as an elongate pair of openings (Er, some Ma[g]) 15c. Anterior foramina indistinct or absent (De, Ph, Tu, Ce[c]) 15d. Middle foramina indistinct or absent (Ch, Ed, Ph, Tu, Ce[c])
16. Short postpalatine canal present	16a. As in L (Sc, So, Te, Ro, Tu, Eup)	16b. Canal not completely enclosed by maxilla and/or palatine (Ma, Sc, Ch, Ph, Ar, Ca) 16c. Canal opens into walls of choanae (De, La, Ca, Hy?, Pe, Pr, Ce, Si, some Er) 16d. Both postpalatine canal and accessory (vertical) canal present (Di, some Er)
17. Posterior margin of palate between last molars	17a. Margin posterior to last molars (Di, Sc, So, Te, Er, Ch, Ed, some Ro, Ca, Tu, Ar, Ce?)	17b. As in L (Hy, Pe, Pr, Si, Eup, some Ro) 17c. Margin far anterior to last molars (De, La)
18. Posterior margin of palate biconcave with strong postpalatine spine	18a. Margin straight or slightly curved, but not biconcave (Di, Sc, Te, some Er, Ch, Ed, Ca, Ph, Tu, Ar, Pe, Pr, Ce, Eup)	18b. As in L (Ma, De, Ro, La, Hy, So) 18c. Posterior margin with distinctly triangular outline (Si)
19. Posterior margin of palate with weak torus	19a. As in L or torus absent (Di, Ma, Sc, Te, Ch, Ed, Ro, La, Ca, Ph, Hy, Ar, Pe, Pr, Ce, Si, Eup)	19b. Postpalatine torus strong, rounded prominence (So, Er, Tu) 19c. Torus developed as a sharp crest along palatal margin (De)

TABLE 3—(*Continued*)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
20. Large common recess for separate sphenopalatine and dorsal palatine foramina	20a. Sphenopalatine and dorsal palatine foramina not closely adjacent in common recess (Di, Ma, Sc, De?, Ed, Ro, Hy, Pe, Ce, Si, Eup)	20b. As in L (So, Te, Er, Ca, Tu) 20c. Foramina united as single foramen or dorsal palatine foramen absent (Ch, La, Ar, Pe)
21. Orbital process of palatine contacts frontal and lacrimal	21a. As in L (Mo, Ma, Di, Sc, De, Ch, Ca, Tu, Hy?, Pe, Ce,[c] Eup?)	21b. Palatine confined to floor of orbit, does not broadly contact frontal and lacrimal (So, Te, Er, Ro?, La?, Ar, Pr, Si?) 21c. Palatine confined to floor of orbit, but contacts ventrally expanded frontal (Ed, Ph)
22. Lacrimal lacking facial process, confined to orbit or antorbital rim	22a. Lacrimal with distinct facial process (Mo, Di, Sc, De, Ch, Ed, Ca, Tu, Ar, Pe, Pr, Ce,[c] Eup)	22b. As in L (So, Te, Er, Ro, La, Ma?, Hy) 22c. Lacrimal restricted to orbital recess for posterior exit of infraorbital canal (Si)
23. Lacrimal foramen opens posterolaterally within orbit	23a. Lacrimal formen (or foramina) opens laterally on antorbital rim or facial process (Mo, Di, Tu, Te, Er, Ch, Ed, Tu, Ar, Pe, Ce,[c] Eup)	23b. As in L (Ma, De, Ca, Ph, Hy) 23c. Confined to orbit but adjacent to antorbital rim, faces laterally (Ro, La) 23d. Foramen indistinct externally (Pr, Si)
24. Lacrimal tubercle present	24a. Tubercle absent (Mo, Di, Ma, Sc, So, Te, De, Ch, Ro, La, Ca, Tu, Ar, Ce, Si, Eup)	24b. As in L (Ed, Ph, Pe, Pr) 24c. Broad lacrimal crest on antorbital rim (Hy)
25. Jugal well developed	25a. As in L (Mo, Di, Ma, Sc, De, Ch, Ed, Ro, La, Ca, Tu, Hy, Ar, Pe, Pr, Ce,[c] Si, Eup)	25b. Jugal small or absent (So, Te, Er, Ph)
26. Frontal with blunt supraorbital ridge, no strong crest or process	26a. As in L or very weak, blunt process present (Mo, Di, Ma, So, Te, Er, Ed, some Ro, some La, some Ca, Ph, Tu, Ar, Pe)	26b. Strong process directed toward or joined with postorbital process of zygoma (Sc, De, Ch, some Ro, some La, some Ca, Hy, Pr, Ce, Si, Eup)
27. Ethmoidal foramen located in orbital wall above and well posterior to palate	27a. As in L (Mo, Di, Ma, Sc, So, Te, Er, Ca, Ph, Tu, Ar, Pe, Eup)	27b. Foramen located more anteriorly, above posterior palate (De, Ch, Ed, La, Hy, Pr, Ce, Si)
28. Orbital wing of frontal large, confines orbitosphenoid and palatine	28a. As in L (Mo, Di, Sc, De, Ch?, Ro, Ca, Tu, Hy, Ar, Pe, Eup)	28b. Frontal orbital wing restricted, maxilla or orbitosphenoid expanded (Ma, So, Te, Er, La) 28c. Ventral expansion of frontal very pronounced, wedges out orbitosphenoid (Ed, Ph) 28d. Frontal shifted anteriorly with expansion of parietal in orbital wall (Ce)
29. Frontal-alisphenoid contact broad	29a. As in L[c] (Di, De, Ch?, Ed, Ro, Ca, Ph, Pr, Si)	29b. Frontal-alisphenoid partly separated by orbitosphenoid (Ma, So, Te, Er, La, Tu, Hy, Ar, Pe, Ce, Eup)

TABLE 3—(Continued)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
30. Optic foramen moderately large, cleftlike or ellipsoidal, opens in posterior orbitosphenoid	30a. As in L (Di, Ed, Ca, Ph, Tu, Hy, Pe, Ce, Eup)	30b. Foramen large, circular, opens laterally (Ma, Sc, De, Ch, Ro, La, Ar, Pe, Si, Pr)
		30c. Foramen small (much smaller than sphenorbital fissure (Mo, Te, So, Er)
31. Suboptic foramen absent or opens in medial wall of sphenorbital fissure	31a. As in L (Di, Sc?, So, Te, some Er, De, Ch, Ed, Ro, La, Ca, Tu, Hy, Ar, Pe, Pr, Ce, Eup)	31b. Suboptic foramen distinct, opens anterior to sphenorbital fissure (Sc, some Er, Ph?, Si)
32. Broad dorsal exposure of alisphenoid in orbital wall	32. Alisphenoid moderately or weakly developed in dorsal orbital wall (Mo, Di, Ma, Sc, So, Te, Er, De, Ch, Ca, Ph, Tu, Hy, Ar, Pe, Pr, Ce,[c] Si, Eup)	32b. As in L (Ro, La)
33. Foramen rotundum confluent with sphenorbital fissure	33a. As in L (Di, Ma, So, Te, Er, De, Ch, Ca, Ph, Tu, Hy, Ar, Pe, Pr, Ce, Si, Eup)	33b. Foramen rotundum distinctly separate from sphenorbital fissure (Ed, Sc, Eup, Ph)
34. Alisphenoid canal shortened with anterior opening lateral and posterior to sphenorbital fissure	34a. Canal indistinct or absent, anterior opening confluent with sphenorbital fissure (some Di, Ma, So, Te, De, Ch, Ed, some Ca, Ph, Tu, Hy, Ar, Pr, Ce, Si, Eup)	34b. As in L (Sc, some Di, Er?, Ro, some Ca, some Pe)
		34c. Canal very short, simple bridge of bone between closely spaced anterior and posterior openings (La, some Pe)
35. No masseteric and buccinator foramina	35a. As in L (Mo, Di, Sc, So, Te, Er, De, Ch, Ed, Ca, Ph, Tu, Hy, Ar, Pr, Ce,[c] Si, Pr)	35b. One or both foramina present (Ma, Ro, La, Pe)
36. Distinct ectopterygoid process on alisphenoid	36a. Process absent (Mo, Di, So, Te, Ed, Ca, Ph, Tu, Hy, Ar, Pe, Pr, Ce,[c] Si)	36b. As in L (Ma, Sc, Er, De, Ch, Ro, La, Eup)
37. Prominent dorsum sellae posterior to hypophyseal fossa[e]	37a. As in L (Sc, Ch, Ca, Tu, some Eup)	37b. Dorsum sellae weak or absent (Mo, Di, Ma, So, Te, Er, De, Ed, Ro, La, Hy, Ar?, Pe, Pr, Ce, Si, some Eup)
38. Squamosal-sinus canals present	38a. As in L (Di, Mo, Ma, Sc, So, Te, Er, Ch?, Ed, Ro, La, Ca, Ph, Pe, Pr, Si, Eup)	38b. Canals absent (De, some Ed, Tu, Hy, Ar, Ce[c])
39. Prominent postglenoid process present	39a. As in L (Di, De, Ch, Ca, Tu, some Hy, Pe, Ce,[c] Eup)	39b. Process weak or absent (Ma, Sc, Er, Ed, Ro, La, Ar, Pr, Si)
		39c. True postglenoid process absent, pseudopostglenoid (entoglenoid) process present (So, Te, some Hy?)
		39d. Squamosal forms broad, blunt flange (Ph)
40. Glenoid fossa oriented transversely, semilunar in outline	40a. As in L (Di, Ma, Sc, So, Te, Er, De, Ch, Ca, Tu, Hy, Ar,[h] Pe, Pr, Ce, Si, Eup)	40b. Fossa oriented anteroposteriorly (some Ed, Ro, La)
		40c. Fossa absent (Mo, Ph)
41. Suprameatal foramen present	41a. As in L (Di, Ed?, Eup)	41b. Foramen absent (Ma, Sc, So, Te, Er, De, Ch, Ro, La, Ca, Ph, Tu, Hy, Ar, Pe, Pr, Ce,[c] Si)

TABLE 3—(*Continued*)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
42. Glaserian fissure distinct, elongate trough on anterolateral wall of tympanic cavity	42a. "Fissure" broadly open, indistinct, or absent (Mo, Di, Ma, De, Ch, Ed, Ro, La, Ca, Ph, Ar,[h] Pe, Pr, Ce,[c] Si, some Eup)	42b. As in L (So, Te, Er, Tu, Hy, some Eup) 42c. Glaserian fissure very narrow cleft originating in epitympanic recess (Sc)
43. Bony lateral wall of epitympanic recess formed primarily by squamosal	43a. As in L (Mo, Di, So, Te, Er, Ch, Ed, Ph, Tu, Ar, Pe, Eup)	43b. Formed by fusion of tegmen tympani of petrosal and the ectotympanic (Ro, La, some Pr, some Ce) 43c. Formed by fused petrosal squamosal (some Ca, Si) 43d. Formed by part of ectotympanic meatal tube (Ma, Sc, De, some Ca, Hy, some Pr) 43e. Formed by mastoid process of petrosal (some Er, some Ce?, some Si?) 43f. Formed partly by membrane distinct from membrane shrapnelli (So, Ch)
44. Meatal arch of squamosal well ventral to level of tympanic roof	44a. Meatal arch slightly below or roughly level with tympanic roof (Mo, Di, Ma, So, Te, Er, Ch, Ed, Ro, Ca?, Ar,[h] Pe, Ce)	44b. As in L (Sc, De, La, Ph?, Tu, Hy, Pr?, Si, Eup)
45. Large postglenoid foramen opens ventrally and posteromedial to glenoid region	45a. As in L (Di, Ma, Sc, So, Te, Er, Ch, Ed, Ca, Ph, Ar,[h] Pr, Eup)	45b. Foramen concealed ventrally by trabeculated flattened auditory bulla (De) 45c. Pseudopostglenoid foramen opens laterally in squamosal-temporal region (Ro, La) 45d. Postglenoid foramen small, absent (Tu, Hy, Pe, Ce?, Si)
46. Prominent post-tympanic ridge of squamosal present	46a. As in L (Di, Ma, Sc, some So, De, Ch, Ed,[i] Ro, La, Ph, Tu, Ca, Ar, Pe, Ce,[c] Si, Eup)	46b. Ridge weak or absent (some So, Te, Er, Hy, Pr)
47. Ectotympanic simple (annular or horseshoe shaped), not greatly expanded laterally or medially into meatal tube or bulla	47a. As in L (Mo, Di, So, Te, Er, Ed, Tu, Eup)	47b. Ectotympanic expanded to form meatal tube and part, most, or all of bulla (Ma, Sc, De, Ch, Ro, La, Ca, Ph, Hy, Ar, Pe, Pr, Ce) 47c. Ectotympanic annular but ventral process somewhat bloated into flask-shaped structure (Si)
48. Rostral ectotympanic crest well developed	48a. Crest weak or absent, but (in simple ectotympanic) medial process present for eustachian tube (Mo, Di, So, Te, Er, some Ch, Tu, some Si, Eup)	48b. As in L (some Ch, Ed) 48c. Rostral ectotympanic largely expanded to form meatal tube and bulla (see 47b) (Ma, Sc, De, some Ch, Ro, La, Ca, Ph, Hy, Ar, Pe, Pr, Ce,[c] some Si)
49. Large bulla formed by caudal (and rostral?) entotympanic	49a. Well-developed bulla absent, tympanic cavity covered by horizontally inclined tensor tympani and membrane medi-	49b. As in L 49c. Bulla largely ectotympanic and entotympanic (Sc, De, some Ch, some Ed, Ca, Ph, Hy)

TABLE 3—(*Continued*)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
	al to ectotympanic (Mo, Di, So, some Te, Tu)	49d. Bulla ectotympanic (some Ch, Ro, La, Ar, Pe, Pr, Ce, Si?)
		49e. Bulla basisphenoid (with minor petrosal contribution) (Te, Er)
		49f. Bulla petrosal (Eup)
		49g. Bulla composite of several elements (Ma)
50. Elongate medial promontorium crest present	50a. Crest weak or absent[j] (Mo, Di, Ch, Ed, some Ro, La, Ca, Ph, Tu, Hy, Ar, Pe, Pr?, Ce,[c] Si, Eup)	50b. As in L, often fused with medial wall of ossified bulla (Ma, Sc, So, Te, Er, De, some Ro)
51. Promontory and stapedial branches of the internal carotid artery present	51a. Main branch of internal carotid artery runs medial to precursor membrane for developing floor of tympanic cavity (Mo, Di, La?)	51b. As in L (Ma,[k] Sc, So, Te, Er, De?, Ch, Ca,[l] Tu, Ar, Ce?, Si?, Eup)
		51c. Main branch runs *within* the fibrous membrane or fully ossified medial wall of the bulla (Ed, Ro, Ph, La?)
52. Inferior ramus of the stapedial artery exits tympanic cavity near facial canal posterior to petrosal-sphenoid suture[e]	52a. Inferior ramus exits tympanic cavity via a ventrally open fissure (sometimes the Glaserian fissure) or bony tube leading out of the anterior tympanic crest (Di?, So, Te, Er, Ch, Ed?, Ca?,[l] Ph, Ar)	52b. As in L[l] (some Di, Ma,[k] Ro, some La, Tu?)
		52c. Inferior ramus small or absent (some Di,[m] Sc, De, some La, Ph?, Eup)
53. Proximal carotid branches[n] conveyed in ventrally open sulci	53a. As in L (Mo, Di, Ma,[k] So, Te, Er, Ch, Ed, Ro, La, Ca, Ph?, Tu, Ar, Ce?, Si?)	53b. Proximal branches conveyed in ossified tubes (Sc, some Eup[o])
54. Fenestra rotunda faces posterolaterally	54a. As in L (Mo, Di, Ma, Sc, So, Te, Er, Ed, Ro, Ca, Ph, Tu, Hy, Ar, Pe, Ce,[c] Eup)	54b. Fenestra opens posteriorly (some La, Ch, De, Si)
55. Fenestra rotunda broadly exposed ventrally	55a. As in L (Di, De, Ch, Ed, La, Ca, Ph, Tu, Ar, Pe, Ce[c])	55b. Fenestra partly concealed by outgrowth of a petromastoid crest (Mo, So, Te, Er)
		55c. Fenestra partly concealed by shelf of tube for entry of the proximal lateral internal carotid artery (Ma, Sc, Ro, Eup)
		55d. Fenestra partly concealed by its vertical orientation and cochlear expansion (Hy, Pr?)
56. Stylomastoid foramen definitivum present	56a. Foramen poorly developed or absent (Mo, Di, Ar, Pe, Pr?, Ce, Si)	56b. As in L (Ma, Sc, So, Te, Er, De, Ch, Ed, Ro, La, Ca, Ph, Tu, Hy)
57. Mastoid process with deep groove for diagastric muscle	57a. As in L (Di, Ma, Sc, So, Te, Ed, Ro, Ce[c])	57b. Groove very faint or absent (Mo, Er, De, Ch, La, Ph, Tu, Hy, Ar, Pe, Pr, Si, Eup)
58. Large mastoid tubercle (incorporates tympanohyal), nearly reaches lateral edge of promontorium cochleae, with distinct ventral depression	58a. Tubercle weak or absent (Mo, Di, Ma, Sc, De, Ch,[p] Ed,[q] Ro, La, Ca, Hy, Ar, Pe, Pr, Ce,[c] Si, Eup)	58b. As in L (So, Te, Er, Tu,[r] some Pe)
		58c. Large mastoid bridge fuses with promontorium, ventrally floors facial canal (Ph)

TABLE 3—(*Continued*)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
59. Very deep, broadly open sub-arcuate fossa	59a. Fossa deep, but not as deep or broadly open as in L (Di, Ma, Sc, So, Te, Er, Ro, some Ca)	59b. As in L (some Ma, De, Ch, La, some Ca, Eup) 59c. Fossa very shallow, or absent (Mo, Ed, Ph, Tu, Hy, Ar, Pe, Pr, Ce, Si)
60. Extensive occipital exposure of mastoid	60a. As in L (Mo, Di, Ma, Sc, So, Te, Er, Pe, Ro, La, Ca, Tu, Eup)	60b. Occipital exposure of mastoid weak, narrow (Ch, Ph?, Hy, Ar, Pe, Pr, Ce,[c] Si, Ed?)
61. Small triangular exposure of parietal on occipital surface	61a. No such exposure of parietal (Mo, Di, Ma, Sc, So, Te, Er, De, Ch, Ed, Ro, La, Ca, Ph, Tu, Hy, Ar, Pe, Pr, Ce,[c] Si, Eup)	61b. Leptictid condition
62. Large mastoid foramen	62a. As in L (Ma, Di, Te, Er, Ch?, Ed, Ro, La, Ca, Ph, Tu, Pe, Eup)	62b. Foramen very small (Ma?, Sc, So, De, some Ar) 62c. Foramen absent (Di, Hy, some Ar, Pr, Ce,[c] Si)
63. Broader exposure of supraoccipital on dorsal roof of skull	63a. As in L (Mo, Di, Sc, Te, Er, De, Ch, some Ed, Ca, Ph, Hy, Pe, Pr, Ce,[c] Si, Eup)	63b. Narrow restriction of supraoccipital on dorsal roof of skull (Ma, Sc, Te, Er, De, Ch, some Ed, Ro, La, Tu, Ar)
64. Lambdoidal crest well developed, partly conceals occiput from dorsal view	64a. As in L (Di, some Ma, some Sc, So, Te, Er, De, Ch, some Ed, Ro, Ca, Tu, Ar, Pe, Ce,[c] Eup)	64b. Lambdoidal crest weak and/or occiput exposed in dorsal view (Mo, some Ma, some Sc, some Ed, La, Ph, Hy, Pr, Si)
65. Paraoccipital process weak	65a. Process strong (Di, So, Te, Er, De, Ch, Ro, La, Ca, Tu, Hy, Ar, Pe, Ce,[c] Si)	65b. As in L (Ma, Sc, Eup) 65c. Process absent (Mo, Ed, Ph, Pr)
66. Foramen magnum faces posteriorly	66a. As in L (Mo, Di, Ma, So, Te, Er, De, Ch, Ed, Ro, La, Ca, Ph, Ar, Pe, Ce[c])	66b. Foramen magnum opens slightly more ventrally (Sc, Tu, Hy, Pr, Si, Eup)
67. Large, circular posterior lacerate foramen for common exit of nerves IX, X, XI, and jugular vein	67a. Posterior lacerate foramen smaller, usually lenticular; jugular vein may exit in separate opening (Mo, Di, Ma, Sc, Ro, La, Hy, Ar, Eup)	67b. As in L (So, Te, Er, Ed, Ca, Ph, Tu) 67c. Posterior lacerate foramen extensive, coalesces with basicochlear fissure that partially separates promontorium cochleae from basisphenoid-basioccipital (De, Ch, Pe?, Ce, Si?)
68. Single hypoglossal foramen located near and slightly anterior to ventral lobes of occipital condyle	68a. As in L (Di, Ma, Sc, So, Te, Er, Ch, Ed, Tu, Hy, Ar, Pr, Si, Eup)	68b. Foramen absent (Mo) 68c. Foramen very large; opens anteriorly into a depression extending to posterior lacerate foramen (De) 68d. Two or three closely spaced hypoglossal foramina present (Ro, La) 68e. Hypoglossal foramen opens far anterior to leading edge of ventral occipital condyles (Ca?, Ph, Ce?)

TABLE 3—(*Continued*)

Leptictid condition	Primitive eutherian condition	Derived conditions[b]
69. Anterior border of ventral occipital condyle with strong sigmoidal curvature	69a. Anterior border with slight or no curvature (Mo, Di, Ma, Sc, De, Ch, Ro, La, some Ca, Ph, Tu, Ar, Pe, Pr, Ce, some Si, Eup)	69b. As in L (some Ma, So, Te, Er,[*] some Ca) 69c. Ventral occipital condyle with large lateral convexity, but weak medial development (Ed, Hy, Si)
70. Ventral basioccipital-basisphenoid with median ridge and pair of shallow depressions for rectus capiti muscles	70a. As in L (Di, Ma, Sc, Er, De, Ro, La, Ca, Hy, Ar, Pr, Eup)	70b. Median ridge, depressions and other sculpturing on ventral basisphenoid very faint or absent (Mo, So, Te, Ch, Ed, Ph, Tu, Pe, Ce, Si)
71. Coronoid process well developed, dorsally rounded, with semivertical anterior ridge	71a. As in L (Di, Sc, So, Te, Er, Ch, Ed, Ca, Ce,[c] Si, Eup)	71b. Process small with anterior margin inclined (Ma, De, Ro, Tu, Hy, Ar, Pe, Pr) 71c. Process highly modified to form mandibular condyle (La) 71d. Process absent, dentary splint-like (Mo, Ph, some Ed)
72. Jaw condyle relatively low in position	72a. As in L (Di, Sc, So, Te, Er, Ch, some Ed, Ca, Ce,[c] Eup)	72b. Relatively high in position (Ma, De, some Ed, Ro, Ph, Tu, Hy, Ar, Pe, Si) 72c. Highest process on mandible (La, Pr)
73. Stapes horseshoe-shaped, with widely spaced crura?[i]	73a. Stapes columnar, with small basal perforation but no widely spaced crura (Mo, some Di, some Ed, Ph)	73b. As in L (Ma, Sc, So, Te, Er, De, Ch, Ro, La, Ca, some Ed, Tu, Hy, Ar, Pe, Pr, Eup) 73c. Stapes without widely spaced crura, but massive or markedly modified (some marine Ca, Ce, Si)

[a] Groups take the following acronyms:

L, leptictids	Ch, chiropterans	Ar, artiodactyls
Mo, monotremes	Ed, edentates	Pe, perissodactyls
Di, didelphid marsupials	Ro, rodents	Pr, proboscideans
Ma, macroscelideans	La, lagomorphs	Ce, cetaceans
Sc, scandentians (tupaiids)	Ca, carnivorans	Si, sirenians
So, soricoids	Ph, pholidotans	Eup, Euprimates
Te, tenrecoids	Tu, tubulidentates	?, primitive character for group uncertain
Er, erinaceomorphs	Hy, hyracoids	
De, dermopterans		

[b] Derived conditions b, c, . . . , n, do not necessarily constitute a morphocline.

[c] Primitive condition in cetaceans is usually shown in archeocetes (e.g., *Prozeuglodon, Basilosaurus,* see Kellogg, 1936). In cases of ambiguity, variation in cetaceans is noted.

[d] The primitive therian condition shows broader posterior exposure of the nasals than in early leptictids; nasals narrow in Oligocene leptictids.

[e] Distribution of character incompletely known or suggested polarity uncertain.

[f] Secondarily deepened in many rodent lineages to accommodate forward migration of masseteric musculature.

[g] Condition secondarily developed in mascroscelidines.

[h] Primitive basicranial features of artiodactyls are described in Coombs and Coombs (1982).

[i] In edentates, post-tympanic usually forms prominent tubercle.

[j] Produced as a small promontorium process in didelphids.

"eutherians." However, most fossil taxa in question (e.g., leptictids) show a number of special features (e.g., entotympanic bulla) found only in some Recent Eutheria. The assignments of *Asioryctes, Barunlestes* (epipubic bones present), or *Kennalestes* to the Eutheria, however, remain open to further inspection (see comments in Novacek, 1982b).

COHORT EDENTATA CUVIER 1798, NEW RANK

DEFINING CHARACTERS: Frontal ventrally expanded in orbit to contact small palatine; orbitosphenoid small and crowded by other orbital elements; posterior lacerate foramen large, circular in outline for common exit of nerves IX, X, XI and jugular vein; subarcuate fossa very shallow depression; paroccipital process very weak or absent; lacrimal tubercle present; foramen rotundum distinctly separate from sphenorbital fissure; depressions for rectus capiti muscles on ventral basisphenoid very weak or absent; anterior teeth small, reduced in number or absent; seven or more ethmoidal scrolls; greatly enlarged epitympanic sinus.

COMMENTS: The association of pholidotans with xenarthrans harks back to Linnaeus's (1758) concept of the Bruta, although the latter grouping was much more inclusive. Linnaeus allied elephants and manatees along with anteaters, sloths, and pangolins (definition: "front teeth none either above or below; gait more or less awkward [incessus ineptior]," see Gregory, 1910, p. 31). Owen (1842) took Bruta to include tubulidentates, as well as xenarthrans and pholidotans.

The possibility of close relationship between pholidotans and xenarthrans has been largely dismissed in mammalian systematic work of this century. Simpson's (1945, p. 195) remarks amply reflect the consensus:

> It cannot be denied that the Xenarthra and the Pholidota may have had a common ancestry, but this has not been demonstrated as a fact or even as a real probability, and if it be true, then the common ancestry must be exceedingly remote (probably before edentates were differentiated clearly from proto-insectivores). Thus ordinal separation is fully justified and superordinal (or ordinal) union is at least as likely to be wrong as right.

Early on, it was suspected that pholidotans took an "edentate-like" form simply because they converged on myrmecophagiids with respect to ant-eating habits. However, it is clear (and somewhat surprising to me) that pangolins share a number of special traits with *all* edentate groups (see above diagnosis). Although some of the "defining" characters are found in several other mammals (e.g., lacrimal tubercle, reduction of teeth, distinct foramen rotundum, etc.), the combination of features provides a reasonably firm definition. Moreover, there are details of musculature peculiar to *Manis* and edentates (Windle and Parson, 1899) that invite modern comparative study.

These conclusions go against the grain of several recent studies (Emry, 1970; McKenna, 1975; DeJong, 1982), including my own brief review of the problem (Novacek, 1982b). Molecular sequence data from alpha crystallin lens proteins fail to show a close association of pangolins with xenarthrans, al-

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[k] In macroscelideans, inferior ramus of stapedial exits skull in a bony tube distal to its passage through the crura of the stapes.

[l] Carnivore condition based on structure of miacids.

[m] The primitive therian and marsupial condition is probably one where the stapedial branch is weak or absent, but in some didelphids the stapedial may have a pathway similar to that in leptictids.

[n] Defined as branches proximal to split of the stapedial (or its passage through the stapes) and the portion of the common internal carotid and promontory that courses over the promontorium.

[o] Carotid tubing claimed not to be homologous in primates and tupaiids (Cartmill and MacPhee, 1980).

[p] Fibrous tympanohyal contact with promontorium in chiropterans.

[q] Tubercle present, but not medially oriented in edentates.

[r] Mastoid tubercle very elongate, thin in tubulidentates.

[s] Condyles secondarily modified, rounded in erinaceines.

[t] Stapes not preserved in leptictids but morphology inferred from pathway and size of stapedial artery (see text).
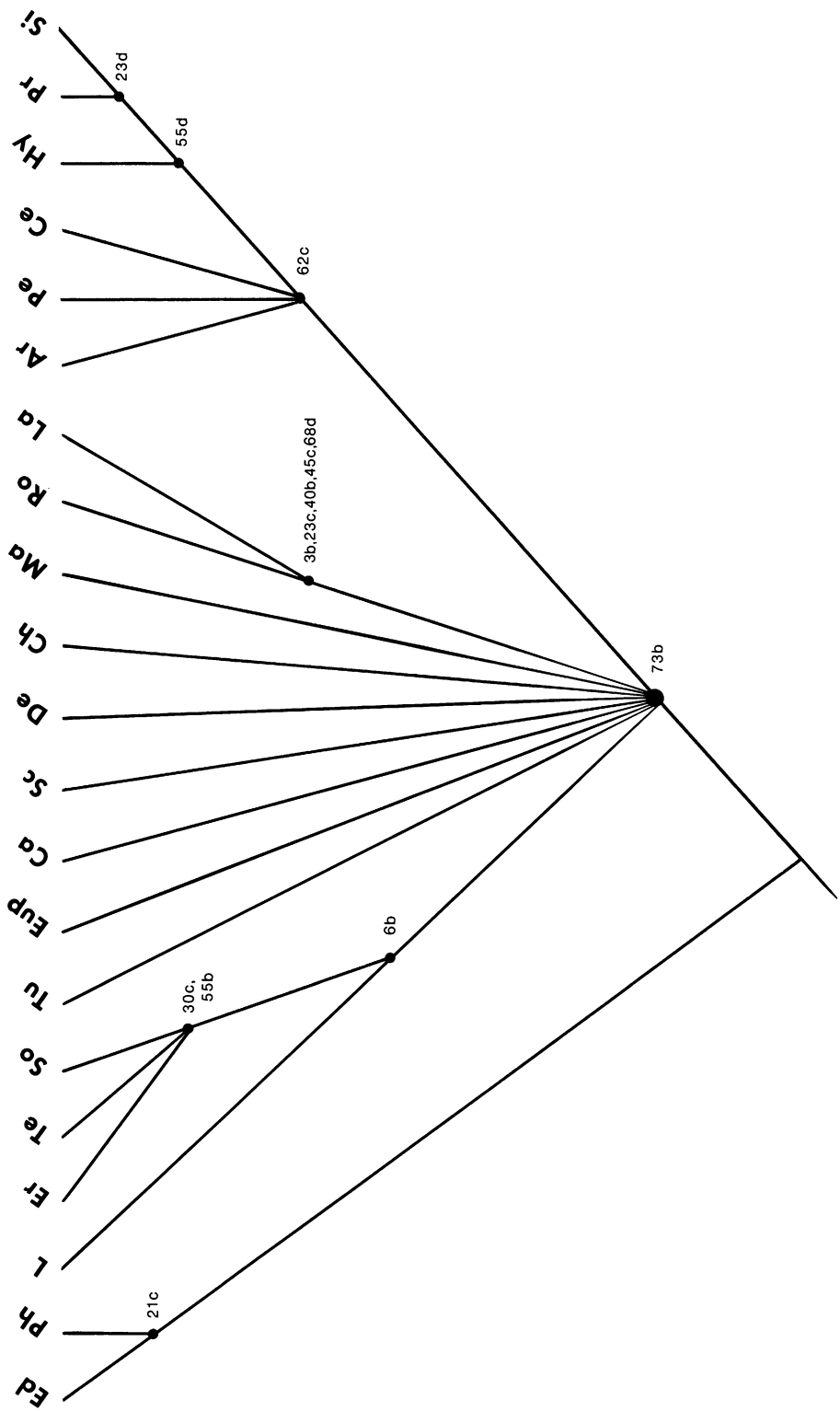
Fig. 31. Cladogram for major eutherian groups based on uniquely derived characters. Acronyms for groups and numbers for characters are defined in table 3. CI, consistency index (the ratio of the number of steps that define monophyletic groups over the total number of steps for the cladogram), 1.00.
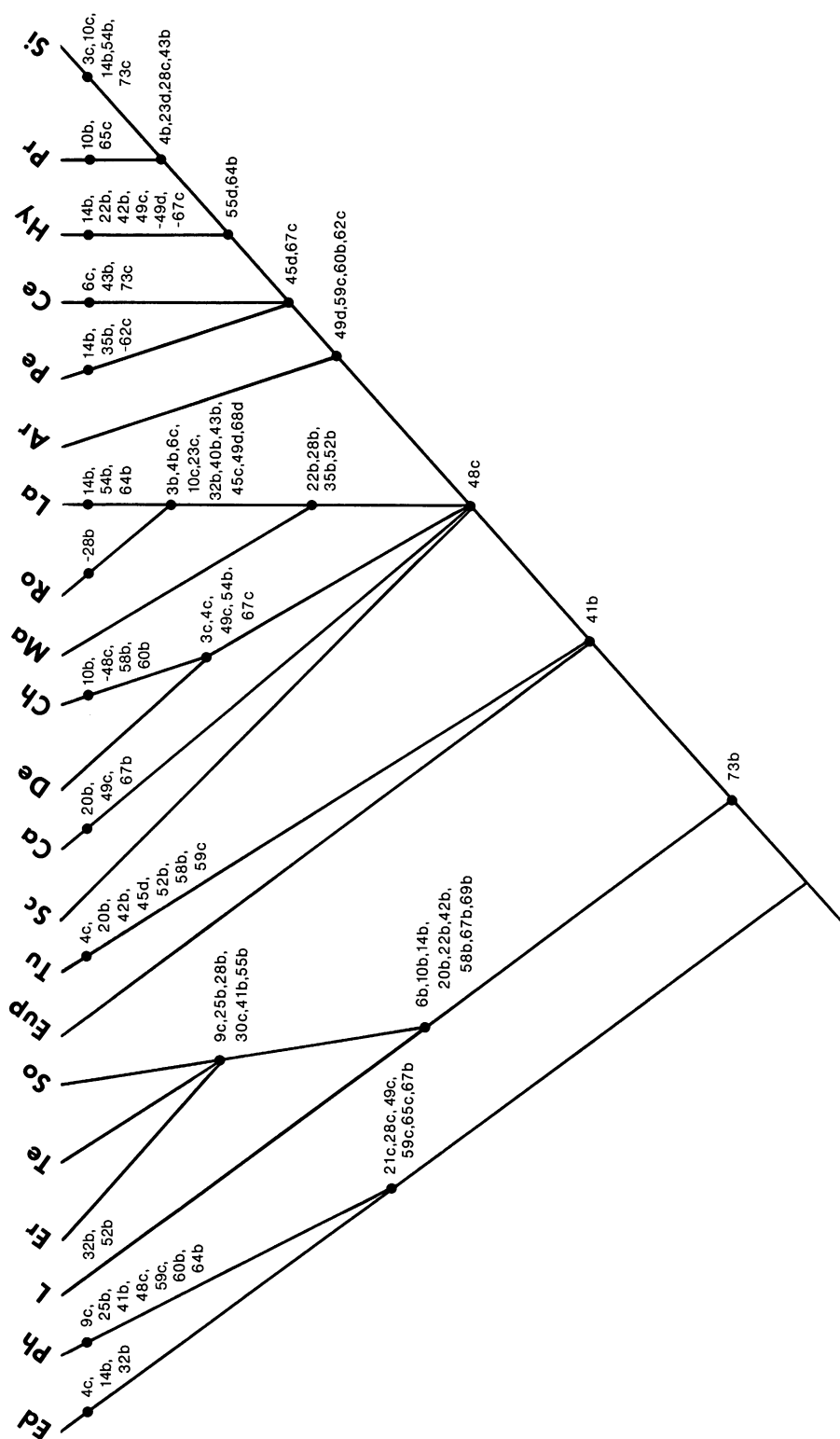
FIG. 32. Cladogram for major eutherian groups based on uniquely derived characters or characters showing relatively low homoplasy (46 traits). Consistency index (CI) is 0.43 (see fig. 31). Symbols are defined in table 3. Minus sign indicates character reversal.
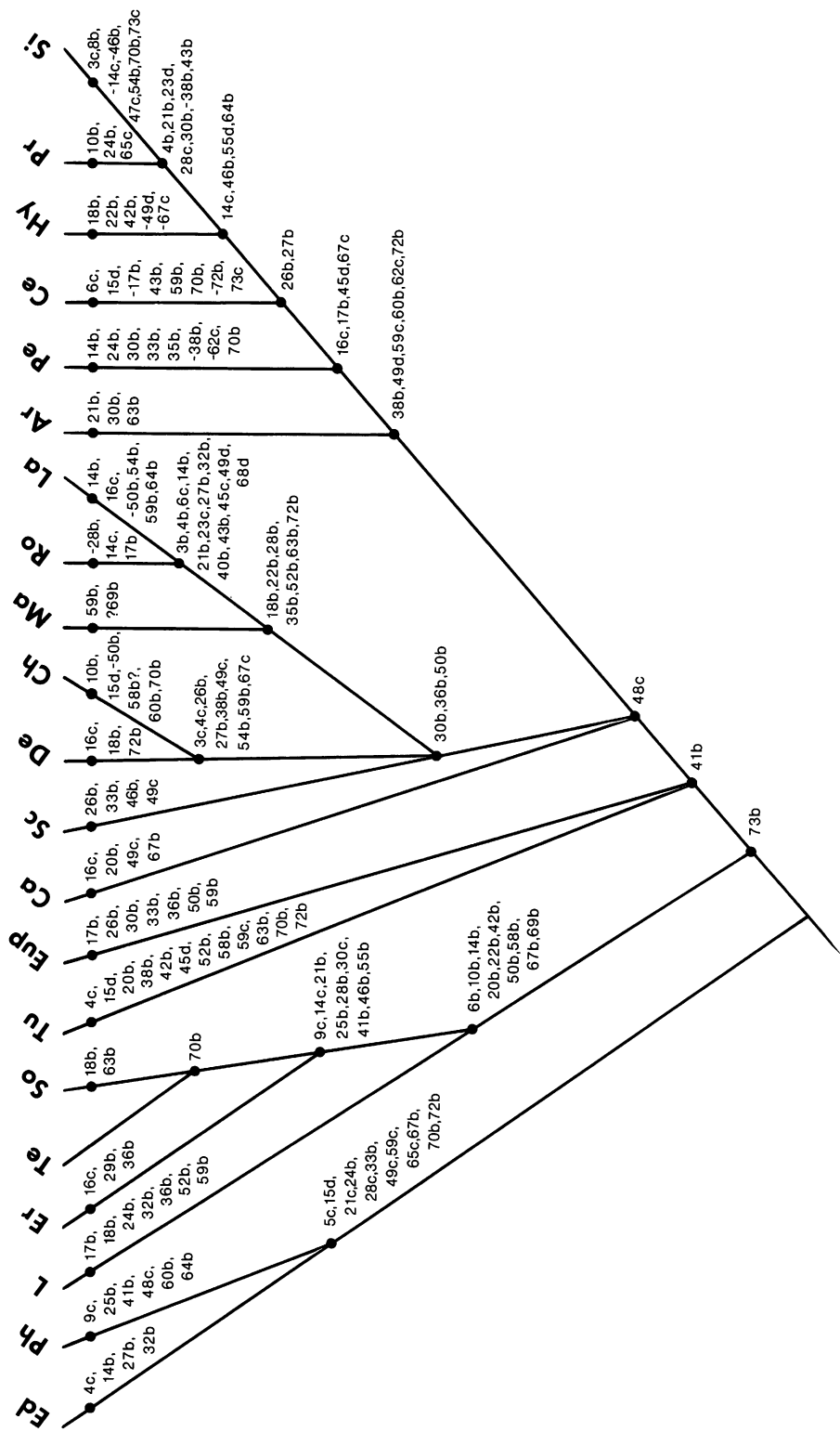
FIG. 33. Cladogram for major eutherian groups based on 67 character states from cranial data set. Consistency index (CI) is 0.35 (see fig. 31). Symbols are defined in table 3. Minus sign indicates character reversal.

though alternative relationships are hardly more definitive (see DeJong, 1982; Goodman et al., 1982). Emry's (1970) detailed analysis of fossil palaeanodonts and pholidotans led him to argue for a close relationship between these groups, but he rejected Matthew's (1918) claim that pholidotans and xenarthrans were closely related through an ancestral palaeanodont stock. Rose (1978), in a detailed review of the epoicotheriids and other palaeanodonts, followed Emry (1970) in linking these groups with pholidotans. He did not, however, exclude xenarthrans from this association. Assessing the morphology of *Amelotabes,* Rose (1978, p. 673) stated:

> The Paleocene *Amelotabes* is older and more primitive than any palaeoanodont known previously. Unfortunately, nothing is known of its cranial or skeletal anatomy, but its mandibular and dental morphology is sufficiently primitive that from something like it xenarthrans as well as pholidotans could have arisen. At this time, the scant fossil evidence precludes a more definitive conclusion, although it suggests once again the possibility that the Pholidota and the Xenarthra are related through common ancestry.

Rose (ibid.) further argued that palaeanodonts might ultimately derive from pantolestids. Since the relationships of the latter are uncertain, this claim has moot significance to the question of pholidotan-xenarthran affinities. At the very least, the fossil evidence fails to contradict the concept of Edentata argued for here (see also Szalay, 1977).

COHORT EPITHERIA MCKENNA, 1975

DEFINING CHARACTERS: Stapes horseshoe-shaped with well-separated stapedial crura; uterus and vagina well differentiated; more than two cochlear turns; small coracoid, no septomaxillary.

COMMENTS: Doran (1879) long ago noted that pangolins, bradypodids, and some dasypodids have columnlike stapes as adults. This condition, also known in several marsupials and in monotremes (Fleischer, 1973) appears to be modified into a broadly open, horseshoe-shaped stapes in the vast majority of eutherians (the anomalous, massive columnar stapes of marine mammals are likely secondary derivations). The variation and

development of this element and its use in defining epitheres is discussed in Novacek (1982b, pp. 17–18). (In leptictids there is no stapes preserved, but a typical "horseshoe," as in other epitheres, may be inferred from the pathway of the stapedial artery.) The primitive therian condition was likely one wherein the columnar stapes had a small perforation, but did not develop a very large opening and stirruplike crura for the stapedial artery (Archibald, 1979; Novacek, 1982b).

Other epithere characters are less certain. Broad-based comparative study of the reproductive tract is sketchy. The septomaxillary is only clearly present in Dasypodidae. Its presumed homology with the reptilian septomaxillary (Broom, 1906) needs further scrutiny.

Epitheres then include all of the major orders of Recent eutherians except the pholidotes and edentates. Further subdivisions of Epitheria constitute separate groupings of ungulates, macroscelidids-lagomorphs-rodents, bats-dermopterans, and leptictid-lipotyphlans. The remainder of the orders show either too few similarities or too many conflicting traits to justify a close association with one or another of these larger groups (fig. 32). These taxa, denoted here as Epitheria incertae sedis, include Tubulidentata, Carnivora (and their extinct relatives, the †Creodonta), Primates, Scandentia (tree-shrews), †Tillodontia, and †Taeniodonta.

SUPERORDER INSECTIVORA ILLIGER, 1811, NEW RANK

DEFINING CHARACTERS: Broad maxillary-frontal contact in facial region; infraorbital canal relatively short; maxilla intrudes into orbit, nearly or extensively contacting frontal; large common recess for separate sphenopalatine and dorsal palatine foramina; lacrimal confined to orbit or antorbital rim; well-defined Glaserian fissure in lateral roof and anterior wall of tympanic cavity; prominent petrosal ridge or crest on promontorium cochleae; large, ossified mastoid tubercle (incorporates tympanohyal) with distinct ventral fossa, medially projecting and nearly contacting promontorium; anterior border of ventral occipital condyle with strong sigmoid outline.

COMMENTS: The justification for allying

leptictids with lipotyphlan insectivores is discussed above. Early statements to this effect were weakly supported. The greatest potential contradiction to this association is the apparent derived similarity between leptictids and macroscelideans in several cranioskeletal traits (Novacek, 1980, fig. 26, and remarks above). However, some of these similarities reflect cursorial specializations not present in early leptictids. Moreover, macroscelideans share many apomorphs with lagomorphs, rodents, and anagalids (Novacek, 1982b, fig. 1, and remarks above) not common to leptictids.

It should be emphasized that this allocation of leptictids to Insectivora does not indicate that leptictids are the nearest sister group of erinaceoids, as was claimed in most early studies (Gregory, 1910). Instead, leptictids are here recognized as the nearest sister group to all Lipotyphla (table 4).

ORDER †LEPTICTIDA MCKENNA, 1975, NEW RANK

DEFINING CHARACTERS: Small, triangular exposure of the parietal on the posterior occiput; deep antorbital fossa for snout muscles; inferior ramus of the stapedial artery exits tympanic cavity near forward apex of facial canal (posterior to alisphenoid-petrosal suture); alisphenoid broadly exposed in orbital wall; bulla solely entotympanic; short alisphenoid canal with anterior exit well behind sphenorbital fissure; subarcuate fossa very (rather than moderately) excavated; elongated femoral trochlea; incipient distal fusion of tibia-fibula (more markedly fused in later leptictids); reduction to two upper incisors; molariform last premolar (P$_3^5$); manubrium of sternum (where known) "inflated" with distinct, robust keel.

COMMENTS: Many of the above-listed characters are present in one or a few other mammals. However, under the relationships favored here, such features were independently acquired in leptictids. Some characters are very distinctive. The triangular parietal on the occiput is known in all well-preserved leptictid skulls, but I am not aware of any other mammals that show comparable shape of this element. The molariform posterior premolars set leptictids apart from most other Mesozoic and Early Tertiary groups with sectorial "in-

sectivorous" dentitions. A deep subarcuate fossa is a likely primitive therian condition, but the extreme to which this fossa is excavated in leptictids is found in few other mammals (Cifelli, 1983; see also table 3, character 59b herein). The posterior exit of the ramus inferior of the stapedial artery is also found in macroscelideans, rodents, and possibly some bats.

The Leptictida as used here provisionally includes *Gypsonictops* (not known from skulls or skeletons), but does not comply with McKenna's (1975) additional inclusion of anagalids, macroscelideans, and lagomorphs. Nor does the Leptictida here equal Szalay's (1977) Leptictimorpha, to which he allocated some "palaeoryctids," pantolestids, taeniodonts, and microsyopids, as well as Tertiary leptictids and *Gypsonictops*. A higher (family-level?) category cannot yet be firmly established for *Gypsonictops*. This genus may be paraphyletic; it has not been defined by unique characters that unite all its named species.

ORDER LIPOTYPHLA HAECKEL, 1866 (MCDOWELL, 1958)

DEFINING CHARACTERS: Orbital wing of palatine very small, confined to floor of orbit; maxilla in orbit strongly expanded, broadly contacts frontal and completely excludes palatine from contact with lacrimal; jugal reduced or absent, does not contact lacrimals; fenestra rotunda partly concealed ventrally, opening into a pit defined posteriorly by the raised rim of the petromastoid; no true postglenoid process (replaced in some lipotyphlans by the expanded entoglenoid process of the squamosal); optic foramen much smaller than sphenorbital fissure; suprameatal foramen absent; pubic symphysis weak or absent; no intestinal caecum.

COMMENTS: The above characterization follows McDowell's (1958) excellent analysis of lipotyphlans. Some of these traits (e.g., loss of the caecum) were noted in Haeckel's (1866) original designation of the Lipotyphla. The classification favored here retains formal recognition of Lipotyphla and a higher category, Insectivora (as opposed to recent moves to equalize these terms—see McKenna, 1975; Novacek, 1980, 1982b). The breakdown of the Lipotyphla (see table 4) corresponds with

the classification described in detail by McDowell (1958). However, McDowell's alliance of soricoids and tenrecoids (in Soricomorpha) and his grouping of talpids with erinaceids (in Erinaceomorpha) is open to further consideration. Also included within lipotyphlans are a number of fossil families: the †Dormaaliidae, †Apternodontidae, †Geolabididae, †Dimylidae, and possibly, certain †"palaeoryctids."

SUPERORDER VOLITANTIA ILLIGER 1811, NEW RANK

DEFINING CHARACTERS: Incisive foramina coalesce, due to modification of the premaxilla; posterodorsal process of premaxillary weak or absent; maxillary-premaxillary suture in nasal-facial exposure nearly vertical; fenestra rotunda opens posteriorly (rather than posterolaterally); posterior lacerate foramen very extensive, coalesces with basicochlear fissure that partially separates promontorium cochleae from basisphenoid and basioccipital; ectotympanic contributes to bulla; patagial membrane continuous between digits; membrane spans between tail and hindlimb; humeropatagialis and coracocutaneous muscles insert into plagiopatagium; marked elongation of fore- and hindlimb; ulna (and radius?) distally reduced; scaphoid-lunate elements fused; extensive pelvic-sacral fusion; greater trochanter smaller than femoral head.

COMMENTS: The grouping of bats and flying lemurs has not been a popular notion. Winge (1941) was doubtless influential here. He argued that many of the similarities between these groups cited in a detailed study by Leche (1886) were merely correlated with their volant lifestyles. However, it does not necessarily follow that such "wing characters" are the result of convergence. Other mammalian "gliders" do not share with dermopterans a chiropteran-like construction of the appendages and flight membranes. Moreover, characters independent of wing structure support the monophyly of the Volitantia (see also Novacek, 1982b). The problem awaits more definitive study (A. Wyss, in prep.).

One objection to the Volitantia might stem from evidence of fossil tarsal elements. Szalay and Drawhorn (1980) described astragali and calcanea from early Eocene faunas that had very dermopteran-like features (e.g., extension of sulcus astragali; deep medially offset cuboid pivot on calcaneum and other features). These authors suggested plausible associations of the isolated foot bones with unknown fossil species of dermopterans, and raised the possibility that the elements might belong to microsyopids. Since the latter have been linked with primates (e.g., Bown and Gingerich, 1973), one might envision a dermopteran-primate affinity via a microsyopid-like ancestor. This concept would either exclude a special grouping for Volitantia or at least broaden a group to include bats, dermopterans, primates, and microsyopids, an assemblage approaching the Archonta (Gregory, 1910) in content. However, the special relationship of microsyopids with primates is poorly established (Szalay, 1969). The fact that microsyopids had dermopteran-like foot bones might merely suggest that this group represents an archaic relative of flying lemurs whose origin predates the divergence of bats and dermopterans. Bat tarsal elements are highly derived and rather bizarre (Novacek, 1980); thus far, they have not helped in identifying the relatives of this order.

SUPERORDER ANAGALIDA, SZALAY AND MCKENNA, 1971, EMENDED

DEFINING CHARACTERS: (Asterisk indicates features not well-known in anagalids.) One or more foramina for masseteric and buccinator nerves present*; orbital wing of frontal restricted dorsally by enlarged orbitosphenoid*; inferior ramus of stapedial exits tympanic cavity posteriorly in an enclosed bony tube (macroscelidids) or through a foramen at apex of facial canal*; jaw condyle relatively high in position; lacrimal lacking strong facial process; posterior margin of palate biconcave with strong postpalatine spine; narrow restriction of supraoccipital on dorsal roof of skull; canine small or absent; molariform "tendencies" of last premolars; wear pattern of molars indicate crushing or grinding occlusion; postglenoid process small or absent; auditory bulla with partial contribution from ectotympanic; lateral border of astragalar trochlea enlarged with distinct crest.

COMMENTS: Anagalida is a broadly defined clade of probable Asian origin. Some of the above-noted characters for Anagalida parallel features in leptictids but the closer relationship of the latter with lipotyphlans seems more compelling. Anagalida here equals McKenna's (1975) grandorder Anagalida with the addition of the Rodentia. Other members of the Anagalida are, potentially, the Eurymylidae [the Eurymylidae may be paraphyletic and include both lagomorph (*Mimotona*) and rodent (true eurymylid) relatives (Li and Ting, 1985; McKenna, personal commun.)]; Pseudictopidae (lagomorph relatives, fide Sulimski, 1969; McKenna and Bleefeld personal commun.), and Zalambdalestidae (see McKenna, 1975, fig. 3; Novacek, 1982b, fig. 1). However, these groups, like anagalids, are incompletely known from relevant cranioskeletal information. Kielan-Jaworowska's (1979) rejection of a connection between zalambdalestids and macroscelideans or lagomorphs seems a bit strong. While she correctly noted the distinctive character of the skeleton of zalambdalestids, a residuum of derived skeletal features shared with elephant shrews and lagomorphs is not necessarily the result of convergence. However, a convergence explanation is easier to apply in the case of leptictids, where features associated with cursorial locomotion are not clearly known for early members of this group (Novacek, 1980).

GRANDORDER GLIRES LINNAEUS, 1735,
NEW RANK

DEFINING CHARACTERS: Incisive foramina large, elongate, and set posteriorly in palate; narrow contact of maxilla with frontal in facial region due to confinement by premaxilla and lacrimal; posterodorsal process of premaxilla elongate, extending to frontals; lacrimal foramen confined to orbit but just adjacent to antorbital rim, faces directly lateral; glenoid fossa oriented anteroposteriorly; pseudopostglenoid foramen opens laterally behind zygoma in squamosal-temporal region; bulla virtually entirely ectotympanic; two or three closely spaced hypoglossal foramina present; broad dorsal exposure of alisphenoid in orbital wall; bony lateral wall of epitympanic recess formed by fusion of teg-

men tympani of petrosal and ectotympanic; palatine exposure in orbital wall somewhat confined by maxilla and alisphenoid; ethmoidal foramen positioned anteriorly, above posterior palate; number of lower incisors reduced; one pair of incisors enlarged above and below; stylar shelves on upper molars markedly reduced; discoidal, hemochorial placenta present; abembryonic portion of bilaminar omphalopleure persists through early or complete duration of gestation; allantoic vesicle small or vestigial.

COMMENTS: Evidence for Glires is discussed extensively in more recent papers by Novacek (1982b, 1985) and Luckett (1985). Despite the general ambivalence for this grouping (see remarks in Simpson, 1945), it remains perhaps the most compelling of the supraordinal categories of placental mammals. Corroborative evidence comes from unique aspects of the skull and fetal development as listed above. New fossil evidence from China shows that rodents and lagomorphs may share a common ancestry with a number of archaic Asian lineages (Li and Ting, 1985).

SUPERORDER UNGULATA LINNAEUS 1766,
NEW RANK

DEFINING CHARACTERS: Weak occipital exposure of the mastoid; subarcuate fossa shallow or absent; occipital-mastoid foramen absent; bulla largely a combination of entotympanic and ectotympanic elements; squamosal-sinus canals vestigial or absent; mandibular condyle relatively high; (primitive forms) with bunodont molar crowns (greatly modified in various lineages); (primitive forms) with consistently well-developed posterolingual cusp (hypocone?) on upper molars; (primitive forms) with swollen metaconids on lower molars and elongated talonid on M_3; terminal phalanges elongated but not fissured (phalanges modified as hooves in many lineages).

COMMENTS: Gregory (1910) recognized the many "ungulate" lineages as united by a remote but single origin. Simpson (1945), however, subdivided "ungulates" into several superorders without explicitly grouping them under one category. The evidence for the monophyly of this great radiation is admit-

tedly sketchy, although the basic pattern from which various lineages derive is well represented by assorted early "condylarths" (see discussion in Gregory, 1910). I thus endorse McKenna's (1975) resurrection of Ungulata, with one modification: namely the exclusion of the tubulidentates from this supergroup. Even though an ungulate association of tubulidentates is weakly supported by molecular data (DeJong, 1982), the ear region of aardvarks is very primitive (Novacek, 1977b, 1982b) compared with that of typical ungulates (e.g., a large ossified bulla is absent). Moreover, the only defining skull character for ungulates shared with tubulidentates is the very shallow subarcuate fossa. Therefore, the Tubulidentata are regarded here as Epitheria incertae sedis, until more detailed work demonstrates otherwise.

GRANDORDER MERIDIUNGULATA MCKENNA, 1975, NEW RANK

COMMENTS: Recognized here is McKenna's (1975) grouping of the South American litopterns, notoungulates, astrapotheres, xenungulates, and pyrotheres within the Meridiungulata. However, this category lacks an explicit definition, and its recognition can only be regarded as highly provisional. As Simpson (1945) noted, the South American isolation of these groups suggests their derivation from a very archaic "condylarth" stock. The striking similarities between South American ungulates, early equids, and other forms of the northern continents have been cited as classic examples of convergence. This theory could, however, use a better argument for the monophyly, and separate origin, of the South American group. Perhaps a stronger definition will come with continued studies of the tarsus and other aspects of the ungulate postcranial skeleton (e.g., Cifelli, 1983).

GRANDORDER PAENUNGULATA SIMPSON, 1945, NEW RANK

DEFINING CHARACTERS: Fenestra rotunda with vertical orientation, partly shielded ventrally by expansion of promontorium cochleae; lambdoidal crest weak and occiput expanded; post-tympanic ridge of squamosal very weak or absent; serial arrangement of

carpal bones; loss of lunar-unciform contact; lunar articulates distally mainly with magnum.

COMMENTS: Simpson's (1945) Paenungulata has been upheld by recent studies of the dentition, skeleton, and protein sequences (Shoshani et al., 1978; DeJong, 1982; Novacek, 1982b). However, the alliance of tubulidentates with these groups, as suggested by Shoshani et al. (1978) and DeJong (1982), is not supported here. McKenna (1975) suggested that hyracoids were most closely related to perissodactyls, but the balance of characters at present seems to favor the alliance of hyracoids with proboscideans and sirenians. It should be noted that Simpson's (1945) original use of Paenungulata was more inclusive, as it also associated the extinct Pantodonta, Dinocerata, Pyrotheria, and Embrithopoda. Such allocations for these archaic groups are by no means certain, and their affinities warrant further study.

MIRORDER TETHYTHERIA MCKENNA, 1975

DEFINING CHARACTERS: Lacrimal foramen opens into common orbital recess for posterior aperture of infraorbital canal; posterodorsal process of premaxilla in broad contact with frontal; ventral expansion of frontal in orbital wall, orbitosphenoid very confined; lateral wall of epitympanic recess formed by composite of squamosal, petrosal, and ectotympanic; palatine confined to floor of orbit; marked retraction of nasals; zygoma robust and laterally expanded; bilophodont molars with tendency to form additional lobe on posterior part of cingulum; ?tendency for forward displacement of worn cheek teeth and replacement by next more posterior tooth of the same dental family (last condition is probably not primitive for this group; it could be acquired independently within Tethytheria several times).

COMMENTS: The association of proboscideans with sirenians actually dates back to DeBlainville's (1834) grouping of these forms under his order "Gravigrades." With the inclusion of the extinct Desmostylia, use of McKenna's mirorder Tethytheria seems appropriate. However, Gravigrades may still prove useful to incorporate the modern tethytheres, if these forms are demonstrably closer to each other than to desmostylians. The

problem has been under consideration by Domning, Ray, and McKenna (MS).

Gregory (1910, p. 407) believed the "Gravigrades" to be well supported. He emphasized features of the Early Tertiary *Moeritherium* from North Africa that showed its "intermediate position" between proboscideans and sirenians. He also suggested, following Andrews (1906), that *Moeritherium* was a fair approximation of the common ancestor of these groups. Some of the characters Andrews (ibid.) cited for this close relationship between proboscideans and sirenians are primitive ones (e.g., abdominal testes). Nevertheless, these groups are clearly linked by specializations in dental, cranial, and possibly fetal structure (Shoshani et al., 1978). Hence, the close relationship of "tethytheres" has attracted little skepticism.

A potential problem for these relationships is the existence of five premolars in the adults of some Eocene sirenians (Domning et al., 1982). This condition seems a retention of the primitive premolar number of eutherians (McKenna, 1975; remarks above). The implications of this evidence are that (1) sirenians are an archaic branch of eutherians that retain a tooth lost at least once in the derivation of all other modern Eutheria, (2) the existence of a "fifth" premolar in these sirenians is the result of a peculiar, derived pattern in dental ontogeny (e.g., supernumerary tooth eruption); or (3) sirenians simply retain a primitive dental condition modified several times in the phylogenesis of other eutherian clades. The preponderance of morphological evidence, which suggests a close affinity between sirenians and other paenungulates, favors the third possibility. However, this argument would admit an uncomfortable degree of parallelism in the loss of a fifth premolar. Note that none of these alternatives requires the acceptance of McKenna's (1975) superclade Tokotheria, which is based on the retention of DP_5^5 and the loss of M_3^3.

CONCLUSIONS

This study has been built on the premise that homology, as a means of identification of monophyletic groups, is most effectively discovered through studies of character distribution. One criticism of an approach so

TABLE 4
A Classification for Higher Categories of Recent and Selected Fossil Eutheria
For details see text.

Class Mammalia Linnaeus, 1758
  Subclass Theria Parker and Haswell, 1897
    Infraclass Eutheria Gill, 1872 (as modified by Huxley, 1880)
      Cohort Edentata Cuvier, 1798
            Order Xenarthra Cope, 1889
            Order Pholidota Weber, 1904
      Cohort Epitheria McKenna, 1975
        Superorder Insectivora Illiger, 1811, new rank
            †Order Leptictida McKenna, 1975, new rank
            Order Lipotyphla Haeckel, 1866 (McDowell, 1958)
                Suborder Erinaceomorpha Gregory, 1910 (Saban, 1954)
                Suborder Soricomorpha Gregory, 1910 (Saban, 1954)
                Superfamily Tenrecoidea Simpson, 1931
                Superfamily Soricoidea Gill, 1872
        Superorder Volitantia Illiger, 1811, new rank
            Order Dermoptera Illiger, 1811
            Order Chiroptera Blumenbach, 1779
        Superorder Anagalida Szalay and McKenna, 1971, emended
            Order Macroscelidea Butler, 1956 (may include Anagalidae fide McKenna, 1975)
          Grandorder Glires Linnaeus, 1735, new rank
            Order Rodentia Bowdich, 1821
            Order Lagomorpha Brandt, 1855
        Superorder Ungulata Linnaeus, 1766, new rank
            †Order Arctocyonia Van Valen, 1969
            †Order Dinocerata Marsh, 1873
            †Order Embrithopoda Andrews, 1906
            Order Artiodactyla Owen, 1848
            Order Cetacea Brisson, 1762
            Order Perissodactyla Owen, 1848
       †Grandorder Meridiungulata McKenna, 1975, new rank
          Grandorder Paenungulata Simpson, 1945, new rank
            Order Hyracoidea Huxley, 1869
          Mirorder Tethytheria McKenna, 1975
            Order Proboscidea Illiger, 1811
            Order Sirenia Illiger, 1811
            †Order Desmostylia Reinhart, 1953
      Cohort Epitheria incertae sedis
            Order Tubulidentata Huxley, 1872
            Order Carnivora Bowdich, 1821
            Order Primates Linnaeus, 1758
            Order Scandentia Wagner, 1855
            †Order Tillodontia Marsh, 1875
            †Order Taeniodonta Cope, 1876

explicitly based on comparative analysis, is that it often forsakes an in-depth understanding of characters that comes with careful paleontological, functional, population, genetic, or other investigations. But any use of such information in systematics is undercut if the distribution of a trait (both its adult expression and its ontogenetic history) is poorly or erroneously known. Thus, a comparative emphasis fosters, rather than denies, other approaches to the study of organisms and their features. It provides a framework and a starting point for further inquiry.

Even with this high regard for the study of character distribution, things go awry. Mistakes in even the simplest mapping exercises occur. Hence, studies of character diversity among organisms are in a state of constant revision. These revisions, in turn, produce new biological classifications. The need for continual revision reflects the varying quality of information on different characters. That is, some characters are better known than others with regard to their "true" similarity among taxa, their distribution at different hierarchical levels (and, coincidentally, their tendency for variation in the lowest taxa considered), and their ontogenetic histories. Systematics requires a compromise here. One must choose a place between practicing the most rigorous selection of "profoundly understood" characters and opting for "all things considered" an approach like those advocated in the most aggressively phenetic techniques. A particular compromise solution is used here to revise some previously mapped character distributions, discover some new ones, and argue for the following points:

1. Lepticids are, as formerly (but not lately) thought, the closest relatives of lipotyphlan insectivores.

2. There are two great divisions of placental mammals: one clade comprising edentates (and possibly pholidotans) and the other clade comprising all other eutherians.

3. There is compelling evidence for several other eutherian supergroups. These are bats–dermopterans, macroscelideans–rodents = lagomorphs, and artiodactyls–perissodactyls–cetaceans–hyracoids = proboscideans ≡ sirenians (additional hyphenation means relatively closer affinity).

Many of these groupings date back to the 19th century. It is, indeed, difficult to conjure the most unlikely higher-level taxa and not find a precedent for them. This seems as true of mammalian "superorders" as anything, because many of the struggles and false starts in systematics are well exemplified in the early fascination with mammalian classification (see Gregory's 1910 superb review on the subject). If one can see a contribution of this and related works, it lies mainly in the proposed resolution of old problems (see also Gaffney, 1983). In addition, the impetus for this study was the impression that mid to late 20th century treatments of higher mammalian classification are depauperate in explicit statements of homology derived from surveys of diverse characters and taxa. The definitions and character tables presented herein are meant to allow others to focus their interests on the characters. I have no doubts that will happen. A growing group of systematists have taken a more rigorous approach to comparative biology and its implications for organismic classification.

APPENDIX: WAGNER TREES

Figures 32 and 33 are attempts to develop the most parsimonious cladogram for selected characters in table 3, without the aid of computer algorithms. These attempts are compared here with Wagner Trees (Farris, 1970) generated by the program in PHYSYS (Mickevich and Farris, 1982; phylogenetic analysis system PHYSYS, FORTRAN V software system of cladistic and phenetic algorithms). A WAG.S. computer run on the 46 character states considered in figure 32 produced a cladogram shown in figure 34. The geometries of the two cladograms display close correspondence. The Wagner Tree shows greater resolution (17 nodes) and is more parsimonious [number of steps (tree length) = 95, consistency index (CI) = 0.48] than the version shown in figure 32 (14 nodes, 107 steps, CI = 0.43).

The most significant discrepancy between the two results is the placement in the Wagner Tree of the edentate-pholidotan clade within a larger set of taxa including carnivorans, chiropterans, dermopterans, and scandentians. In contrast, figure 32 shows the edentate-
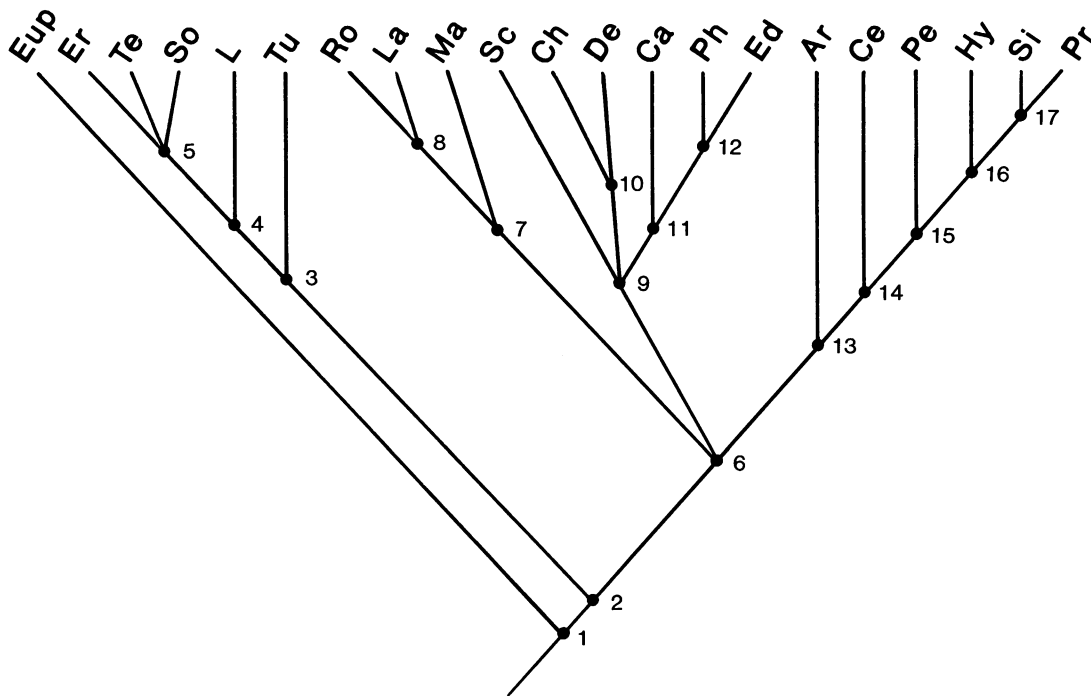
FIG. 34.   Cladogram for major eutherian groups generated by PHYSYS algorithm for computing Wagner Trees. Data are 46 cranial traits also used in figure 32. Consistency index (CI) is 0.48. Numbers refer to nodes given with character states in text. Acronyms for groups are defined in table 3.

pholidotan clade as the sister group of all other eutherians. The main reason for the discrepancy appears to be the secondary reversal of the stapes character (73) at node 12 in the Wagner Tree. In the "free-hand" version, the stapes condition in edentates and pholidotans is simply scored as a primitive retention. Nodes 9, 11, and 6 of the Wagner Tree in figure 34 are weakly supported (see below). Therefore, the position of edentates and pholidotans at a lower level in the cladogram is less than compelling.

This suspicion is borne out by the results of a WAG.S. run of 104 character states (fig. 35), which represent a high percentage of all the distribution data (147 character states) provided in table 3. Here, many characters are considered in addition to the 46 states analyzed for the results shown in figures 32 and 34 (in fig. 33, 67 character states are considered). Figure 35 shows higher resolution (20 nodes) but less parsimony (number of steps = 327, CI = 0.32) than other solutions. These statistics support the above assertion

that many of these additional characters are of ambiguous polarities, or are highly homoplastic. Nevertheless, the geometry of figure 35 is remarkably close to that of figures 32 and 33. Note that in this more robust solution the edentate-pholidotan clade once again is identified as the sister-group of all other eutherians. Note also the alliance of tubilidentates with other "ungulates" and the grouping of an archontan clade (sensu McKenna, 1975). Again, data supporting these nodes are of interest, but are not compelling enough to promote changes in the classification (table 4).

Character distributions (see table 3) for the 46-character Wagner Tree (fig. 34) are as follows (minus sign indicates character reversal):

Node 1: Traits defining Eutheria discussed in text.
Node 2: 41b
Node 3: 20b, 58b
Node 4: 6b, 10b, 14b, 22b, 42b, 67b, 69b
Node 5: 9c, 25b, 28b, 30c, 55b
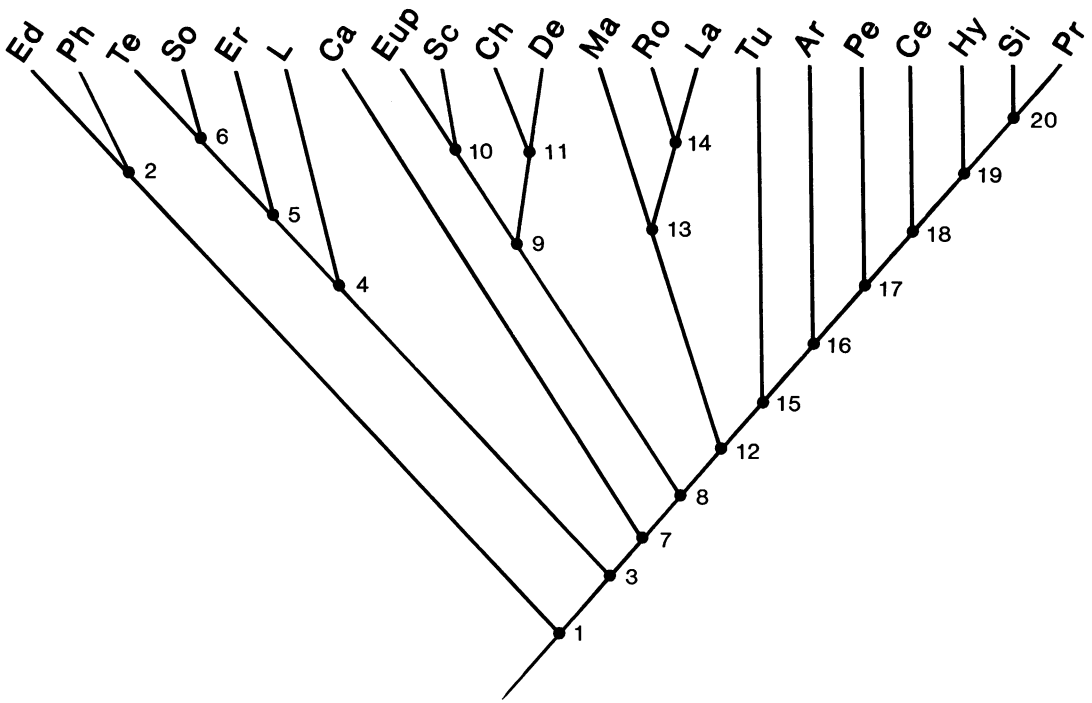Node 6: 48c
Node 7: 22b, 35b, 52b

FIG. 35. Cladogram for major eutherian groups generated by PHYSYS algorithm for computing Wagner Trees. Data are on 104 cranial traits taken from table 3. Consistency index (CI) is 0.32. Numbers refer to nodes given for character states in text. Acronyms for groups are defined in table 3.

Node 8: 3b, 4b, 6c, 10c, 23c, 32b, 40b, 43b, 45c, 49d, 68d
Node 9: 49c
Node 10: 3c, 4c, 54b, 67c
Node 11: 67b
Node 12: 21c, 28c, 65c, −73b
Node 13: 49d, 59c, 60b, 62c
Node 14: 45d, 67c
Node 15: 14b
Node 16: 55d, 64b
Node 17: 4b, 10b, 23d, 43b
Leptictids: 32b, −41b
Tubilidentates: 4c, 45d, 52b, 59c
Lagomorphs: 14b, 28b, 54b, 64b
Macroscelideans: 28b
Chiropterans: 10b, 58b, 60b, −48c
Carnivorans: 20b
Pholidotans: 9c, 25b, 59c, 60b, 64b
Edentates: 4c, 14b, 32b, −41b, −48c
Cetaceans: 43b, 73c
Perissodactyls: 35b, −62c
Hyracoids: 22b, 49c, −49d, −67c
Sirenians: 3c, 10b, 54b, 73c
Proboscideans: −14b, 65c

Character distributions (see table 3) for the 104-character Wagner Tree (fig. 35) are as follows:

Node 1: Traits defining Eutheria discussed in text.

Node 2: 5c, 11b, 15d, 21c, 24b, 28c, 33b, 49c, 51c, 65c, 70b
Node 3: 51b, 73b
Node 4: 6b, 10b, 14b, 20b, 22b, 42b, 50b, 58b, 69b
Node 5: 9c, 21b, 25b, 28b, 29b, 30c, 55b
Node 6: 39c, 70b
Node 7: 47b, 48c
Node 8: 30b, 57b, −67b
Node 9: 26b, 36b
Node 10: 11b, 33b, 37b, 44b, 50b, 52c, 53b, 66b
Node 11: 1b, 4c, 27b, 38b, 45d, 49c, 54b, 59b, 67c
Node 12: 63b, 65c, 71b, 72b
Node 13: 18b, 22b, 35b, 36b, 39b, 52b
Node 14: 3b, 4b, 6c, 8b, 10c, 13b, 21b, 23c, 27b, 32b, 40b, 43b, 45c, 49d, 68d
Node 15: −2b, 7b, 38b, 59c
Node 16: 49d, −56b, 60b
Node 17: 16c, 45d, −63b, 67c
Node 18: 1b, −7b, 8b, 26b, 27b, 59c
Node 19: 5b, 17b, 44b, 55d, 64b, 66b
Node 20: 2b, 4b, 10b, 21b, 23d, −29b, −38b, 39b, 43b
Edentates: 4c, 7b, 14b, 27b, 32b, 39b, −41b, 69c
Pholidotans: 1b, 9c, 15c, 16b, 23b, 25b, 31b, 37b, 40c, 44b, 47b, 48c, 57b, 59c, 60b, 64b, 72b
Tenrecoids: 1b, 47b, 49e

Soricoids: 18b, 19b, 43f, 46b, 63b

Erinaceomorphs: 1b, 16c, 19b, 24b, 34b, 36b, 39b, 46b, 49e, 57b

Lepticids: −2b, 5b, 9b, 12b, 17b, 18b, 23b, 24b, 32b, 34b, 36b, 37b, −41b, 44b, 59b, 61b, 65b

Carnivorans: 9b, 16b, 16c, 20b, 23b, 49c

Euprimates: 7c, 17b, 29b, −30b, −41b, −47b, −48c

Scandentians: 16b, 34b, 39b, 43d, 46b, 49c, −57b, 65b

Chiropterans: 9b, 10b, 15d, 16b, 20c, 37b, 43f, −48c, 58b, 60b, 70b

Dermopterans: −2b, 5b, 11b, 15c, 16c, 17c, 18b, 23b, 43d, 44b, 50b, 52c, 71b, 72b

Macroscelideans: 1b, 12b, 16b, 23b, 28b, 31b, 43d, 50b, −57b, 59b, 65b

Rodents: 17b, −29b, 34b, −51b, 51c, −57b

Lagomorphs: 11b, 14b, 16c, 17c, 20c, 28b, 44b, 54b, 59b, 64b

Tubilidentates: 1b, 4c, 5b, 15c, 15d, 19b, 20b, −30b, 37b, 44b, 45d, −47b, −48c, 52b, 58b, 66b, 70b

Artiodactyls: 9b, 16b, 20c, 21b, 39b, 62c

Perissodactyls: 14b, 17b, 20c, 24b, 33b, 34b, 35b, −38b, −51b, 70b

Cetaceans: 2b, 11b, 15c, 15d, −30b, 43b, −57b, 59b, 70b, −71b, −72b, 73c

Hyracoids: 11b, 14b, 18b, 22b, 23b, −30b, 39c, 43d, 46b, 49c, −49d, −51b, 56b, −67c, 69c

Sirenians: 3c, 10c, 11c, 14b, 31b, −47b, 51c, 54b, 70b, −71b, 73b

Proboscideans: −8b, 12b, 24b, 46b, −51b, 65c

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