Cranial Anatomy and Phylogenetic Position of *Tsaganomys altaicus* (Mammalia: Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia*

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ABSTRACT

Tsaganomys altaicus from the early Oligocene Hsanda Gol Formation, Mongolia, is the oldest hystricognathous rodent known from a complete skull. "*Cyclomylus lohensis*" is a junior synonym of *T. altaicus*. "*Cyclomylus*" *minutus*, *Sepulkomys eboretus*, *Beatomus bisus*, *Pseudotsaganomys mongolicus*, and *Pseudotsaganomys turgaicus* are most likely also junior synonyms of *T. altaicus*. Characters aligning *Tsaganomys* with Hystricognathi are hystricognathous jaw and reduced lacrimal. In addition, *Tsaganomys* has multiserial enamel and lacks an internal carotid artery, derived characters shared with Hystricognathi and its sister taxa. *Tsaganomys* retains plesiomorphic characters such as unfused malleus and incus, unexpanded malleus head, and imperforate pterygoid fossa. Parsimony analysis indicates that *Tsaganomys* is the nearest outgroup of all living

Hystricognathi. A definition of Hystricognathi is proposed based on the taxic content of the crown group, which does not include *Tsaganomys*. The traditional "Phiomorpha" and "Caviomorpha" are not monophyletic. The non-erethizontid "caviomorphs" are a monophyletic group for which a crown group definition and the name Caviida are proposed. The living Ctenodactylidae is the sister taxon to *Tsaganomys* plus Hystricognathi. The name Hystricognathiformes is proposed for rodents more closely related to the crown group Hystricognathi than to Ctenodactylidae. Previously proposed exclusive relationships among *Tsaganomys*, Bathyergidae, and *Ardynomys occidentale* are not supported. *Tsaganomys* was widely distributed in Asia throughout the Oligocene. The presence of hystricognathous rodents in the earliest Oligocene of northern Africa and South

America, at about the same time as *Tsaganomys* in Asia, indicates that the origin and early diversification of hystricognathous rodents is poorly known and was not restricted to Africa. Two independent introductions of hystricognathous rodents to South America now seem necessary, one for Caviida and one for Erethizontidae.

INTRODUCTION

The American Museum of Natural History and the Mongolian Academy of Sciences resumed joint paleontological exploration of Mongolia in 1990. The 1990, 1991, 1993, 1994, and 1995 Mongolian-American Expeditions (MAE) visited the Tsagan Nor Basin in central Mongolia to prospect the Oligocene Hsanda Gol Formation. Fossiliferous localities in the Hsanda Gol Formation were first discovered in 1922 by the Central Asiatic Expeditions (CAE). The Hsanda Gol Formation (Berkey and Granger, 1923) is well known for its fossil rodents (Matthew and Granger, 1923a, 1923b; Kowalski, 1974). *Tsaganomys altaicus*, the oldest hystricognathous rodent known from a complete skull, is common in the collections but has been described inadequately.

Isolated jaws and teeth of tsaganomyids were recovered by the 1990 MAE from a new locality in the Hsanda Gol Formation called Oortsog (table 1). More complete tsaganomyid material was collected from the Hsanda Gol Formation by the 1991, 1993, and 1994 MAE, when field parties returned to several localities discovered by the CAE in 1922 and 1925 and prospected for new localities. The MAE recovered many new *Tsaganomys altaicus* specimens from Tatal Gol, Oortsog, Zavlia, and other localities (table 1), including well-preserved skulls and mandibles. The specimens are often preserved in carbonate-cemented, silty sandstone and mudstone amenable to acid preparation, allowing examination of extremely fine structural details in the middle ear and orbital wall. Several specimens collected by the 1922 and 1925 CAE have been prepared more completely as well. The purposes of this report are to (1) reexamine the tsaganomyids in the CAE collections, (2) describe new specimens collected by the MAE, and (3) place *Tsaganomys altaicus* into a phylogenetic context with a new consideration of morphological characters widely used in hystricognathous rodent phylogeny.

PHYLOGENETIC HISTORY

Matthew and Granger (1923a) described two new genera and species of protrogomorphous, hystricognathous rodents recovered by the 1922 CAE from the Tsagan Nor Basin. The fossil material consisted of a few crushed, incomplete skulls, several mandibles, and partial dentitions. Matthew and Granger (1923a) referred the two taxa, *Tsaganomys altaicus* and "*Cyclomylus lohensis*," to the Bathyergidae, based on the protrogomorphous infraorbital foramen, very hypsodont cheek teeth that lose their occlusal pattern early in wear, hystricognathous jaw, and other similarities. *T. altaicus* and "*C. lohensis*" were distinguished from one another principally by size. Matthew and Granger (1923a) provisionally placed *T. altaicus* and "*C. lohensis*" in an exclusive subfamily, Tsaganomyinae. Landry (1957) agreed with Matthew and Granger (1923a) that *T. altaicus* and "*C. lohensis*" are bathyergids, but considered tsaganomyids to be more closely related to *Bathyergus* than to other bathyergids. Patterson and Wood (1982: 515) raised the tsaganomyids to family rank in their horizontal classification scheme. Since their description, *T. altaicus* and "*C. lohensis*" have figured prominently in discussions of rodent phylogeny with much speculation, incorrect characterization, and little new work. Although additional material has been recovered from Kazakhstan, Mongolia, and China (Teilhard de Chardin, 1926; Bohlin, 1937; Vinogradov and Gambaryan, 1952; Mellett, 1966, 1968; Shevyreva, 1972; Kowalski, 1974; Li and Ting, 1983; Russell and Zhai, 1987; Huang, 1993), tsaganomyids remain among the least-investigated groups of early hystricognathous rodents (Luckett and Hartenberger, 1985).

Interpretations of the phylogenetic position of tsaganomyids have generally followed one of three hypotheses. One hypothesis places tsaganomyids in or very close to Bathyergidae within Hystricognathi. Essentially this
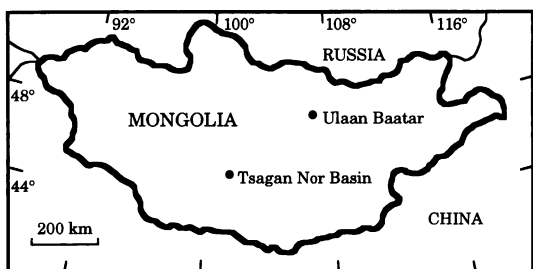
Fig. 1. Location of the Tsagan Nor Basin in Mongolia.

TABLE 1
Coordinates of Localities in the Tsagan Nor Basin Discussed in the Text

Locality	Latitude	Longitude
Oortsog	45°16'20"N	101°39'49"E
Tatal Gol localities		
Main exposures	45°17'50"N	101°37'16"E
Dike locality	45°17'19"N	101°37'17"E
Zavlia localities		
Zavlia #1	45°17'10"N	101°33'41"E
Zavlia #2	45°16'45"N	101°33'35"E
Loh localities		
Loh well	45°17'00"N	101°47'44"E
Ridge SW of Loh	45°16'35"N	101°46'17"E
Localities east of Loh		
Argalant	45°17'50"N	102°04'53"E
Serendipity hills	45°17'24"N	101°57'55"E
Goonbold hills	45°18'22"N	102°04'28"E
Rodent heaven	45°17'22"N	101°58'03"E

was first proposed by Matthew and Granger (1923a) when they placed *T. altaicus* and "*C. lohensis*" within the Bathyergidae. The idea has been supported by Landry (1957) and Martin (1992). The second hypothesis, first proposed by Burke (1936), postulates that tsaganomyids are cylindrodontids related to *Ardynomys occidentale*, an arrangement most forcefully argued by Wood (1970, 1974a) and accepted by Simpson (1945), Wilson (1949), Wood (1955), Mellett (1966), Chaline and Mein (1979), Parent (1993), and Huang (1993), among many others. The third hypothesis, first suggested by Wood (1974a) but more clearly defined by Patterson and Wood (1982), includes elements from each of the others: tsaganomyids and bathyergids are closely related to each other and derived from a cylindrodont (such as *A. occidentale*), ultimately sharing a common ancestor with other hystricognathous rodents among the "Franimorpha."

Our current understanding of rodent phylogeny and the position of tsaganomyids can be summarized as follows (see reviews in Luckett and Hartenberger [1985], Jaeger [1988], and Korth [1994]). (1) Numerous molecular and morphological analyses strongly support monophyly of the living hystricognathous rodents, including the Bathyergidae. Phylogenetic relationships within, and derivation of, hystricognathous rodents are not well understood. (2) The "Franimorpha," including cylindrodonts, is paraphyletic and removed from ancestry of hystricognathous rodents (Korth, 1984; Meng, 1990; Martin, 1992). (3) Hystricognathous rodents are most likely closely related to Paleogene "ctenodactyloids" (Flynn et al., 1986). The problem of the position of

T. altaicus can be outlined with three questions. Are the similarities between bathyergids and *T. altaicus* convergent or evidence of relationship? Is *T. altaicus* more closely related to cylindrodonts or to living hystricognathous rodents? Is *T. altaicus* significant in the early diversification of hystricognathous rodents? These questions can best be approached by analysis of the new material collected by the MAE.

LOCALITIES AND GEOLOGIC SETTING

The localities described here are in the Tsagan Nor Basin in central Mongolia (fig. 1). Berkey and Morris (1927) published the first geologic map of the Tsagan Nor Basin. New field data gathered by the MAE have shown that the map published by Berkey and Morris (1927) is, in general, topographically accurate but the coordinate system is displaced slightly and the geologic mapping is not very accurate (McKenna et al., in prep.). More recent or accurate topographic maps are not currently available to us, but the coordinates of important sites (based on satellite global positioning system data) are provided in table 1.

The Hsanda Gol Formation was named by Berkey and Granger (1923) for deposits ex-

posed in badlands along Shand Gol (a "gol" is a stream or drainage) near a well called Loh (Camp Loh of Berkey and Morris [1927: plates 28, 29]). Berkey and Granger (1923) believed the Hsanda Gol Formation to be over 900 m thick and Miocene in age. Berkey and Morris (1927) revised their age estimate to Oligocene based on biostratigraphy. An important marker bed in the local stratigraphy is a lava flow mapped within the Hsanda Gol Formation by Berkey and Morris (1927). The ages of two samples of this lava were determined by K-Ar methods (Evernden et al., 1964: 193) as 31.5 and 32.2 Ma (no error estimates provided; corrected for revised radioisotope decay constants [Steiger and Jäger, 1977]). The precise locations from which the CAE lava samples were collected are not known. Similar age results were reported by Devyatkin and Smelov (1979). Based on new bio- and lithostratigraphic evidence gathered by the MAE (McKenna et al., in prep.), it is clear that the geology of the area was not fully understood by the CAE. Rocks included in the Hsanda Gol Formation by Berkey and Granger (1923) and mapped by Berkey and Morris (1927) range in age from Cretaceous to Quaternary.

The exact localities and stratigraphic horizons of the CAE collections are generally not well known. Most of the Hsanda Gol fossils collected by the 1922 and 1925 expeditions were from badlands near Camp Loh and especially about 14 km west of Camp Loh in an area called the "Grand Canyon" (or "Grand Cañon") along Tatal Gol (table 1; Berkey and Granger, 1923; Berkey and Morris, 1927; see summary by Mellett, 1968). Several other localities in the region were also collected, e.g., near Dzun Hsir (about 6 km northeast of Camp Loh) and badlands 19 to 24 km east of Camp Loh. The stratigraphic position of fossils relative to the lava or other units usually was not recorded. Berkey and Morris (1927: 365) claimed that all of the fossils collected from the type section "near Loh" came from above the level of the lava flow, and that most fossils from further west along Tatal Gol were collected below the level of the lava (some fossils were also collected above the lava along Tatal Gol, however [Granger, MS, 1922]).

In 1994 the MAE spent three weeks pros-

pecting the Hsanda Gol Formation in the Tsagan Nor Basin and collecting fossils within a stratigraphic framework. A new understanding of the litho- and biostratigraphy of the region is emerging (McKenna et al., in prep.) that differs in many respects from interpretations by the CAE and by the Joint Soviet-Mongolian Expeditions (Badamgarav et al., 1975; Goroshko and Kurotchkin, 1979). In summary, the Hsanda Gol Formation in the region of Shand Gol and Tatal Gol can be divided into three lithostratigraphic and two biostratigraphic units (fig. 2), which are considered informal (sensu ISSC, 1994) until completion of the stratigraphic work. The lowermost lithostratigraphic unit (informally referred to as the Tatal member) is predominantly a dark-red, fine-grained, clay-rich sandstone. The lava (informally referred to as the Mellett lava) provides an excellent local marker bed near the middle of the Hsanda Gol Formation. The uppermost lithostratigraphic unit (informally referred to as the Shand member) is lighter in color with numerous variegated, calcic paleosols and lower clay content, representing a change in paleoecologic conditions. The Tatal and Shand members are divided at the level of the lava (where present), or at a horizon stratigraphically correlative to the lava where the lava is not present. Where the lava is not present, the contact of the Tatal and Shand members is topographically higher than the projected level of the lava because the basalt flow filled valleys present at the time of eruption. The Tatal and Shand members, however, can be distinguished without the presence of the lava. As also noted by Badamgarav et al. (1975), the total thickness of the Hsanda Gol Formation does not exceed 60 m in any outcrop. The thickness is far less than the 900 m proposed by Berkey and Granger (1923) and Mellett (1968).

The presence of two faunas within the Hsanda Gol Formation was first recognized by Kowalski (1974). The lower fauna (informally referred to as the Ulaan Khongil fauna) is dominated by the rodents Tsaganomys altaicus and Cricetops dormitor, with abundant smaller rodents including Karakoromys, Selenomys, and Eucricetodon. The upper fauna (informally referred to as the Zavlia fauna) represents a reduction in apparent diversity

of the rodent fauna to three dominant taxa: the local first appearances of a very large tataromyid and *Tachyoryctoides*, and the continued presence of *Tsaganomys*. The Ulaan Khongil and Zavlia faunas are typically separable at a stratigraphic level approximately 5 to 10 m above the lava (where present) or at a correlative level within the basal part of the Shand member. *Tsaganomys* occurs throughout the Hsanda Gol Formation.

The stratigraphic levels within the Hsanda Gol Formation from which the holotypes of *Tsaganomys altaicus* and "*Cyclomylus lohensis*" were collected are not well known. The field notebook of Granger (MS, 1922) records the holotype of "*C. lohensis*" (AMNH 19096, field number 51) as collected from "variegated beds—lower red strata" from "badlands around Camp Loh." Thus the holotype specimen of "*C. lohensis*" was likely collected from the Tatal member, which is well exposed along a ridge two miles southwest of Camp Loh (although not at Loh itself), low in the section, and dark red in color. The origin of the holotype of *Tsaganomys altaicus* (AMNH 19019, field number 72) is more uncertain. Granger's fieldnotes (MS, 1922) record the horizon only as "variegated beds," which suggests (although certainly does not prove) the specimen is from the Shand member, which is well exposed at Loh and along the ridge extending southwest from Loh. The published description of *T. altaicus* (Matthew and Granger, 1923a) records the horizon as Hsanda Gol Formation, red strata, near Loh, which implies the Tatal Member and appears to contradict Granger's fieldnotes. The new material described here, mostly collected by the 1991 and 1993 expeditions, was recovered from the Tatal member and Ulaan Khongil fauna, below the lava. Some tsaganomyid specimens were collected from above the level of the lava at localities near Tatal Gol in 1990, 1994, and 1995, but this material is not very well preserved and is not included in the measurements or discussion presented here.

INSTITUTIONAL ABBREVIATIONS

AMNH   American Museum of Natural History
PIN   Paleontological Institute, Russian Academy of Sciences, Moscow

GENERALIZED COMPOSITE SECTION
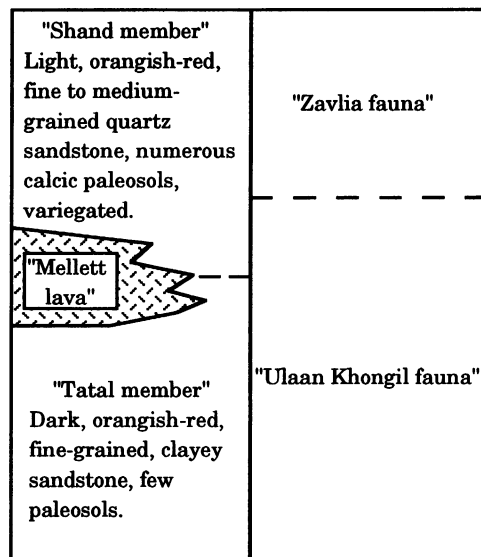LITHOSTRATIGRAPHY   BIOSTRATIGRAPHY

Fig. 2. Schematic composite section illustrating relationships between litho- and biostratigraphic subdivisions of the Hsanda Gol Formation in the region of Shand Gol and Tatal Gol. Subdivisions are informal pending completion of a detailed stratigraphic analysis (McKenna et al., in prep.). Thicknesses are schematic only and do not imply an actual lithostratigraphic scale. The boundary between the Zavlia and Ulaan Khongil faunas is approximately 5 m above the level of the lava.

M   Mongolian Academy of Sciences–American Museum of Natural History Paleontological Expeditions, collection to be deposited at the Mongolian Academy of Sciences, Ulaan Baatar

SYSTEMATIC PALEONTOLOGY

Rodentia Bowdich, 1821

TSAGANOMYS ALTAICUS MATTHEW AND GRANGER, 1923A

HOLOTYPE: AMNH 19019, partial skull and mandibles.

HORIZON AND LOCALITY: Hsanda Gol Formation, "red strata," near Loh, Tsagan Nor Basin, Mongolia.

DISTRIBUTION: Early to late Oligocene of China, Mongolia, and Kazakhstan.

REVISED DIAGNOSIS: Large, protrogomorphous rodent with fossorial adaptation in cranial and postcranial skeleton; in lateral view skull low, occiput sloping forward, incisors very procumbent and extending into orbit with posterior end of alveolus lateral to molar roots; in dorsal view zygomatic arches almost forming a circle, braincase nearly triangular in shape with narrow interorbital constriction. Anterior end of zygoma formed by broad vertical maxillary root; jugal extending mediodorsally to meet the premaxilla; bulla heavily septate, malleus and incus not fused, internal carotid artery system absent. Mandible hystricognathous with large angular and coronoid processes, incisors extending posteriorly into the condyloid process. Enamel of upper and lower incisors multiserial with prisms perpendicular to the surface in the *portio externa* and interprismatic matrix at an acute angle to the prisms; cheek teeth cylindrical, extremely hypsodont, tetralophodont, without a hypocone, occlusal pattern lost very early in wear.

SYNONYMY: *Cyclomylus lohensis* Matthew and Granger, 1923a; also probably *"C."* *minutus* Kowalski, 1974; *Pseudotsaganomys mongolicus* Vinogradov and Gambaryan, 1952; *P. turgaicus* Vinogradov and Gambaryan, 1952; *Sepulkomys eboretus* Shevyreva, 1972; and *Beatomus bisus* Shevyreva, 1972.

REFERRED SPECIMENS: Besides the holotype and paratypes collected by the 1922 CAE and described by Matthew and Granger (1923a), a collection of several hundred jaws, partial skulls, postcranial bones, and teeth, collected by the 1925 CAE and the 1991, 1993, and 1994 MAE. Most notable for preservation are AMNH 21675 (collected in 1925), and M 350, M 1798, M 468, M 360, and M 367 (collected in 1991).

DISCUSSION: By modern standards Matthew and Granger (1923a) did not sufficiently diagnose, describe, or provide measurements of the tsaganomyid material available to them. Two line drawings illustrated a reconstructed skull of *Tsaganomys altaicus*, both rather undiagnostic beyond gross morphology and not representative of the holotype. *"Cyclomylus lohensis"* was not illustrated. It was distinguished principally by being smaller and less hypsodont than *T. altaicus*. Additional distinguishing characters of *"C. loh-*

ensis" were narrower skull, orbits "not built out so much as in *Tsaganomys"* (Matthew and Granger, 1923a: 4), and the presence of a small dP3.

Two morphotypes of tsaganomyids appear to be represented in the Hsanda Gol collection, a large and a small form. Body size, however, is an extremely variable character in fossorial rodents (Nevo, 1979; Lessa and Thaeler, 1989; Lessa, 1990). In bathyergids and *Thomomys*, body size may relate to age or sex, as well as the presence of a breeding female, colony size, food resources, predation, soil types, and other factors (Jarvis et al., 1991; Rogers, 1991). Sexual dimorphism is evident in virtually all cranial matrices in *Thomomys* (Rogers, 1991). All of the complete *Tsaganomys* dentitions collected by the CAE and the 1991 and 1993 MAE expeditions (over 400 specimens) were measured for toothrow length and incisor widths. Toothrow length and incisor width are the only presumably age-independent characters available with sufficient sample sizes to determine if *Tsaganomys altaicus* and *"Cyclomylus lohensis"* are distinct. Bivariate plots of specimens for which both incisor width and toothrow length could be measured (fig. 3A, B) show no significant size groupings among the specimens. Histograms of toothrow length (fig. 3C, D) are bimodal. We interpret this distribution to reflect sexual dimorphism. Histograms of incisor width (fig. 3E, F) are unimodal. The range in size appears to represent a growth series; only small individuals retain vestiges of the deciduous dentition and cheek teeth with light wear.

In addition to the problem of determining growth series, the amount of time likely represented in the Hsanda Gol Formation must also be considered. As discussed above, there is a faunal turnover within the Hsanda Gol Formation approximately 5 to 10 m above the level of the lava. Although the stratigraphic distribution of specimens collected by the 1922 and 1925 expeditions was not usually recorded, *Tsaganomys* is found in both faunas (Kowalski, 1974; McKenna et al., in prep.). The new material described here, collected mostly by the 1991 and 1993 expeditions, is from the lower fauna and includes the full morphologic range observed in *Tsaganomys altaicus* and *"Cyclomylus*
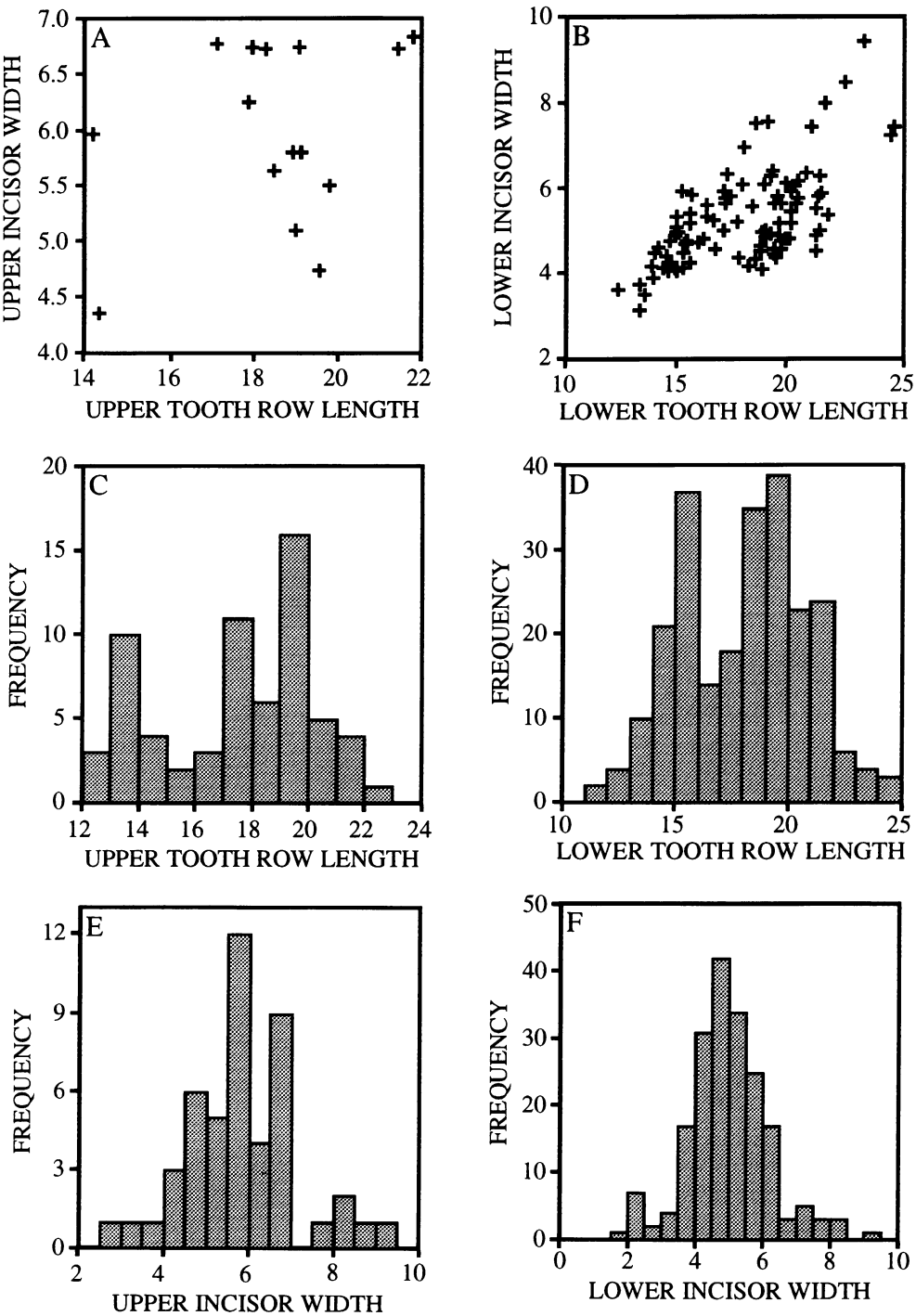
Fig. 3. Graphs of dental measurements of *Tsaganomys altaicus* specimens. All measurements are in millimeters. **A**, Scatterplot of measurements of paired upper incisor widths and toothrow lengths. **B**, Scatterplot of paired lower incisor widths and toothrow lengths. **C–F**, Histograms of individual measurements. Toothrow lengths (C–D) are slightly bimodal, interpreted as representing sexual dimorphism.

lohensis." Thus it does not appear that *T. altaicus* and "*C. lohensis*" are end members of a stratophenetic cline.

Two other characters have been used to differentiate *Tsaganomys altaicus* and "*Cyclomylus lohensis*." The first character is the presence of a diminutive, peg-like dP3, cited by Matthew and Granger (1923a) in their description of "*C. lohensis*." The tooth is not present in the holotype but is preserved in six other small maxillae. The homology and presence of this tooth are important because the presence of a permanent P3 replacing dP3, as opposed to early loss of dP3 with no replacement by P3, is plesiomorphic for rodents. Confusion over the interpretation of homology and the distribution of the tooth described as dP3 or P3 among *T. altaicus* specimens has led paleontologists to describe additional species. A reconstruction of the ontogenetic replacement of the cheek teeth (see below) reveals that the tooth in question is actually a dP3 that is lost early in life and not replaced. The presence or absence of this tooth, therefore, is age-related.

The second character is a difference in the inclination of the Hunter-Schreger bands in incisor enamel. Martin (1992) found that the bands were inclined at about 10–15° in the *portio interna* of *T. altaicus* and about 30° in specimens identified as "*C. lohensis*," but said these are within the range of natural variation, including ontogenetic change. Large differences in inclination can be found between upper and lower incisors of the same individual in modern rodents (Martin, 1992). Because these characters are not diagnostic and no other apomorphies could be identified to separate *T. altaicus* from "*C. lohensis*," we consider them synonymous.

Holotypes of the remaining tsaganomyid taxa described from Asia were not examined during the course of this study, but all appear to be referable to *Tsaganomys altaicus*. *Pseudotsaganomys* was described by Vinogradov and Gambaryan (1952) with two species, *P. turgaicus* (from the Oligocene of Kazakhstan) and *P. mongolicus* (from the Hsanda Gol Formation in Tsagan Nor Basin). Mellett (1966, 1968) and Kowalski (1974) have previously argued that *Pseudotsaganomys* is a junior synonym of "*Cyclomylus*." Specimens illustrated by Vinogradov and Gambaryan

(1952) do not show any differences between *Pseudotsaganomys* and *Tsaganomys altaicus*.

Shevyreva (1972) described two new genera and species of tsaganomyids, *Sepulkomys eboretus* and *Beatomus bisus*, from the Hsanda Gol Formation at Tatal Gol. *Sepulkomys* was differentiated from *T. altaicus* and "*C. lohensis*" by the presence of a "P3." As Shevyreva (1972) noted, the holotypes of *T. altaicus* and "*C. lohensis*" do not have a dP3, even though Matthew and Granger (1923a) mentioned the presence of dP3 in their description of "*C. lohensis*" (based on the occurrence of a dP3 in the paratypes). Shevyreva's figure of the holotype of *Sepulkomys eboretus* (PIN 475-50) shows that it is a young individual in which the "P3" is a dP3, the dP4-M2 are also present, M1-2 are lightly worn, and M3 is unerupted. Based on our observations, this specimen represents a juvenile *T. altaicus*. A mandible (PIN 475-460) referred to *Sepulkomys* by Shevyreva (1972) also retains the deciduous dentition and is indistinguishable from *T. altaicus*.

The holotype of *Beatomus bisus* (PIN 475-1899) was not figured by Shevyreva (1972). *Beatomus* was differentiated from *T. altaicus* by the absence of a core of "honeycomb fibrous fabric" in the histological construction of the cheek teeth that is distinct from dentine and enamel. Figured specimens referred to *Beatomus bisus* (Shevyreva, 1972: fig. 6; 1974: figs. 1–3) do not indicate clearly what is meant by this ambiguous character and there are no specimens in our collections that suggest such a feature. Furthermore, Shevyreva (1972: 143) admitted that there are no distinct external features to distinguish *Beatomus bisus* from *T. altaicus*. Kowalski (1974) examined the holotype and referred specimens and also doubted the validity of *Beatomus bisus*.

"*Cyclomylus*" *minutus* was described by Kowalski (1974) from a skull and mandible (probably associated) from Khatan Khayr-khan in the southwestern Gobi Desert (Gradzinski et al., 1968). "*C.*" *minutus* was distinguished from "*C. lohensis*" by smaller size, lack of a "P3," incisors without longitudinal ridges, teeth more hypsodont, and "structure of the M3 more ephemeral and otherwise distinctive" (Kowalski, 1974: 160). Kowalski admitted, but apparently did not accept,

Shevyreva's (1972) statement that the holotype of "*C. lohensis*" (AMNH 19096) also lacks dP3. Huang (1993) placed "*C.*" *minutus* within *Tsaganomys*, but also confused the homology of the dP3. The measurements provided for the holotype skull and mandible of "*C.*" *minutus* (Kowalski, 1974) and referred specimens (Huang, 1993) indicate individuals within the range of small *T. altaicus*. The illustrated tooth rows of the type specimen show that the anteriormost lower cheek tooth is a dp4, not a p4 as indicated by Kowalski (1974). The M3 and m3 have not fully erupted. This is also a very young individual, which explains its small size. Hypsodonty cannot be judged from the figures, but considering the variation observed in Hsanda Gol *Tsaganomys*, it is doubtfully significant. Incisor "ridges" or striations are a highly variable feature present even on large *T. altaicus* specimens, including the holotype. These are not longitudinal grooves as found in some rodents, but an irregular surface texture which tends to originate in the center of the incisor and extend outwards in a roughly radial pattern. Among the small individuals, those retaining a deciduous premolar or unworn permanent molars have no noticeable surface texture on the incisor enamel. Thus, "*C.*" *minutus* also appears to be a junior synonym of *T. altaicus*.

In summary, there are no characters, aside from those attributable to sexual dimorphism or ontogenetic stage, that appear to distinguish described specimens of *Cyclomylus*, *Pseudotsaganomys*, *Beatomus*, or *Sepulkomys* from *Tsaganomys altaicus*.

MORPHOLOGY

SKULL

Terminology of the cranial foramina follows Wahlert (1974, 1983), and that of the masseteric musculature follows Woods (1972). The skull is broad with a low lateral profile, very similar to those of other fossorial rodents (fig. 4). The rostrum comprises about a third of the total length of the skull (from tip of snout to anterior zygoma), and the incisors are very procumbent. In dorsal view the braincase has a triangular outline due to a narrow interorbital constriction, very wide squamosals, and a flat occiput. The occipital region slopes forward, similar to that of *Myospalax* but much flatter. There are pronounced antorbital crests arising on the frontals. The crests form ridges that unite posteriorly as a sagittal crest. There is a strong lambdoidal crest which, with the sagittal crest, forms a tripartite ridge across the top of the braincase.

The infraorbital foramen is small, ovate, and inclined slightly in anterior view, with no evidence for passage of the masseter onto the rostrum (fig. 5). The anterior zygomatic root is expanded to a wide, thin plate. The jugal forms the laterodorsal margin of the anterior zygomatic root. The jugal meets the lacrimal and extends beyond it anteromedially to make contact with the premaxilla. The jugal-premaxillary contact appears to be autapomorphous for *Tsaganomys altaicus*. In some rodents (e.g., *Paramys*, *Castor*) the jugal extends dorsally to the lacrimal but does not reach the premaxilla. In most rodents the jugal is restricted to the zygomatic arch and excluded by the maxilla from reaching the anterior zygomatic root. There is a distinct pocket in the root of the zygoma anterolateral to the nasolacrimal foramen (fig. 5). This pocket is bordered dorsally by the jugal, maxillary, and lacrimal bones, which form a small crest overhanging the orbit. We interpret this pocket as the origin of the anterior part of the *masseter medialis*, a condition found in some other fossorial rodents (e.g., *Aplodontia*, *Thomomys*, and *Cryptomys*). The nasolacrimal foramen, bordered by the lacrimal and maxilla, opens upward into the pocket. The ventral margin of the zygomatic arch has a horizontal scar for attachment of the masseter.

The incisors extend far into the orbit and end lateral to the molars (figs. 4, 5). The molar alveoli extend high into the orbit medial to the incisor sheath (fig. 4). The premolar alveolus follows a slightly different path and passes anteroventral to the incisor within the orbital wall. The molar alveoli and incisor sheath produce a very prominent, swollen maxillary bone in the orbital region. This creates a distinct groove in the orbit, mediodorsal to the swollen region, that extends from the anterior alar fissure anteriorly into the sphenopalatine foramen. The orbital lamina of the frontal and alisphenoid form most of the orbital wall dorsal to this groove with a
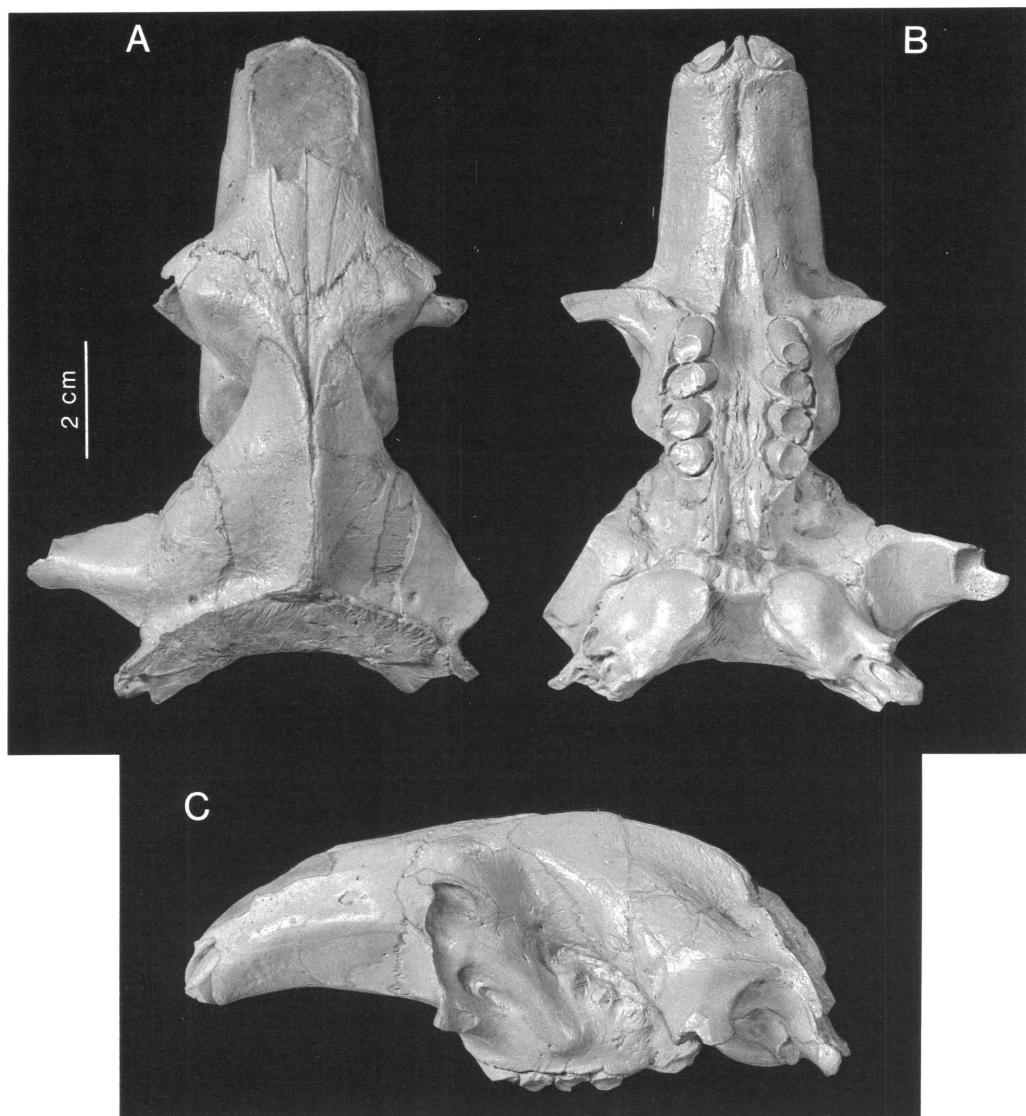
Fig. 4. Skull of *Tsaganomys altaicus* (AMNH 21675). A, Dorsal view. B, Ventral view. C, Lateral view. Abbreviations used throughout the figures: lower teeth indicated by lower case letters (p4, m1, etc.); upper teeth indicated by upper case letters (P4, M1, etc.); **aal**, anterior alar fissure; **aasc**, anterior opening of the alisphenoid canal; **aav**, anterior alveolar foramen; **aoc**, antorbital crest; **as**, alisphenoid; **az**, anterior zygomatic root; **b**, auditory bulla; **bo**, basioccipital; **bs**, basisphenoid; **bu**, buccinator foramen; **eam**, external auditory meatus; **eth**, ethmoid foramen; **f**, frontal; **fnt**, tube for facial nerve; **fo**, foramen ovale; **fov**, fenestra ovalis; **fr**, fenestra rotunda; **fsm**, fossa for origin of the stapedius muscle; **gf**, glenoid fossa of squamosal; **hy**, hypoglossal foramen; **i**, incisor; **iav**, extension of upper incisor alveolus into orbital region; **iof**, infraorbital foramen; **is**, internal septae (bulla); **j**, jugal; **ju**, jugular foramen; **l**, lacrimal; **lp**, pocket in dorsal anterior zygoma region, formed by lacrimal, jugal, and maxilla; **m**, maxilla; **mal**, malleus; **mav**, upper molar alveolus (in orbital region); **mf**, mental foramen; **mlf**, medial lacerate foramen; **msc**, masticatory foramen; **mst**, mastoid; **mstp**, mastoid process; **n**, nasal; **nl**, nasolacrimal foramen; **occ**, occipital; **op**, optic foramen; **os**, orbitosphenoid; **p**, parietal; **pasc**, posterior opening of the alisphenoid canal; **pl**, palatine; **pm**, premaxilla; **pmt**, promontorium; **ser**, bony shelf separating the external auditory meatus from the epitympanic recess; **spf**, sphenofrontal foramen, **spl**, sphenopalatine foramen; **sq**, squamosal; **sty**, stylomastoid foramen; **t**, temporal foramen.
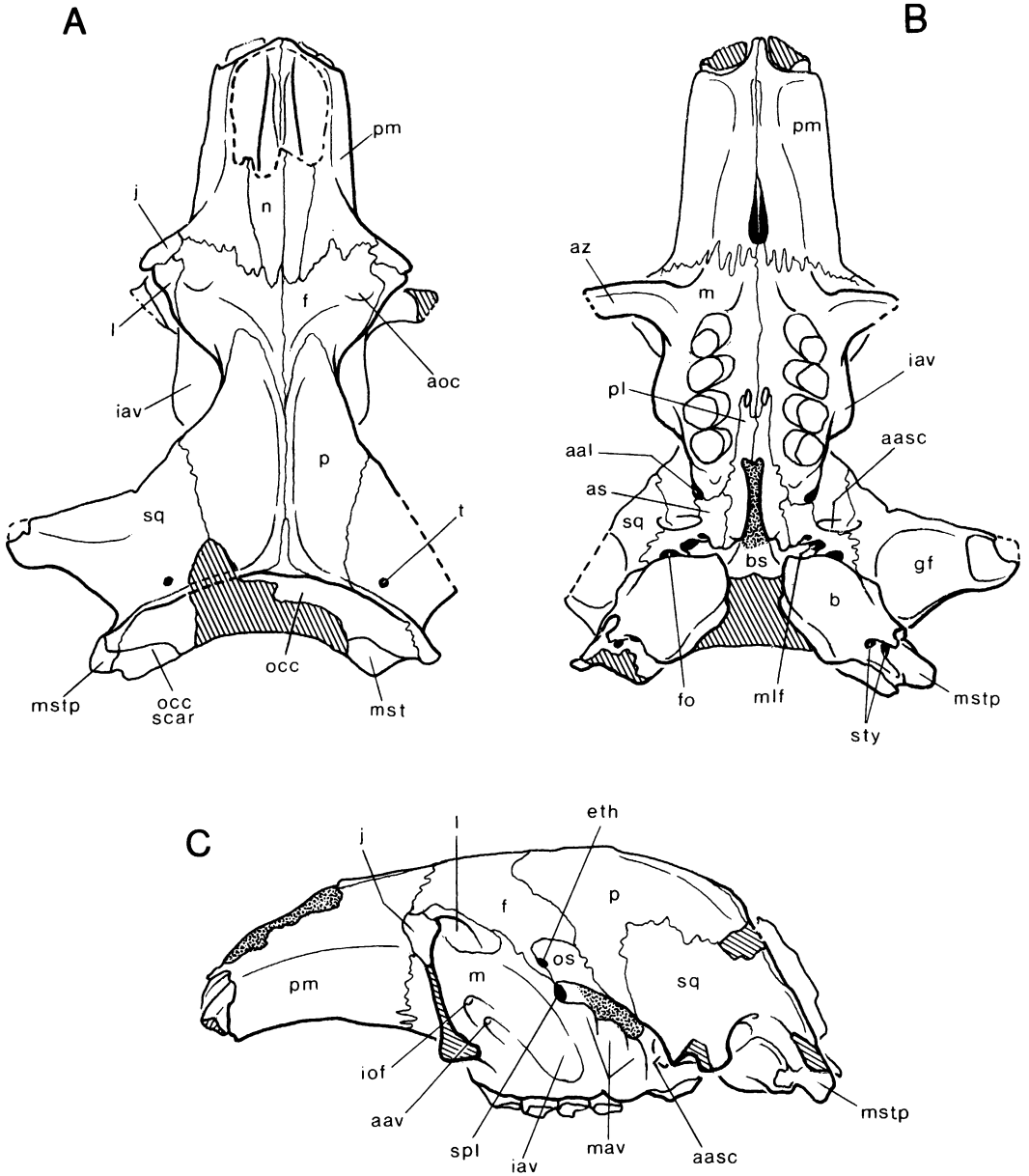
A

B

C

Fig. 4.   Continued.

small contribution by the orbitosphenoid. The orbital wing of the alisphenoid contacts the parietal dorsally. The frontal-maxillary suture descends into the sphenopalatine foramen. An ethmoid foramen occurs entirely within the frontal and may be single (AMNH 21675) or paired (AMNH 19021). The optic foramen is situated above the groove, and a sphenofrontal foramen opens into an external canal dorsal to the optic foramen.

The alisphenoid, as the lateral pterygoid flange, descends ventrally to the level of the occlusal surface of the cheek teeth (fig. 5). The masticatory and buccinator foramina are separate from the anterior alar fissure (fig. 6). A transverse canal opens near the posterior end
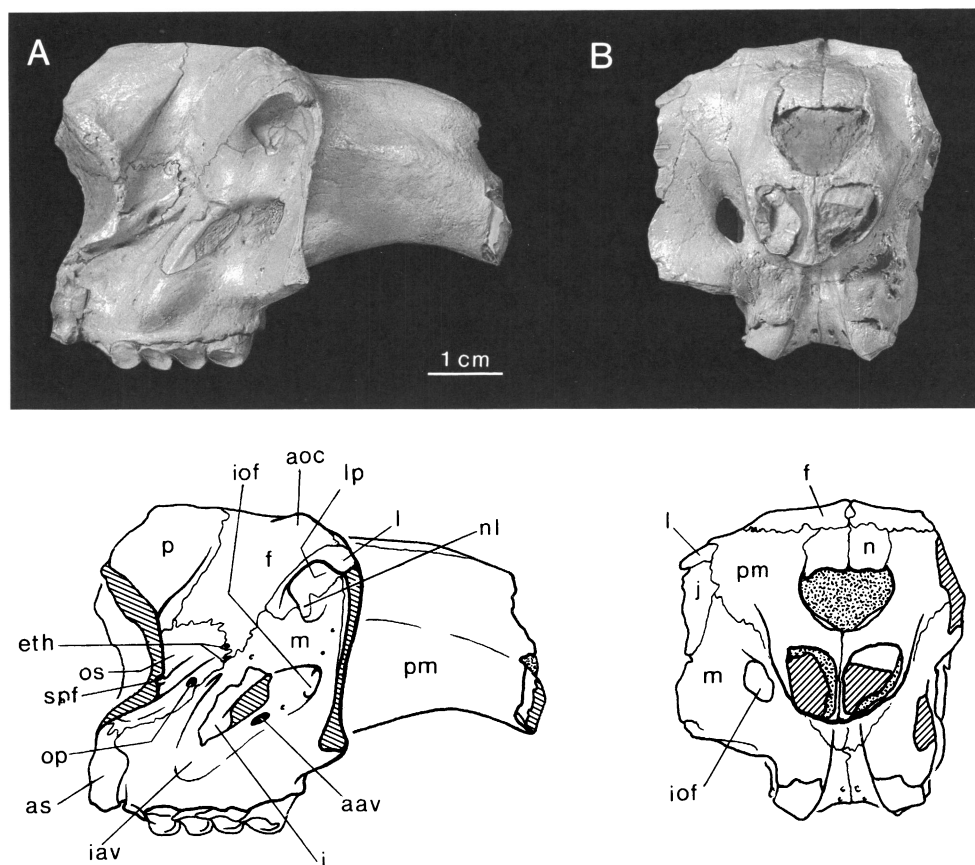
Fig. 5. Skull of *Tsaganomys altaicus* emphasizing the orbital wall and anterior view (AMNH 19021). A, Lateral view. B, Anterior view. Abbreviations are given in figure 4.

of the alisphenoid canal, but the expression of the transverse canal is slightly different on the two specimens in which this area is well preserved (AMNH 21675 and M 350). The transverse canal and alisphenoid canal are separate but lie immediately adjacent to each other in AMNH 21675, but in M 350 the foramina share a confluent opening and are divided internally by a recessed septum. The foramen ovale is relatively small and situated dorsal to the posterior opening of the alisphenoid canal, adjacent to the medial lacerate foramen. A deep or perforate pterygoid fossa is not present.

The occiput is not well preserved in any of the specimens and it is difficult to identify sutures of the mastoid and occipital elements and their relations to foramina. The following details are identifiable principally in three

specimens. On the right side of the occiput of AMNH 21675, the occipital overlaps the mastoid and a thin lamina of the mastoid penetrates between the occipital and squamosal on the lambdoidal crest (fig. 4). The portion of the occipital that overlies the mastoid is mostly broken, but a scar across the mastoid indicates its ventral extent; the scar is also visible on the left mastoid where the overlap of the occipital is not so obvious. M 93-3 preserves the occipital (although the region is slightly crushed) and confirms the extent of the occipital overlap of the mastoid. The mastoid foramen may be represented by a canal that is exposed along the fractured medial portion of the mastoid on both sides. A rounded, blunt mastoid process extends laterally beyond the auditory meatus (fig. 4). The stylomastoid foramen is split into two
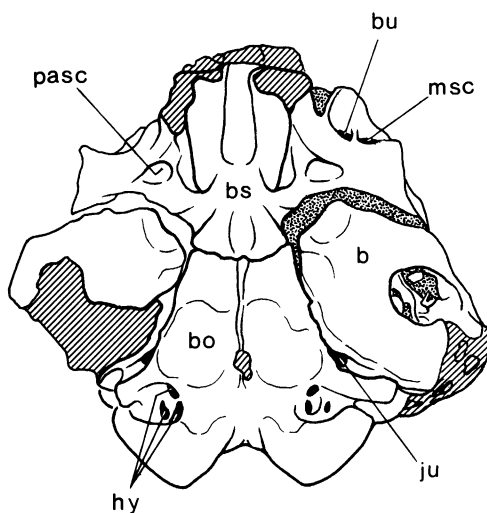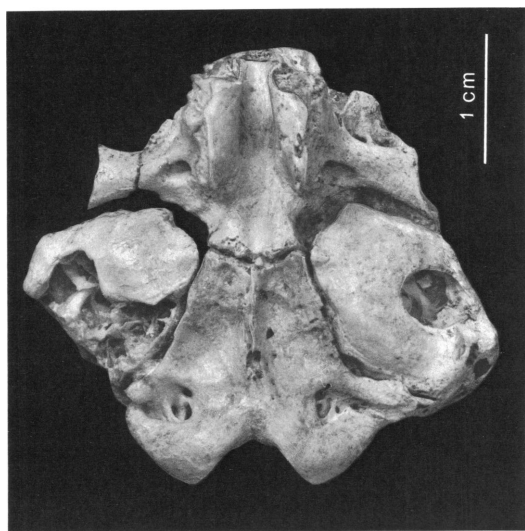
Fig. 6. Basicranium of *Tsaganomys altaicus* (M 350). The right auditory bulla (on the left side in this ventral view) is slightly displaced with the anteromedial end rotated laterally. The left bulla is in life position. Both bullae (and several from other individuals) were dissected to expose the middle ear. Abbreviations are given in figure 4.

foramina of equal size, implying that branches of the facial nerve emerge separately.

M 350 is a well-preserved basicranium with the basioccipital, occipital condyles and most of the foramen magnum (fig. 6). Two hypoglossal foramina and a condyloid canal are recessed in a pit. The condyloid canal passes dorsolaterally and opens into the posterior lacerate region between the bulla and basioccipital. There is a small jugular foramen. The foramen magnum is roughly square in outline, with well-developed dorsal atlantal facets. Two sulci of indeterminate homology are present lateral and slightly dorsal to the foramen magnum.

AUDITORY REGION

The following discussion supplements the brief descriptions by Parent (1980, 1993) and notes specific characters of phylogenetic interest. Terminology generally follows Parent (1980). Most of this description is based on acid preparation of the left bulla of M 350 (figs. 6, 7), although several bullae were dissected to expose the middle ear. The bulla is relatively flattened dorsoventrally, inclined

slightly from horizontal (lateral margin higher than medial), with a long, tubular external auditory meatus. The bulla is fused to the petrosal. The tympanic cavity consists of a single chamber with numerous radial septa around the promontorium (fig. 7). The septa end ventrally on the tympanic annulus of the bulla. The epitympanic sinus is separated by a bony shelf from the external auditory meatus. The cochlea bears three full coils with the axis oriented anterolaterally; the last portion (at the fenestra rotunda) is not coiled. The fenestra rotunda (= fenestra cochlea) faces posteriorly, is ovate in shape, and oriented vertically. The fenestra ovalis (= fenestra vestibuli) is horizontal, relatively large, with a distinct bordering lip. A deep stapedius fossa lies posterior to the fenestra ovalis and is bordered laterally by a fully enclosed tube for the facial nerve. The posterior semicircular canal can be traced encircling the stapedius fossa in the petrosal of M 350. The canal crosses the hypotympanic sinus into the mastoid bone and returns toward the fenestra ovalis in a tube that is ventral to the enclosed facial nerve. A rudimentary fossa, possibly for insertion of the tensor tympani, is present anterolateral to the cochlea in a recess be-

tween internal septa. There is no evidence for passage of an internal carotid or stapedial artery.

The intracranial surface of the petrosal has a very large, deep subarcuate fossa. A sulcus for the prootic and sigmoid sinuses forms the border of the petrosal with the mastoid. The internal auditory meatus is smaller than the subarcuate fossa and does not lie in a fossa itself. The internal auditory meatus is filled with sediment in most specimens, but a septum that divides the superior and inferior acoustic foramina is visible in M 320. The vestibular and cochlear aqueducts are represented by small foramina located posteriorly and ventrally to the subarcuate fossa.

The ear ossicles are preserved in four specimens, M 350, M 1798, M 1729, and M 360. All three ossicles of the left ear remain in the bulla of M 350, disarticulated and fallen into the epitympanic recess before the bulla filled with sediment. The right bulla of M 350 was deeply dissected to locate the ossicles, from which a complete malleus (still in the bulla) and the stapes footplate were recovered. A malleus and incus with preserved articular surfaces were recovered from M 1798. M 1729 preserves a complete incus. These specimens form the basis of this description and reconstructions. The malleus and incus are not fused (fig. 8). The malleus is robust with a round head and thick neck, not laterally expanded as in other hystricognathous rodents. An extremely thin lamina is preserved in the mallei of M 350, particularly the left malleus. In M 1798 the lamina was either damaged during preparation or was not preserved. The manubrium is very elongated and spatulate. The incus has an extended *processus brevis* and a thin *processus longus*. The incus is nearly as large as the malleus. The articular surfaces of the incus and malleus are saddle-shaped and slightly twisted. In articulation the manubrium of the malleus and the *processus longus* of the incus lie adjacent to one another for much of their length. The stapes is bicrurate, roughly symmetrical, with a large stapedial foramen. The crura are flattened, and the head of the stapes is thin and does not taper from the crura. The footplate is ovate and slightly concave (into the fenestra rotunda), imperforate, and symmetrical about the crura.
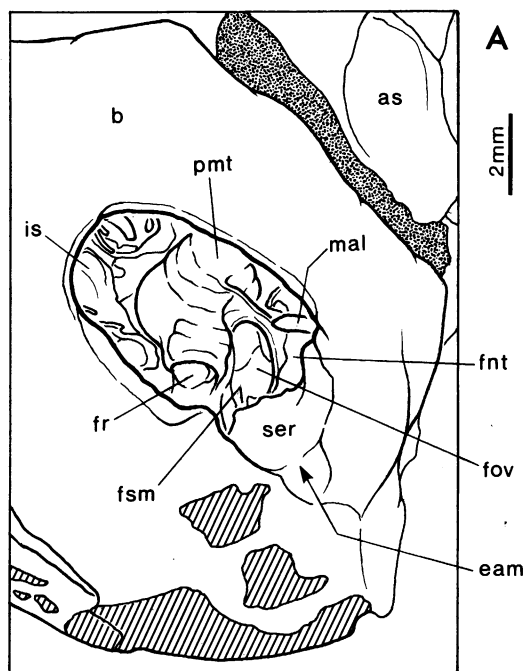

Fig. 7. Detailed interior views through the aperture dissected in the left auditory bulla of M 350. **A**, Stereo photographs and line drawing of the middle ear. **B**, Photograph through the aperture from a ventral perspective (with the same orientation as figure 6), showing the stapes and manubrium of the malleus in place. **C**, Photograph through the aperture from a lateral perspective, showing the internal septa.

MANDIBLE

The mandibles are massive and hystricognathous (fig. 9). The angular process arises lateral to the plane defined by the incisor, at a point between m1 and m2, flares laterally, and does not recurve medioventrally. The incisor passes ventral and slightly medial to the cheek teeth and extends nearly into the condyloid process, above the occlusal surface of the lower cheek teeth. A coronoid process arises lateral to the m1 and m2, dorsal to the origin of the angular process. The masseteric fossa is moderately developed and the masseteric crest has a wide, nearly flat ventral margin. There is a groove for passage of the *masseter superficialis pars reflexa* onto the posteromedial side of the angle (Tullberg, 1899; Woods, 1972), but it is not so well developed as in most modern hystricognathous rodents. There is a single mental fora-
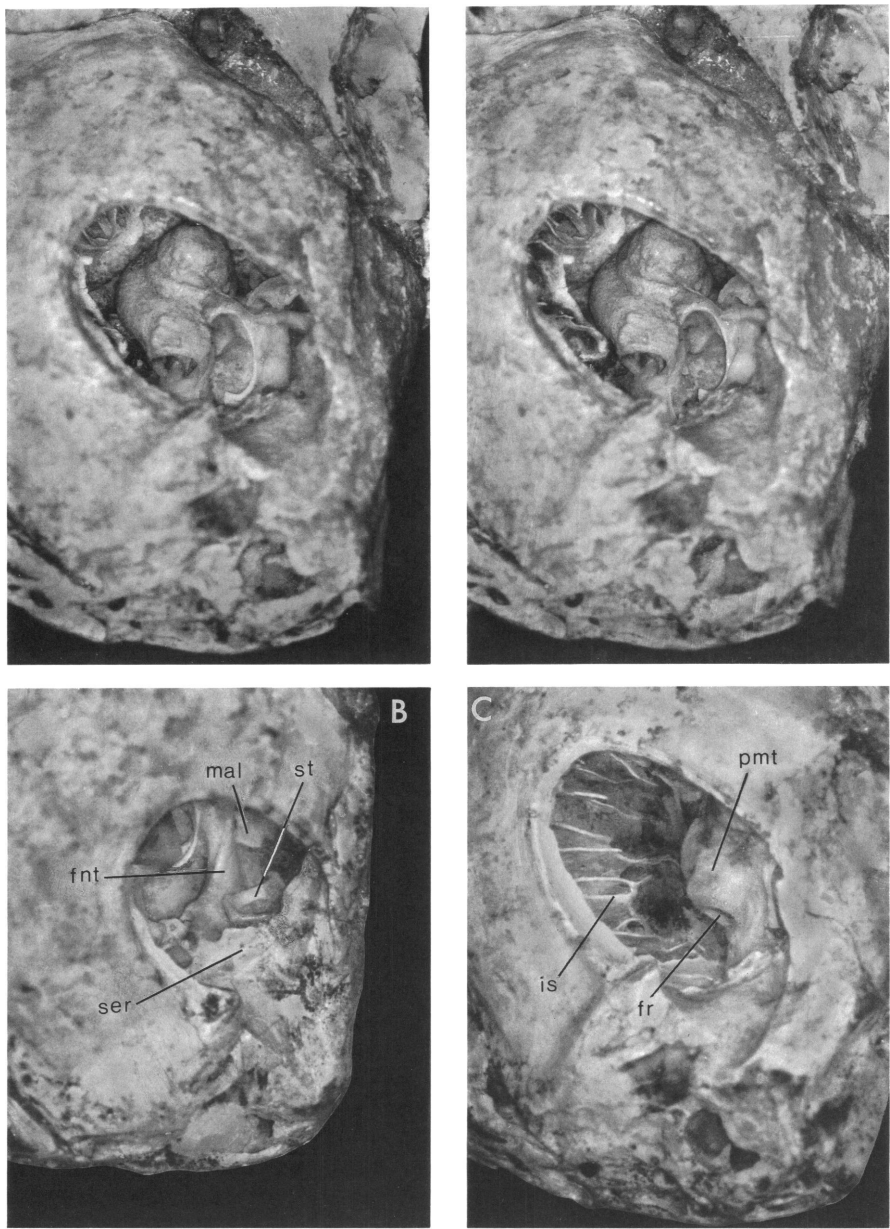
Fig. 7.   Continued.

men. Anterior to the p4, the dorsal margin of the mandible drops steeply to the diastema with a strong ridge extending anteriorly to the incisor.

INCISOR ENAMEL MICROSTRUCTURE

Martin (1992) studied the incisor enamel microstructure of *Tsaganomys altaicus* as part of his survey of hystricognathous rodents. Martin (1992) differentiated *Tsaganomys altaicus* and "*Cyclomylus lohensis*," but the differences in the enamel microstructure are not significant (see below). *T. altaicus* has multiserial enamel with 4–6 enamel prisms per Hunter-Schreger band (HSB). The interprismatic matrix forms an acute angle with the

Fig. 8. Auditory ossicles, based on specimens from M 350, M 1798, and M 1729. **A**, Stapes. **B**, Incus. **C**, Malleus.

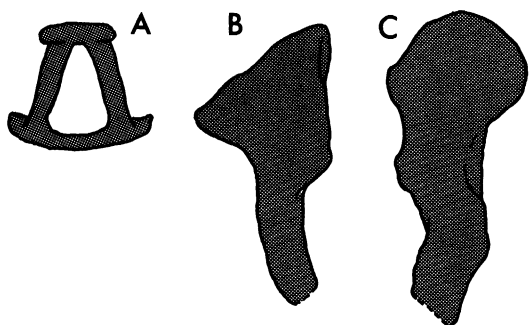HSB, and the HSB have an inclination of 10–30° relative to the enamel-dentine junction in the *portio interna* that changes to horizontal (90° relative to the enamel-dentine junction) in the *portio externa*. The enamel band is 80–185 μm thick, and the *portio externa* comprises 20–40% of the band. The horizontal HSB in the *portio externa* is a derived condition in multiserial enamel, which Martin (1992) otherwise found only in bathyergids.

DENTITION

The tooth crown pattern of *Tsaganomys altaicus* is poorly known because the occlusal pattern is worn away so quickly. The large collection from the Tsagan Nor Basin permits reconstruction of the ontogenetic replacement sequence, tooth homology, and the unworn crown pattern. Four subjective stages for the upper and lower dentition demonstrate patterns of tooth replacement (tables 2, 3; figs. 10, 11). The wear stages are certainly related to age but are not interpreted as cohorts. The homology of dp4 is evident in AMNH 85737, in which p4 is beginning to erupt below dp4. In several other specimens dp4 is clearly rooted, while m1-3 are not rooted and not heavily worn. As in other rodents there is no evidence of dp3 or p3 in any specimen. For the upper dentition, nine specimens (AMNH 19023, 19098, 19095, 83624, 83625, 84516, and 84544; M 429 and 557) have dP4 and a small, peg-like dP3 (fig.

10). Several other maxillae have an alveolus for dP3, which is lost very early and is never present after dP4 is lost and P4 has begun to erupt. The homology of dP4 is clear from AMNH 19098 and M 472. In AMNH 19098, the maxillary bone is broken away on the lingual side of the cheek teeth. The dP4 is rooted and heavily worn, in contrast to the hypsodont, unrooted M1-M2. The position of P4 is indicated by a matrix-filled slot on the labial margin of the jaw. In M 472, dP3 has been shed and the dP4 is nearly lost with P4 erupting below it. Several specimens record a stage in which M1-3 are beginning to wear and P4 is erupting from the jaw.

The upper molars are tetralophodont (fig. 10). In M1-2, the protocone is large and the hypocone absent. The protoloph and metaloph are roughly parallel, oriented transversely across the crown, and have no accessory cusps or lophules. With wear, the anteroloph and posteroloph join lingually to form a crescent to which the protoloph and metaloph unite. With progressively more wear all lophs unite labially and finally the occlusal patterns are lost. M3 is smaller than M1-2, more ovate in outline, and the protocone is more distinctly separated from the protoloph. P4 is molariform.

The lower molars are also tetralophodont (fig. 11). The protoconid and hypconid are pronounced cusps on m1-2. The hypoflexid remains prominent until heavy wear. The anterolophid and posterolophid connect buccally and define a nearly continuous cingulum around the lingual margin; the metaconid and entoconid are rudimentary or indistinct. A hypolophid extends transversely across the tooth. A metalophid and ectolophid are lower than the adjacent crests, but become distinct after light wear. The m3 differs by being slightly smaller than m1-2, and the ectolophid enters wear earlier relative to other crests on the tooth.

All of the cheek teeth acquire a round outline and flattened occlusal surface very early in wear. The roots of the cheek teeth do not close until the latest stages of wear. Wear may continue until P4 and p4 are almost worn away. In older animals that have formed roots for the cheek teeth, the roots sometimes extend above the bone and the anterior root of p4 and P4 may enter wear.
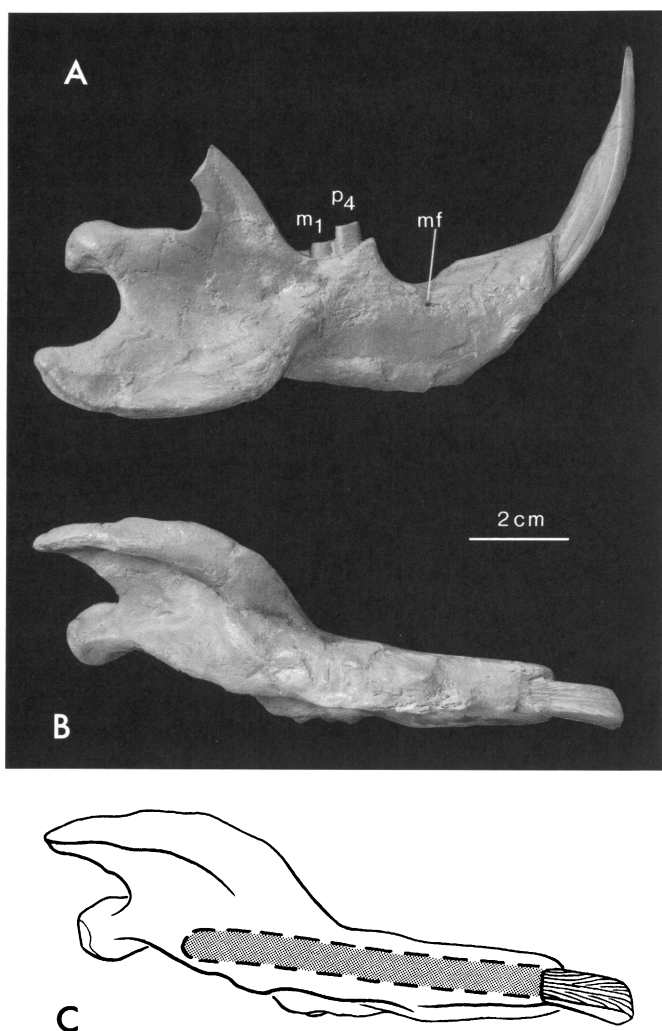
Fig. 9.   Mandible of *Tsaganomys altaicus* (AMNH 19037). **A**, Lateral view. **B**, Ventral view. **C**, Ventral view illustrating the path of the incisor through the corpus of the mandible.

PHYLOGENETIC ANALYSIS

ANALYZED TAXA

Taxa were selected on the basis of studies by Parent (1980), Lavocat and Parent (1985), and Meng (1990). Preliminary analyses of our data set suggested that *Tsaganomys* is allied with Hystricognathi; therefore, many taxa analyzed by Lavocat and Parent (1985) and Meng (1990) were excluded (Sciuridae, Myoxidae, etc.). The fossil taxa included in this analysis are known from relatively complete material. Many very important taxa are excluded because they are known only from teeth, jaws, or partial skulls that can be scored for only a few of the analyzed characters. These include Paleogene "ctenodactyloids" such as *Chapattimys*, *Birbalomys*, and *Advenimus*, and early "phiomorphs" such as *Protophiomys*, *Metaphiomys* and *Phiomys*. Several Deseadan "caviomorphs" are known from skulls (e.g., *Branisamys*, *Incamys*, and *Platypittamys*) but were excluded because they also cannot be scored for over half of the characters analyzed.

Ingroup taxa are hystricognathous rodents,

hystricomorphous rodents considered possible sister taxa of Hystricognathi in other studies (Ctenodactylidae, Anomaluridae, and Pedetidae), and putative ancestors of *T. altaicus* and other hystricognathous rodents (*Ardynomys occidentale* and Theridomyidae). As a member of "Franimorpha," *Reithroparamys delicatissimus* has also been considered an ancestor of hystricognathous rodents (Wood, 1975), a proposal refuted by Meng (1990) but tested again here. *Cocomys lingchaensis* and *Paramys copei* are included as primitive rodents. *Rhombomylus* and lagomorphs are considered closely related outgroups of Rodentia (Li and Ting, 1993; Meng et al., 1994) and serve to determine character polarity when it is ambiguous in Rodentia.

Modern representatives of each living taxon are, of course, much better known than fossil representatives, and in most cases character scores are assigned from modern taxa. However, fossil representatives are in some cases known from very well-preserved material (e.g., Fields, 1957; Vucetich, 1975; Parent, 1980), and character scores were checked against illustrations and descriptions to insure the scores were valid for each taxon analyzed. With the exception of Theridomyidae, extinct taxa are represented by a single species in order to minimize the possibility of non-monophyly of higher-level taxa. Within the Theridomyidae no single species was identified for which most of the characters could be scored. Scores for Theridomyidae are, therefore, assigned from multiple species, as noted below. The living Ctenodactylidae appears to be monophyletic but is almost certainly paraphyletic if many poorly known Paleogene forms are included; hence only living ctenodactylids are explicitly included in this analysis. Monophyly is assumed, not tested, for the remaining taxa, but by consensus appears supportable.

CHARACTER ANALYSIS

Cranial characters (table 4) were drawn from the literature and scored for phylogenetic analysis. Principal sources for characters were papers on middle ear anatomy by Parent (1980), Lavocat and Parent (1985), and Meng (1990). Other characters of the middle ear, zygomasseteric musculature, and
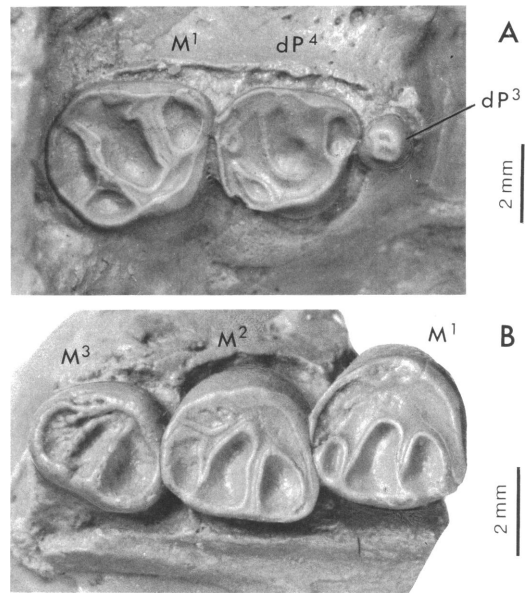

Fig. 10.   Unworn and lightly worn upper dentitions of *Tsaganomys altaicus*. A, Right maxilla (AMNH 19023) with dP3–4 and M1 present. The peglike dP3 is lost in all individuals in which the dP4 is lost. This maxilla is typical of wear stage 1 (table 3). B, Left maxilla (AMNH 84545) with M2–3 erupted but unworn or lightly worn, typical of wear stage 3. C, Complete maxilla (M 472) with P4 erupting below the dP4 and dP3 lost, also typical of stage 3. The occlusal patterns of M1 and M2 are worn to simple cylinders.

dentition often used in rodent phylogeny were drawn from Tullberg (1899), Landry (1957), Li et al. (1989), and Martin (1992), and our own survey. Landry (1957), Patterson and Wood (1982), and Luckett and Hartenberger (1985) provide lucid discussions of many characters. Character scores (table 5) were checked against specimens, published illustrations, and descriptions and generally agree with scores assigned in other analyses, but some changes are discussed below. Several characters and character states from other studies were uninformative among the taxa analyzed and were excluded. The following discussion focuses on characters that are controversial, characters for which scorings have been changed relative to previous studies or that were rejected in this analysis, and characters that were not included in discussions by Lavocat and Parent (1985) or Meng (1990).
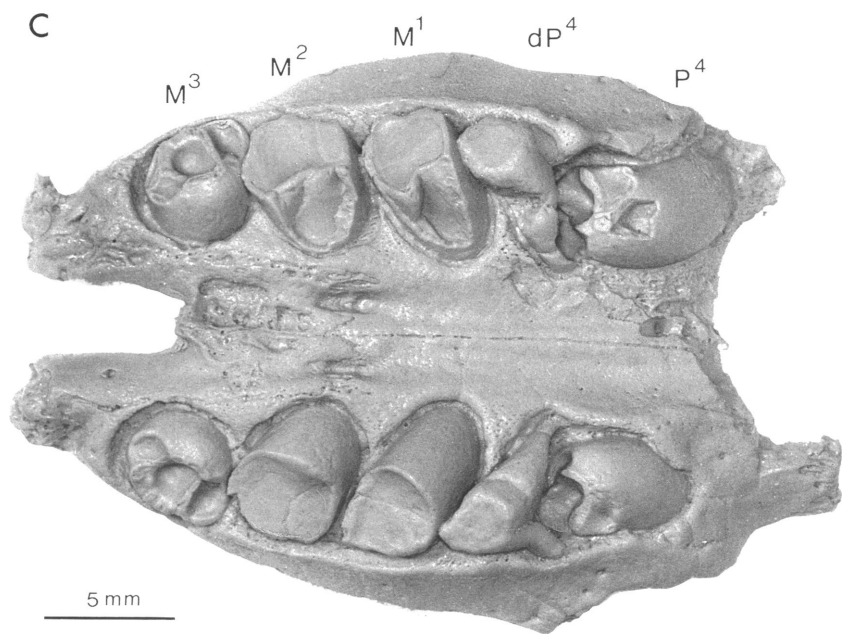
Fig. 10. Continued.

The numbers preceding each character description refer to tables 4 and 5. Characters used in previous analyses but rejected here have no number.

2. BULLA INFLATION AND THE HYPOTYMPANIC SINUS. The hypotympanic sinus, as defined by Klaauw (1931: 19), ". . . covers a part of the tympanic cavity that contains none of its principal elements, including the auditory ossicles and the fenestrae in the periotic. It is formed when the ventral wall loses its flatness and becomes inflated on the medial or caudal side." An inflated bulla must, therefore, have an enlarged hypotympanic sinus, but the presence of a complete bony bulla does not necessitate the presence of a large hypotympanic sinus (Klaauw, 1931). Lavocat and Parent (1985) and Meng (1990) apparently misinterpreted this character. Lavocat and Parent (1985) recognized three conditions for the hypotympanic sinus (referred to as the hypotympanic recess by them): absent, present, and an intermediate condition. The hypotympanic sinus may be small but

TABLE 2
Wear Stages for Upper Dentition (fig. 10)
(Wear stages are not used as age classes but to demonstrate tooth replacement.)

Wear stage	Description	Representative specimens
1	dP3–M1 erupted and wearing, M2 beginning to erupt.	AMNH 19023, AMNH 19095, AMNH 84544, M 557, M 429
2	dP3-dP4 heavily worm, dP3 sometimes shed; M1-M2 in early wear. M3 not erupted.	AMNH 19098, AMNH 83625, AMNH 84535, AMNH 84543, AMNH 84546
3	dP3 shed, P4 beginning to erupt beneath dP4; M3 erupted and wearing.	M 472, M 461, M 315, AMNH 84545, AMNH 82290
4	All permanent cheek teeth (P4–M3) erupted and worn to simple cylinders.	Many specimens

TABLE 3
Wear Stages for Lower Dentition (fig. 11)

Wear stage	Description	Representative specimens
1	dp4 and m1-m2 erupted and wearing; m3 not erupted.	AMNH 81218, AMNH 83503, AMNH 81927, AMNH 85538, AMNH 85738, AMNH 82260, AMNH 19023, M 532
2	dp4 roots showing above jaw line; m1-m2 lightly worn; m3 beginning to wear.	AMNH 82276, AMNH 82275, AMNH 85747, M 1778, AMNH 85737, AMNH 19098, AMNH 82268, AMNH 84545
3	dp4 shed, p4 beginning to erupt and wear; m1-m2 beginning to lose occlusal pattern; m3 moderately worn.	AMNH 85545, AMNH 82252, AMNH 26187, AMNH 85300, AMNH 85296, AMNH 85310, AMNH 82183, M 1775
4	All permanent cheek teeth (p4–m3) erupted and worn to simple cylinders.	Many specimens

cannot be absent if a bony bulla is present (the bulla is present in several taxa scored by Lavocat and Parent [1985] as having no hypotympanic sinus). Meng (1990) distinguished an inflated bulla and size of the hypotympanic sinus as different characters and provided different scoring for each (e.g., Sciuridae is scored by Meng [1990] as having an inflated bulla [his character 1] but no hypotympanic sinus [his character 21]). However, as defined above, there is no difference between these characters. Many rodents have one or more septa within the bulla that serve to partition regions of the hypotympanic sinus (see below). These regions are wholly within the ectotympanic bulla, unlike the epitympanic sinus or mastoid sinus, which are formed in part by other bones.

All rodents either have a bulla or preserve evidence that a bulla was present. Most modern rodents have an enlarged bulla that extends beyond the surrounding bones, and a relatively huge bulla occurs in many desert-dwelling rodents. This hyper-inflated condition, often involving the mastoid, epitympanic, and hypotympanic sinuses, is an adaptation for improved hearing in arid environments and also occurs outside the Rodentia (Fleischer, 1978), and thus adds little phylogenetic information. Two conditions, however, can be identified in Rodentia that appear to be of phylogenetic value. *Cocomys* has a very small, rounded bulla (Li et al.,

1989), which we interpret to represent the primitive state for rodents. Sciuravids also have a very small bulla similar to *Cocomys*, and *Paramys* likely had a small bulla based on the distribution of bulla-petrosal contacts. The bulla in each of these taxa is limited to within the surrounding bones. Among modern rodents, muroids generally have small bullae. The derived condition, in which the bulla is inflated and extends ventrally or laterally beyond the surrounding bones, is typical for most other rodents.

BULLA INTERNAL SEPTA. Development of internal septa within the bulla was treated as a character by Lavocat and Parent (1985). In the primitive state the bulla has a smooth internal surface and no septa. In the derived state there are one or more strong ridges or septa that may divide the hypotympanic sinus. These septa are usually restricted to the interior surface of the bulla and do not extend to the promontorium. The number of these septa appears to be related to the degree of bulla inflation; the greater the inflation, the more septa within the bulla, possibly to provide internal support. We interpret this character to be dependent upon bulla inflation and, therefore, do not consider it to be phylogenetically informative at this level.

Tsaganomys altaicus and *Octodon* (among taxa included in this analysis) have numerous septa within the hypotympanic sinus. These septa are strongly developed rather than ex-
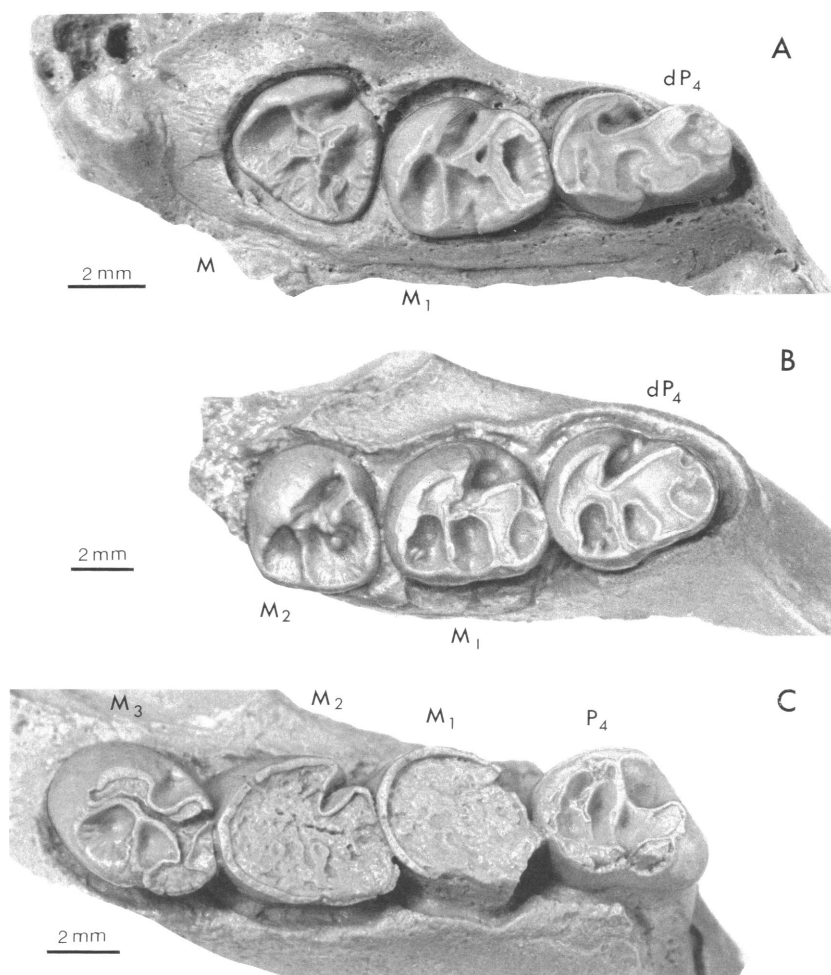
Fig. 11. Unworn and lightly worn lower dentitions of *Tsaganomys altaicus*. **A**, Left mandible (AMNH 19023; see associated upper dentition in figure 10) with dp4 still present, m1 lightly worn, and m2 beginning to erupt, typical of wear stage 1 (table 2). **B**, Left mandible (AMNH 81927) with dp4 present, and m1 and m2 in wear, typical of later phase of stage 1. **C**, Left mandible (AMNH 82183) with dp4 lost, p4 and m3 lightly worn, and m1-2 worn to cylinders, typical of wear stage 3.

pressed as a ridge for support. The septa, however, are structurally different (and therefore not homologous) in each taxon. In *Tsaganomys* the septa radiate from the promontorium to the tympanic annulis (fig. 7). In *Octodon* the septa do not radiate from the promontorium but instead connect to form a second interior ring within the bulla. Although these characters may provide phylogenetic information at a lower taxonomic level, we interpret these characters to have little phylogenetic significance at the level considered in this analysis.

3. PROMONTORIUM RELIEF AND COCHLEAR SHAPE. Lavocat and Parent (1985) proposed a character that describes the degree of relief of the promontorium from the body of the petrosal. In the primitive condition the promontorium has little relief and is hardly distinguishable from the body of the petrosal. In the intermediate condition the promontorium is more pronounced and swollen,

TABLE 4
Selected Characters and Character Polarity

(Characters are ordered unless noted below. The primitive state is 0 for all characters except incisor enamel microstructure (#25), for which state 1 is primitive (see fig. 12). For all other ordered characters, states 1 and 2 are sequentially more derived.)

1. Bulla-petrosal contact: (0) very loose, (1) tight, (2) fused.
2. Bulla inflation: (0) not inflated, (1) inflated.
3. Promontorium, relief: (0) low, (1) slightly expanded, (2) swollen with bulging cochlea.
4. Promontorium, orientation: (0) horizontal or slightly tilted, (1) vertical.
5. Cochlea, coils: (0) uniform, (1) last portion uncoiled.
6. Epitympanic sinus relations: (0) overlies the roof of the external auditory meatus, (1) separated by a shelf from the external auditory meatus.
7. Epitympanic sinus, form: (0) small shallow fossa, (1) dorsally expanded.
8. Proximal internal carotid artery system: (0) complete, (1) absent, (2) distal internal carotid artery absent, (3) stapedial artery absent (unordered).
9. Fenestra ovalis, orientation: (0) vertical relative to the antero-posterior plane of the skull, (1) inclined, (2) horizontal.
10. Fenestra ovalis, size: (0) relatively small, (1) intermediate, (2) large.
11. Fenestra rotunda, shape: (0) normal (rounded or ovate), (1) twisted.
12. Fenestra rotunda, size: (0) relatively small, (1) intermediate, (2) large.
13. Stapedius muscle, size (based on size of attachment scar): (0) large, (1) reduced, (2) absent.
14. Stapedius muscle, enclosure: (0) exposed in tympanic cavity, (1) partially covered within a fossa.
15. Tensor tympani muscle origin: (0) uncovered, (1) partially covered, (2) completely covered.
16. Facial nerve: (0) exposed in tympanic cavity, (1) partially enclosed by bony element, (2) completely enclosed by bony tube.
17. Malleus and incus: (0) separated, (1) fused.
18. Malleus head shape: (0) small and rounded with a thin bony lamina, (1) large and anteriorly expanded.
19. Optic foramen: (0) confluent between orbits, (1) not confluent.
20. Pterygoid fossa: (0) solid, (1) perforate.
21. Infraorbital foramen: (0) protrogomorphous, (1) hystricomorphous.
22. Lacrimal size: (0) large orbital wing, (1) reduced orbital wing.
23. Alisphenoid: (0) enlarged, meets parietal (no squamosal-frontal contact), (1) reduced, does not meet parietal (squamosal-frontal contact).
24. Mandible: (0) sciurognathous, (1) hystricognathous.
25. Incisor enamel microstructure: (0) uniserial, (1) pauciserial (primitive), (2) multiserial-acute angular, (3) multiserial-right angular (see fig. 12).
26. Mesolophule: (0) absent, (1) present.

while in the most derived condition there is a bulging cochlea whose apex is oriented roughly perpendicular to the promontorium. A related character proposed by Lavocat and Parent (1985) is the cochlear shape. In *Cocomys, Paramys*, and other early rodents the cochlea is in line with the promontorium, such that a line passing through the apex and helical axis of the cochlea would parallel the longest axis of the promontorium and exit through or near the fenestra rotunda. In the most derived condition the helical axis of the cochlea is strongly bent in an elbow-shape relative to the promontorium. This character is dependent upon promontorium relief; the cochlea cannot have a strongly elbowed shape relative to the promontorium if the cochlea has no relief relative to the body of the petrosal. These two characters describe the same feature.

4. PROMONTORIUM ORIENTATION. Parent (1980), Lavocat and Parent (1985), and Meng (1990) refer to this character as "petrosal" orientation. In order to avoid confusion with the intracranial (or cerebral) wall of the petrosal (which is tilted to some degree in all rodents for which the area is known), this character should be referred to as "promontorium orientation." In most rodents the promontorium is located dorsally (on the roof) within the bulla. This condition is known in *Rhombomylus* (Li and Ting, 1985) and early rodents including *Paramys, Cocomys*, and sciuravids (Li et al., 1989; Meng, 1990) and is, therefore, scored as primitive. In pedetids and anomalurids the entire bulla is rotated vertically and the promontorium lies on the medial wall of the bulla.

8. INTERNAL CAROTID ARTERY SYSTEM. Terminology of the internal carotid artery system (ICAS) follows Meng (1990), in which the proximal internal carotid artery is the portion of the internal carotid artery before the stapedial-promontory artery bifurcation, and the distal internal carotid artery is the portion after the bifurcation, regardless of position. Bugge (1985), Lavocat and Parent (1985) and Meng (1990) provide excellent discussions of the evolution of the ICAS in rodents. The primitive condition in rodents is a complete ICAS, with the stapedial and distal internal carotid arteries branching off the proximal internal carotid artery as it pass-

TABLE 5
Data Matrix of Selected Taxa and Character States
(Characters and states given in table 4.)

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Cocomys lingchaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?	0	0	0	0	0	0	1	0
Paramys copei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	1	0
Reithroparamys delicatissimus	1	1	1	0	0	0	1	2	2	1	0	0	0	0	0	1	?	?	?	0	0	0	?	0	1	0
Theridomyidae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Ardynomys occidentale	1	1	?	?	?	?	?	3	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0	0	1	0
Anomaluridae	1	1	2	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0
Pedetidae	1	1	2	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	0	0	1	0	0	3	0
Ctenodactylidae	2	1	2	0	1	1	1	1	1	1	1	1	2	2	0	1	2	1	1	1	0	1	0	0	3	0
Tsaganomys altaicus	2	1	2	0	1	1	1	1	2	1	0	1	0	1	0	2	0	0	1	0	0	1	0	1	2	0
Erethizontidae	2	1	2	0	1	1	1	3	1	1	0	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1
Hystricidae	1	1	2	0	0	1	1	1	1	1	0	1	2	0	1	2	1	1	1	1	1	1	1	1	2	1
Thryonomyidae	2	1	2	0	1	1	1	1	1	1	0	1	1	0	2	2	1	1	1	1	1	1	1	1	3	1
Bathyergidae	2	1	2	0	1	1	1	1	0	2	0	0	2	0	2	2	1	1	1	1	1	1	1	1	3	1
Octodontoidea	2	1	2	0	1	1	1	1	2	2	0	2	1	0	2	2	1	1	0	1	1	1	1	1	3	1
Chinchillioidea	2	1	2	0	1	1	1	1	2	2	0	2	1	0	2	2	1	1	0	1	1	1	1	1	2	1
Cavioidea	2	1	2	0	1	1	1	1	2	2	0	2	1	0	2	2	1	1	0	1	1	1	1	1	2	1

es over the promontorium (Bugge, 1985; Meng, 1990). The distal internal carotid, stapedial, or entire ICAS is lost in various rodents, but that transformation is not understood. The character is therefore coded with four unordered states. Alternatively the character could be split into three binary characters for presence and absence of each branch, but the resulting tree topologies are identical. Coding as one unordered character more clearly represents the state of our knowledge.

The path of the proximal internal carotid artery, if present, across the promontorium is phylogenetically informative (Lavocat and Parent, 1985; Meng, 1990) but is not variant in the taxa analyzed in this study. In fossil rodents the presence and path of the ICAS are not directly observable. Passage of the internal carotid artery and its branches in fossil taxa is assumed if evidence (carotid foramen, promontory groove, or stapedial tube) is present in the bones. Conroy and Wible (1978) demonstrated that this assumption is not always valid in primates. Lacking other evidence, however, we assume it is valid for rodents.

10, 12. SIZE OF THE FENESTRA OVALIS AND FENESTRA ROTUNDA. There is a degree of variation in the size of these fenestrae relative to other features of the middle ear, especially the promontorium. An objective or quantitative measure relative to other structures, however, cannot be satisfactorily defined. A ratio of a dimension of the fenestrae (e.g., circumference, diameter, or area) relative to the promontorium length, for example, fails because the margin of the promontorium cannot be defined adequately nor are the possible allometric effects known. Thus this character is subjectively coded.

17. FUSION OF THE MALLEUS AND INCUS. Fusion of the malleus and incus with a suture nearly always visible between the elements was noted by Tullberg (1899) as an important character diagnosing his concept of Hystricognathi. Patterson and Wood (1982) pointed out that a small proportion of adults of several hystricognath rodents have incompletely fused ossicles. They used this as evidence to refute this character and monophyly of Hystricognathi. Unfused ossicles, however, are not typical of any hystricognathous rodent described previously. Juveniles of many hystricognaths do not have fused ossicles and there is an ontogenetic transformation to complete fusion in adults (Doran, 1879; Fleischer, 1973); it is reasonable, therefore, to expect some individual variation in the timing of fusion, or that fusion might never occur in some individuals. Bathyergids, on the other hand, fuse the ossicles over

a considerable distance along the neck of the malleus and the *processus longus* of the incus. The condition of the ear ossicles is unknown in *Rhombomylus* and early rodents. The malleus and incus are fused in Miocene hystricognaths in which the ossicles are known (Fields, 1957; Lavocat, 1973; Vucetich, 1975). The primitive eutherian condition is unfused which, along with the ontogenetic transformation towards increased fusion, is evidence of polarity. The ear ossicles are not fused in *Tsaganomys*.

Only a two-state transformation is recognized in this study. Lavocat and Parent (1985) and Meng (1990) coded *Pedetes* as having an intermediate condition ("tightly joined"). The ossicles in *Pedetes* are separable and the "tightness of joining" is no greater than in other rodents with unfused ossicles (e.g., Tullberg, 1899: plate 24). The ossicles are joined to a greater degree, but not fused, in *Rhizomys* and *Tachyoryctes*, so an intermediate score for *Pedetes* is not supportable. The malleus and incus are known in one theridomyid, *Paradelomys*, and are apparently not fused (Hartenberger, 1973).

18. MALLEAR HEAD SHAPE. Doran (1879) and Tullberg (1899) noted that the head of the malleus in hytricognathous rodents is swollen and expanded anteriorly, and the malleus does not have a thin lamina. This expanded condition is derived in contrast to the head of the malleus in other rodents, lagomorphs, and insectivores, in which the head is small and rounded, often with a thin lamina of bone extending anteriorly from the neck (Doran, 1879; Tullberg, 1899; Cockerell et al., 1914; Fleischer, 1973). The malleus of Miocene hystricognathous rodents in which the ossicles are known is of typical hystricognath form, i.e., laterally expanded and fused (Fields, 1957; Lavocat, 1973; Vucetich, 1975). The malleus of *Tsaganomys* is not swollen or expanded anteriorly and has a thin lamina. The malleus of *Paradelomys* has a large lamina (Hartenberger, 1973).

19. OPTIC FORAMINA. The optic foramina are confluent between the orbits in *Rhombomylus*, lagomorphs, and *Cocomys lingchaensis* (Meng et al., 1994). Li et al. (1989) cited this as evidence that *Cocomys* is more primitive than *Paramys*, which they did not believe to have confluent optic foramina. *Par-*

amys copei (AMNH 4756), however, does have a confluent optic foramina, while *Paramys delicatus* (AMNH 12506) does not. The region is not preserved in the only known skull of *Reithroparamys*. The foramina are not confluent in *Tsaganomys* and many other rodents because of a posterior extension of the orbitosphenoid between the foramina. The confluent condition is scored as primitive within Rodentia, based on the condition in *Rhombomylus*, lagomorphs, *Cocomys*, and *Paramys copei*. Among the rodents analyzed in this study, Anomaluridae, Pedetidae, and non-erethizontid "caviomorphs" (Octodontoidea, Chinchilloidea, and Cavioidea) do have confluent foramina.

20. PTERYGOID FOSSA. The perforate condition, in which the pterygoid fossa is open anterodorsally, is found in all living hystricognathous rodents except *Hydrochaeris*, in which it is blocked by a posteriorly expanded M3. In bathyergids (except *Bathyergus*) the pterygoid fossa is perforate but passes dorsally into the braincase rather than into the orbit. This likely reflects the posterior extension of the incisors into the pterygoid region (Landry, 1957). In *Bathyergus* the incisors extend posteriorly only to the level of the infraorbital foramen and the pterygoid fossa opens into the orbit as in other hystricognaths. In *Tsaganomys* there is no perforation or pocket developed in the pterygoid region. Outside the hystricognathous rodents the perforate condition is found in living geomyoids, *Spalax*, and *Aplodontia* (Tullberg, 1899; Landry, 1957; Patterson and Wood, 1982). With the exception of *Tsaganomys*, a perforate fossa occurs in all fossil hystricognathous rodents in which the area is known, but not in any other fossil sciurognathous rodent, and thus the condition in geomyoids, *Spalax*, and *Aplodontia* is most parsimoniously interpreted as convergence (Luckett and Hartenberger, 1985). Lavocat (1974b: 11) reported that *Tsaganomys* has a perforate pterygoid fossa, which is incorrect based on specimens available to us.

Tullberg (1899) and Woods (1972) argued that the transformation of the internal pterygoid muscle favored elongation (through a perforated pterygoid fossa) and horizontal positioning of the muscle, resulting in an increased degree of propalinal chewing. Pro-

palinal chewing is not, however, restricted to hystricognaths (Landry, 1957) and occurs in taxa without a perforate pterygoid fossa. The earliest confirmed hystricognathous rodents, from the late Eocene—early Oligocene of the Fayum Depression of Egypt, did not have propalinal chewing (Holroyd, 1992) but unfortunately are not reported from skulls. Thus it appears that the perforate pterygoid fossa associated with propalinal chewing may be a derived feature within Hystricognathi. Confirmation of this hypothesis must await description of skulls of the Fayum hystricognathous rodents.

21. INFRAORBITAL FORAMEN. The protrogomorphous condition is generally considered to be the most primitive because it is found in the oldest rodents and in rodent outgroups. All living hystricognathous rodents are hystricomorphous (or derived from an hystricomorphous condition), but many hystricomorphous rodents are not hystricognathous. The Bathyergidae have long been a problem because adults are protrogomorphous but hystricognathous. Based on paleontological evidence, Lavocat (1973) proposed that bathyergid protrogomorphy is derived from an hystricomorphous condition. This is supported by myological studies; Parsons (1896), Tullberg (1899), and Boller (1970) have described a small slip of the masseter passing through the infraorbital foramen in bathyergids, whereas Maier and Schrenk (1987) show that bathyergids derive their protrogomorphous condition from an hystricomorphous one during fetal development. Although bathyergid protrogomorphy is clearly derived for modern hystricomorphs, such a transformation opens the possibility that other protrogomorphous rodents may have similarly derived this character state.

Coues and Allen (1877) first described a slip of the masseter and the maxillary nerve passing through the infraorbital foramen in *Aplodontia*. Eastman (1982) also described a slip of the masseter passing through the infraorbital foramen in *Aplodontia* and proposed that hystricomorphy was, therefore, primitive for rodents. Wahlert (1984) argued that multiserial enamel was the primitive condition for incisor enamel and that, therefore, so was hystricomorphy (since multiser-

ial enamel is found only in hystricomorphous rodents). We find the proposal that hystricomorphy is primitive for rodents to be very unlikely, because the protrogomorphous condition is widely distributed among the earliest rodents (e.g., Wood, 1962), outgroups such as lagomorphs (Lopez Martínez, 1985), *Rhombomylus* (Li and Ting, 1985), and taxa not included in this analysis such as Primates, and pauciserial enamel is now recognized as primitive (see character 25 below). Only protrogomorphy and hystricomorphy are relevant states in this analysis, so the transformation is ordered because we interpret protrogomorphy as primitive. The Bathyergidae are scored as hystricomorphous based on the arguments outlined above.

22. LACRIMAL. The lacrimal bone in rodents can have a large orbital wing or be reduced to the immediate border of the anterior zygoma. In *Rhombomylus* the lacrimal has a large facial wing anterior to the zygoma and no orbital wing posterior to the zygoma (Li and Ting, 1985). This is plesiomorphous in mammals and a similar facial wing is not found in rodents. *Rhombomylus*, therefore, cannot be used to determine polarity of the lacrimal bone shape within rodents. Lagomorphs have a small facial wing and a large orbital wing. In most specimens of early rodents the lacrimal region is damaged or the element is missing. The lacrimal was apparently loosely attached. The left lacrimal is preserved in one specimen of *Paramys copei* (AMNH 4755). The element has a significant orbital wing and is not restricted to the border of the lacrimal foramen. On the left side of a skull of *Paramys delicator* (AMNH 12506) a portion of the lacrimal is preserved, showing the suture of the lacrimal with the maxilla and frontal and also indicating a large orbital wing. The size of the lacrimal in these specimens, compared to the missing area in other paramyid skulls, indicates that the missing area generally marks the borders of the lacrimal bone in taxa in which it is not preserved. *Cocomys lingchaensis* (Li et al., 1989) and theridomyids (Hartenberger, 1973) also have lacrimals with large orbital wings. This state is therefore scored as primitive. In more derived rodents the lacrimal is reduced from a large orbital wing, to the immediate border of the lacrimal foramen, and does not extend

posteriorly into the orbital region. This is the condition in hystricognathous rodents. *Thryonomys* and *Hydrochaeris* have a lacrimal that is enlarged anterolaterally and forms a large part of the anterior zygoma bordering the infraorbital foramen. The lacrimal does not extend posteriorly into the orbit and hence represents a different condition.

23. ALISPHENOID. The alisphenoid bone in hystricomorphous rodents is generally reduced relative to other rodents (Landry, 1957). In the primitive condition the anterodorsal part of the alisphenoid extends around the squamosal anteriorly to meet the parietal and exclude a squamosal-frontal contact. This condition is known in *Paramys* and *Cocomys*. In most hystricomorphous rodents the alisphenoid is reduced anteriorly and the squamosal and frontal meet in the orbital wall. Landry (1957) also noted an expansion of the posterior portion of the alisphenoid in many hystricomorphs, but bones in this region undergo a much more complex rearrangement, and posterior expansion is not even consistent within a single genus (*Erethizon*). In *Tsaganomys* the orbital wing of the alisphenoid is not reduced and contacts the parietal. Bathyergids have a very large squamosal that forms a large part of the braincase, and the alisphenoid and parietal are far apart. *Ctenodactylus* has the primitive condition. The condition for theridomyids is based on *Theridomys* cf. *T. gregarius*, in which the alisphenoid is reduced and there is a large squamosal-frontal contact (Hartenberger, 1973).

24. MANDIBLE. In the original concept of hystricognathy, the anterior portion of the angular process begins fully outside the main body of the mandible in a plane separate from that defined by the incisor and cheek teeth, and the angular process is posteriorly elongate (Tullberg, 1899). Woods (1972) identified a difference in the area of insertion of the *masseter superficialis*, which separates hystricognaths (Hystricomorpha *sensu stricto* of Woods, 1972) from other rodents. In all living hystricognathous rodents the *masseter superficialis* inserts along the entire ventral margin of the angular process, including the posteriorly elongated tip. Insertion of the *masseter superficialis pars reflexa* has migrated around to the posteromedial side of

the mandible underneath the *masseter pterygoideus*. This new course is associated with a groove on the anterior margin of the angle. Such migration does not occur in other rodents or in lagomorphs. In *Tsaganomys* the angular process extends posteriorly beyond the condyle with clear areas for insertion of the *masseter superficialis*. The groove for passage of the *masseter superficialis pars reflexa*, however, is not so well developed in *Tsaganomys* as in other hystricognathous rodents and insertion of the muscle may not have extended posteriorly under the *masseter pterygoideus*.

The concept of "incipient hystricognathy" was first proposed by Wood (1962). This state was an important character for Wood's (1975) "Franimorpha" and was used by him in numerous papers (1980a, 1980b, 1984, 1985). "Incipient hystricognathy" was based on a condition in which the angular process of the lower jaw was displaced slightly laterally relative to the toothrow. The condition has been questioned by Dawson (1977) and Korth (1984). Korth (1984) argued that "incipient hystricognathy" is merely a heavy ridge bounding the masseteric fossa, and that the groove on the ventral surface of the mandible in some "franimorph" taxa is not homologous to the groove for passage of the *masseter superficialis pars reflexa* in hystricognaths. Furthermore, the mandibles do not exhibit a posterior expansion of the angle for insertion of the *masseter superficialis*. "Incipient hystricognathy" is, therefore, not recognized here. Since sciurognathy is most like the condition in other eutherians and is widely distributed among all early rodents and rodent outgroups, it is interpreted as the primitive condition.

25. INCISOR ENAMEL MICROSTRUCTURE. The incisor enamel microstructure in rodents has received considerable attention in view of its potential usefulness for phylogenetic inference. The primitive condition for rodents has been argued to be either multiserial (Wahlert, 1984; Koenigswald, 1985) or pauciserial (Wahlert, 1968, 1989; Martin, 1992, 1993, 1994). Martin (1992) surveyed the incisor enamel microstructure in 110 fossil and recent rodents, particularly hystricognathous taxa. He concluded that pauciserial enamel

is primitive for rodents based on outgroup comparison with *Rhombomylus*, occurrence of pauciserial enamel in the earliest rodents, and comparison with other mammals that have Hunter-Schreger bands. Uniserial and multiserial enamel are independently derived from the pauciserial condition.

Martin (1992) further recognized three subtypes of multiserial enamel based on the angle at which interprismatic matrix crystallites intersect the Hunter-Schreger bands. Two subtypes, one in which the prisms and interprismatic matrix are parallel and one in which the prisms and matrix are at a low angle, are not always differentiable and sometimes occur in upper and lower incisors of the same individual. These two subtypes are therefore grouped together for this analysis and referred to as acute-angular matrix. In the remaining subtype the interprismatic matrix forms narrow sheets perpendicular to the prisms and is referred to as right-angular matrix. Martin (1992, 1993, 1994) favored a transformation with the right-angled condition derived from the acute-angled condition, based on stratigraphical and biomechanical arguments. Outgroup comparison also supports this interpretation. Among rodents with pauciserial enamel (e.g., paramyids) and *Rhombomylus*, the interprismatic matrix intersects the Hunter-Schreger bands at an acute angle or is parallel (e.g., Wahlert, 1989; Martin, 1992). The transformation series is ordered with pauciserial as the primitive state, with independent derivations of uniserial and multiserial enamel from the pauciserial condition. Right-angular matrix is coded as derived from acute-angular matrix. This character is therefore coded as shown in figure 12, with pauciserial scored as 1 to allow this type of transformation.

Tsaganomys and bathyergids share a condition in which the prisms in the *portio externa* are oriented perpendicular to the enamel surface, which Martin (1992) interpreted as evidence of a close relationship. *Tsaganomys* and bathyergids, however, have different multiserial enamel subtypes. These subtypes were considered by Martin (1992) to be intraspecifically invariant, arguing against a close relationship. Patterson and Wood (1982: 516) cited unpublished data claiming
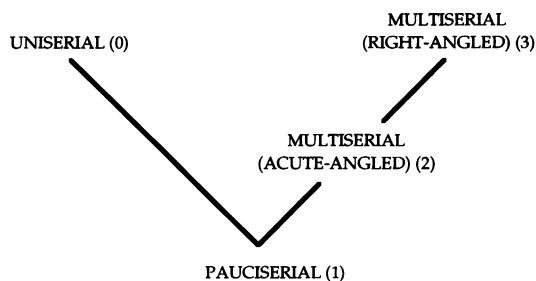

Fig. 12. Incisor microstructure character transformation tree. Pauciserial enamel (state 1) represents the primitive state, with independent derivation of uniserial (0) and multiserial (2, 3) enamel. Multiserial enamel with right-angled interprismatic matrix relative to enamel prisms (3) is considered more derived than multiserial enamel with acute-angular matrix (2). This organization forces a minimum of two steps for a transformation from uniserial to multiserial enamel, consistent with the independent derivation of each microstructural type from a pauciserial form.

Tsaganomys to have enamel microstructure intermediate between multiserial and pauciserial, which is incorrect, *fide* Martin (1992: 135).

26. MESOLOPHULE. One series of related dental characters has figured prominently in all discussions of hystricognath phylogeny: the number and homology of lophs on the upper molars of "phiomorphs" and "caviomorphs." The problem revolves around two questions: (1) what are the homologies of the crests in question (the third and fourth from the anterior margin)? and (2) is the presence of five or four crests the primitive condition for South American "caviomorphs"? Lavocat (1973, 1974a, 1974b, 1976, 1980), Hoffstetter and Lavocat (1970), and Hoffstetter (1972, 1975) have long argued that a five-crested pattern is plesiomorphic for "caviomorphs," and that crest 3 is a mesoloph and crest 4 is a metaloph. Lavocat used this as evidence to argue that "caviomorphs" were derived from African "phiomorphs," which also have five crests. Wood (1974b, 1980c, 1984, 1985; Wood and Patterson, 1959, 1970; Patterson and Wood, 1982), on the other hand, has argued that a four-crested pattern was primitive for "caviomorphs" and that crest 3 is a metaloph and crest 4 is a "neo-
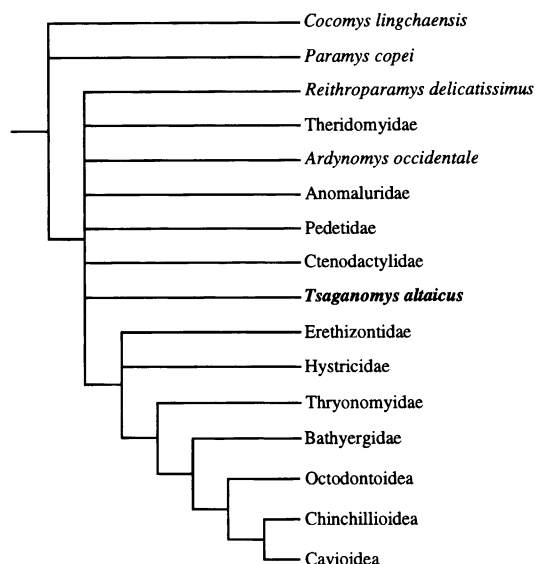
Fig. 13. Strict consensus tree of 45 equally most parsimonious trees resulting from a branch-and-bound search of the full data set. The individual trees each have 68 steps, a consistency index of 0.56, and a retention index of 0.77.

loph" of new origin, and used this as evidence to refute derivation of "caviomorphs" from "phiomorphs."

The discovery of chapattimyids (possibly the nearest outgroup to all hystricognathous rodents) from the middle Eocene of Pakistan (Hussain et al., 1978) and the late Eocene of northern Africa (Jaeger et al., 1985; Flynn et al., 1986) prompted reconsideration of the problem by Flynn et al. (1986). A central cusp (the metaconule) occurs on the metaloph in chapattimyids (Jaeger et al., 1985; Flynn et al., 1986). A small crest (the third from the anterior margin) extends labially from the metaconule (Jaeger et al., 1985). Flynn et al. (1986) called this third crest a mesolophule. This crest is not homologous with a mesoloph, which occupies the same topographic location (between the protoloph and metaloph) but originates from a mesocone on a mure connecting the protocone and hypocone (hystricognaths do not have a mure or mesocone). Thus it is clear that five crests is the primitive condition for "phiomorphs" and the third crest is not a mesoloph.

Jaeger (1989) suggested that the third crest in early non-erethizontid "caviomorphs" is

formed as a loph that extends lingually from a mesostyle, and, therefore, is not homologous to the mesolophule in "phiomorphs." If correct, this would imply that non-erethizontid "caviomorphs" and "phiomorphs" are monophyletic sister groups whose nearest common ancestor predates middle and late Eocene chapattimyids. Jaeger's (1989) interpretation was based on the condition in the P4 of Branisamys, in which the mesolophule is not continuously high (the lingual portion is topographically lower than the labial portion). With light wear there appears to be a mesostyle before the entire crest has entered wear. Jaeger's (1989) hypothesis appears unlikely to us because the mesolophule in premolars and molars of Metaphiomys schaubi (e.g., Wood, 1968: fig. 11D) shows the exact same condition. This condition is, therefore, not restricted to "caviomorphs," and the mesolophule in "phiomorphs" and "caviomorphs" is homologous.

Absence of a mesolophule is the primitive state. The presence or absence of a mesolophule is ambiguous in most of the living taxa due to the development of extreme hypsodonty but can be ascertained from fossil representatives. The mesolophule and other crests merge early in wear, but this is different from the primitive condition in which the mesolophule is not present at all. The condition in bathyergids is difficult to determine because at their earliest appearance (early Miocene; Lavocat, 1973), bathyergids already have very hypsodont cheek teeth. The presence of a mesolophule in the Bathyergidae is based on the condition in Bathyergoides neotertiarus. Lavocat (1973) illustrated several dentitions of B. neotertiarus, but most are worn and the crests generally obliterated. In Lavocat's (1973) plate 29, fig. 1, however, the unworn M2 of B. neotertiarus has five crests. The fourth crest (metaloph) is small and oriented anteroposteriorly from the posteroloph, and with very early wear the mesolophule and metaloph merge into one crest.

ANALYTICAL METHODS AND RESULTS

Most characters were analyzed as polarized and ordered. As an ordered character type,

A

- Cocomys lingchaensis
- Paramys copei
- Theridomyidae
- Reithroparamys delicatissimus
- Anomaluridae
- Pedetidae
- Ctenodactylidae
- **Tsaganomys altaicus**
- Erethizontidae
- Hystricidae
- Thryonomyidae
- Bathyergidae
- Octodontoidea
- Chinchillioidea
- Cavioidea

B

- Cocomys lingchaensis
- Paramys copei
- Theridomyidae
- Reithroparamys delicatissimus
- Anomaluridae
- Pedetidae
- Ctenodactylidae
- **Tsaganomys altaicus**
- Erethizontidae
- Hystricidae
- Thryonomyidae
- Bathyergidae
- Octodontoidea
- Chinchillioidea
- Cavioidea

C

- Cocomys lingchaensis
- Paramys copei
- Theridomyidae
- Reithroparamys delicatissimus
- Anomaluridae
- Pedetidae
- Ctenodactylidae
- **Tsaganomys altaicus**
- Erethizontidae
- Hystricidae
- Thryonomyidae
- Bathyergidae
- Octodontoidea
- Chinchillioidea
- Cavioidea

D

- Cocomys lingchaensis
- Paramys copei
- Theridomyidae
- Reithroparamys delicatissimus
- Anomaluridae
- Pedetidae
- Ctenodactylidae
- **Tsaganomys altaicus**
- Hystricidae
- Erethizontidae
- Thryonomyidae
- Bathyergidae
- Octodontoidea
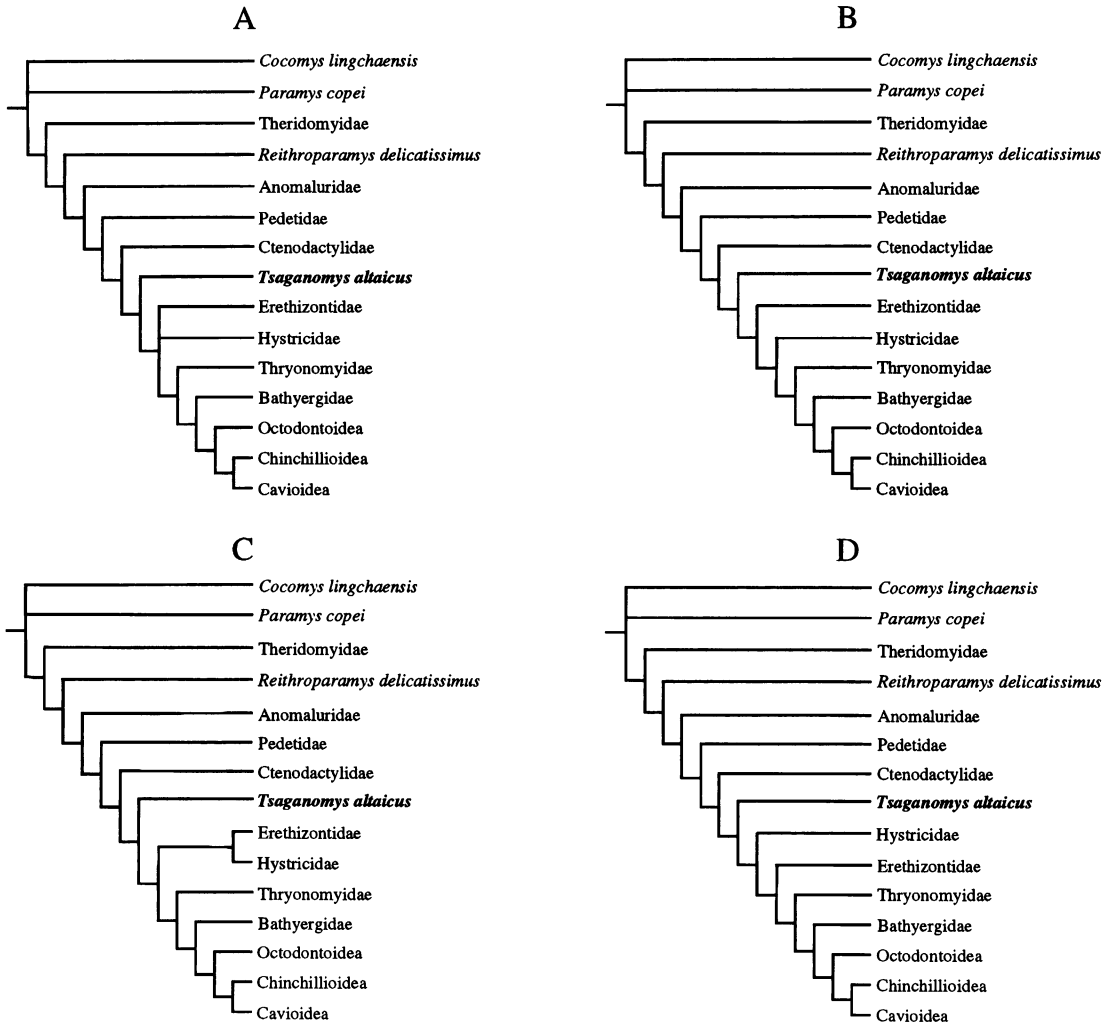- Chinchillioidea
- Cavioidea

Fig. 14. Equally most parsimonious trees resulting from a branch-and-bound search of the data set excluding *Ardynomys occidentale*. A search with ordered characters yields three trees (A-C). Each tree has 66 steps, a consistency index of 0.58, and a retention index of 0.77. The trees differ only in the placement of Erethizontidae and Hystricidae. The strict consensus is shown in figure 15. A search with unordered characters also yields three trees (B–D). Each tree has 62 steps, a consistency index of 0.61, and a retention index of 0.79. Note that two of the trees (B and C) result from searches with both ordered and unordered characters. Only the placement of Erethizontidae and Hystricidae varies among trees B–D. The strict consensus of trees B–D has the same topology as the tree in figure 15.

transformations follow the sequence 0-1-2 and are polarized with 0 as the primitive state unless otherwise noted. A transformation from state 0 to state 2 without the intermediate state 1 is counted as two steps. Character 8, internal carotid artery system (table 4), is coded as an unordered character be-

cause the transformation series could not be deduced although the plesiomorphic state is known (see character analyses above). As an unordered character type, a character state may transform to any other and is counted as one step. Character 25, incisor enamel microstructure, is coded following the transfor-
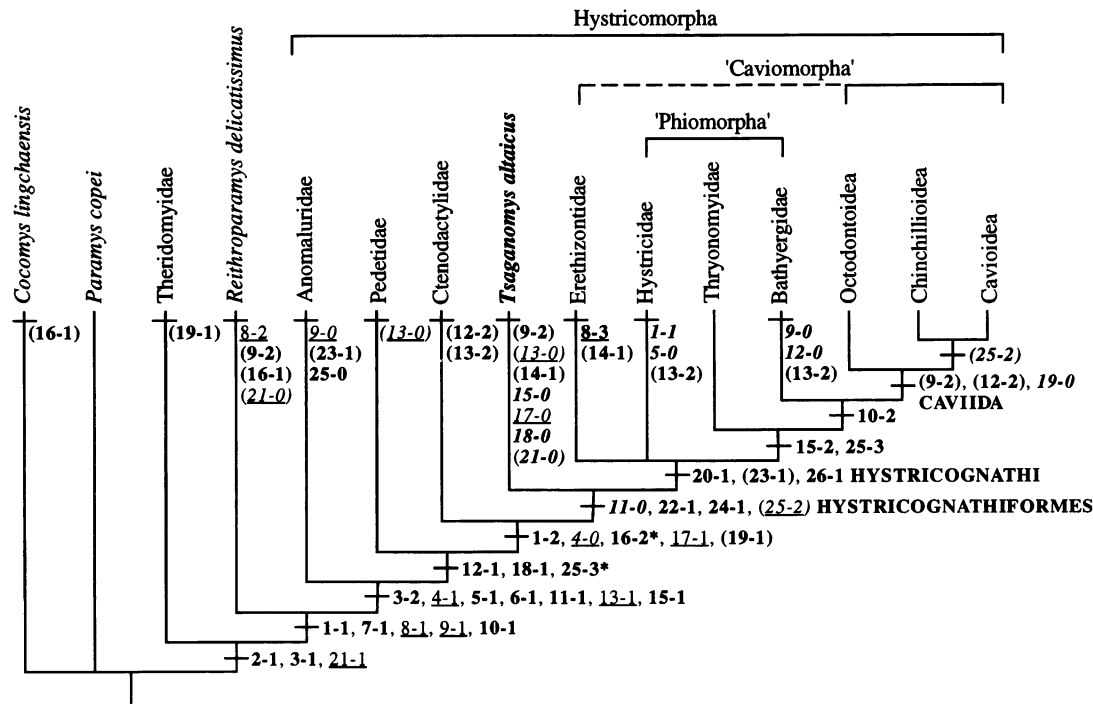
Fig. 15. Strict consensus of trees A–C in figure 14, based on a branch-and-bound search with ordered characters. Apomorphies correspond to characters and states in table 4. Transformations that are unambiguous for that branch are in boldface. Transformations that are reversals of ordered characters are italicized. Transformations that are dependent upon the optimization method (ACCTRAN versus DELTRAN) are underlined. Transformations that occur more than once are enclosed in parentheses. Transformations that are part of an ordered series but are longer than one step are indicated by an asterisk. Individual character statistics are presented in table 6. The traditional groupings of "Phiomorpha" (*sensu* Lavocat, 1973: 20; Hystricidae + Thryonomyidae + Bathyergidae), "Caviomorpha" (Erethizontidae + Octodontoidea + Chinchillioidea + Cavioidea), and Hystricomorpha are shown above the cladogram. Caviida and Hystricognathiformes are new taxa defined phylogenetically (see text).

mation shown in figure 12. The character matrix was analyzed with PAUP 3.1.1 (Swofford, 1993) with ACCTRAN optimization and resulting trees were manipulated with MacClade 3.04 (Maddison and Maddison, 1992).

A branch-and-bound search of the full data set of 16 taxa yielded 45 equally most parsimonious trees, each with 68 steps, a consistency index of 0.56, and a retention index of 0.77. The strict consensus tree (fig. 13) resolves the living hystricognathous rodents as a monophyletic clade with a polytomy for most of the remaining taxa. Only 11 of the 26 characters could be scored for *Ardynomys occidentale*, which introduces considerable uncertainty in the position of this taxon and

overall tree instability. *Ardynomys occidentale* was therefore excluded from further consideration and the analysis repeated with the 15 remaining taxa. A branch-and-bound search yielded three most parsimonious trees, each with 66 steps, a consistency index of 0.58, and a retention index of 0.77 (fig. 14A, B, C). The strict consensus tree (fig. 15) has a basal tritomy for Erethizontidae + Hystricidae + other living hystricognathous rodents. Character diagnostics for the tree in figure 15 are presented in table 6. In order to test the *a priori* assumptions of character transformations, the analysis was repeated with all characters unordered. Three most parsimonious trees were generated, each with 62 steps, a consistency index of 0.61, and a

retention index of 0.79 (fig. 14B, C, D). Two of the three trees have the same topology as trees recovered from the search with ordered characters (fig. 14B, C), and again the trees differ only in the position of Erethizontidae and Hystricidae. Topology of the strict consensus of trees B–D in figure 14 is the same as the tree in figure 15.

DISCUSSION

TSAGANOMYS AND CYLINDRODONTIDAE

Burke (1936) and Wood (1937, 1970, 1974a) have argued for a close relationship between *Tsaganomys* and cylindrodonts, specifically *Ardynomys occidentale*. Most classifications (e.g., Simpson, 1945; Wilson, 1949; Wood, 1955; Chaline and Mein, 1979; Stucky and McKenna, 1993) consider *Tsaganomys* a cylindrodont and this is the most commonly accepted placement (e.g., Shevyreva, 1974; Kowalski, 1974; Parent, 1980, 1993). The similarities between *Tsaganomys* and *Ardynomys* mentioned by Burke (1936) are strictly superficial or plesiomorphous: development of an antorbital crest overhanging the orbit, expanded anterior zygoma, and ovate infraorbital foramen, which are shared by most protrogomorphous rodents. Wood (1970) pointed out that the incisor in *Ardynomys* extends into the orbit as in *Tsaganomys* and also argued that the angular process of *Tsaganomys* could by derived from the condition in *Ardynomys*. Wood (1970, 1974a), however, noted that the modifications in the incisors and angular process and other similarities could be due to fossorial modification. The dentition of *Tsaganomys* is strikingly similar to that of some cylindrodonts, particularly the Cylindrodontinae of Wood (1974a): the upper molars have a large protocone and have lost the hypocone; the anteroloph, protocone, and posteroloph are united to form a continuous cingulum; cusps are not distinct on the lophs; the protoloph and metaloph converge slightly towards the protocone; the cheek teeth are notably cylindrical in shape; and the hypoconid is distinct from the mure on the lower molars.

Ardynomys lacks all of the derived features of hystricognathous rodents and is different in this respect from *Tsaganomys*. Neither the middle ear region of *Ardynomys* nor that of

TABLE 6
Character Diagnostics for the Tree in Figure 15
(Character numbers correspond to those in tables 4 and 5.)

Character	Consistency index	Homoplasy index	Retention index
1	0.667	0.333	0.875
2	1.000	0.000	1.000
3	1.000	0.000	1.000
4	0.500	0.500	0.000
5	0.500	0.500	0.750
6	1.000	0.000	1.000
7	1.000	0.000	1.000
8	1.000	0.000	1.000
9	0.333	0.667	0.500
10	1.000	0.000	1.000
11	0.500	0.500	0.500
12	0.500	0.500	0.750
13	0.333	0.667	0.429
14	0.500	0.500	0.000
15	0.667	0.333	0.875
16	0.500	0.500	0.750
17	0.500	0.500	0.667
18	0.500	0.500	0.500
19	0.333	0.667	0.667
20	1.000	0.000	1.000
21	0.333	0.667	0.333
22	1.000	0.000	1.000
23	0.500	0.500	0.800
24	1.000	0.000	1.000
25	0.500	0.500	0.625
26	1.000	0.000	1.000

any other cylindrodont has been described. Wahlert (1974) identified a carotid canal entering the bulla and the absence of a stapedial foramen in *Ardynomys* and *Cylindrodon*. This implies the presence of an internal carotid artery and the absence of a stapedial artery, which is less derived than the condition in *Tsaganomys* and most other hystricognaths in which the entire ICAS is lost. The incisor enamel in three cylindrodonts (*Dawsonomys*, *Mysops*, and *Ardynomys*) has the primitive pauciserial state (Martin, 1992), while Hystricognathi and its outgroups share multiserial enamel. *Ardynomys* has also lost the transverse canal (Wahlert, 1974), a derived condition that is not shared with *Tsaganomys* or any other hystricognathous rodent. *Ardynomys* also retains the enlarged alisphenoid and lacrimal, which are reduced in most hystricognathous rodents.

Although this analysis does little to determine where cylindrodonts fit in rodent phylogeny, it is clear that there is little evidence to unite *Ardynomys* with *Tsaganomys* or with Bathyergidae. The fact that *Ardynomys* and other cylindrodonts can only be coded for less than half of the analyzed characters precludes any further, supportable, discussion. The only conclusion that we reach is that *Tsaganomys* has little in common with *Ardynomys*.

TSAGANOMYS AND BATHYERGIDAE

Evidence cited by Matthew and Granger (1923a) and Landry (1957) for allying *Tsaganomys* with Bathyergidae includes protrogomorphy, hystricognathy, procumbent incisors extending into the orbit, hypsodont cheek teeth, and certain superficial similarities. With the exception of hystricognathy, none of these characters provides strong evidence of relationship between *Tsaganomys* and bathyergids. The protrogomorphous condition in bathyergids is secondarily derived from an hystricomorphous one (Maier and Schrenk, 1987), and the transformation from hystricomorphy to protrogomorphy is demonstrated in the fossil record of bathyergids since the Miocene (Lavocat, 1973). If the protrogomorphous condition in *Tsaganomys* is similarly derived from an hystricomorphous condition, a close relationship with bathyergids would require two separate origins of protrogomorphy within the Bathyergidae (one in the Oligocene for *Tsaganomys* and a second in the Miocene for "true" bathyergids) and, therefore, seems unlikely.

Most of the resemblance between *Tsaganomys* and bathyergids is related to fossorial adaptation. Cranial specializations for fossorial life include forward-sloping occiput, narrow interorbital constriction, and triangular braincase, as found in *Tsaganomys*, bathyergids, and other fossorial rodents including *Myospalax*, *Spalax*, *Thomomys*, *Aplodontia*, and *Spalacopus* (e.g., Ellerman, 1940; Nevo, 1979; Lessa and Thaeler, 1989; Jarvis and Bennett, 1991). Fossorial adaptations are also highly developed in the postcranial skeleton of *Tsaganomys* (Vinogradov and Gambaryan, 1952). Extension of the upper incisor well into the orbit is a specialized feature of *Tsaganomys*, but also occurs in some bathyergids, *Ardynomys occidentale*,

and notably in *Spalacopus*. Landry (1957) allied *Tsaganomys* more closely with *Bathyergus* than with other bathyergids based on incisors that extend posteriorly only to the infraorbital foramen. This is incorrect for *Tsaganomys*, in which the incisors extend well into the orbit and end lateral to M1-2. In bathyergids the shape and posterior extension of the incisors is related to mode of tunnel excavation. *Bathyergus* digs with well-developed claws (Jarvis and Bennett, 1991) and has incisors like those of many other rodents, which do not extend posteriorly into the orbit and anteriorly curve sharply downwards. All other bathyergids dig with their incisors, which extend posteriorly through the orbit into the pterygoid region posterior to the M3 and are anteriorly very procumbent (i.e., do not turn strongly downward). Only the fossorial hystricognathous rodent *Spalacopus* has a similar condition among living taxa, in which the incisors extend posteriorly into the orbit and anteriorly are very procumbent, also an adaptation for using the incisors to dig (Nevo, 1979). In fact, Vinogradov and Gambaryan (1952) interpreted the functional morphology of *Tsaganomys* to represent a "tooth-digger" rather than a "claw-digger" based mostly on the postcranial skeleton, not the posterior penetration of the incisors. Increased procumbency (although not quite to the degree of bathyergids, *Spalacopus*, and *Tsaganomys*) is correlated with the method of digging (Lessa and Thaeler, 1989).

No evidence in favor of a special relationship between *Tsaganomys* and bathyergids to the exclusion of other hystricognathous rodents could be identified in this study. Several characters argue for a closer relationship between bathyergids and other hystricognathous rodents than between *Tsaganomys* and bathyergids. These include states of multiserial enamel microstructure subtype, pterygoid fossa, fusion of the malleus and incus, shape of the mallear head, stapedial fossa, and other characters (fig. 15).

TSAGANOMYS, HYSTRICOGNATHI, AND PHYLOGENETIC DEFINITIONS OF TAXON NAMES

It is clear from the results of this analysis (fig. 15) that (1) hystricognathous rodents are monophyletic, and (2) *Tsaganomys* is the

nearest outgroup of living hystricognathous rodents. Two characters found in all members of the clade uniting *Tsaganomys* with living hystricognathous rodents are reduced lacrimal (22-1) and hystricognathous mandible (24-1). In addition *Tsaganomys* has two other features that characterize hystricognathous rodents and their outgroups (fig. 15), loss of the internal carotid artery system (8-1) and multiserial incisor enamel (25-2 and 25-3). However, *Tsaganomys* also lacks two characters often used to characterize hystricognathous rodents, fusion of the malleus and incus (17-1) and an expanded mallear head (18-1). Living hystricognathous rodents are more derived than *Tsaganomys* in having a perforated pterygoid fossa (20-1), reduced alisphenoid (23-1; also in Anomaluridae) and a mesolophule on the cheekteeth (26-1, the "five-crested" condition).

The results of this study imply a rather different organization of Hystricognathi than historical classifications such as those of Tullberg (1899), Simpson (1945), Wood (1955), and Patterson and Wood (1982). The traditional groups "Caviomorpha" and "Phiomorpha" are not monophyletic, and Erethizontidae is well isolated from other "caviomorphs" (Chinchilloidea, Cavioidea, and Octodontoidea). Thryonomyidae and Bathyergidae are sister taxa to the non-erethizontid "caviomorphs." These arrangements are not new ideas and are also supported by myology (Woods, 1972; Woods and Hermanson, 1985) and macromolecular systematics (Sarich, 1985).

The phylogenetic organization proposed in figure 15 brings into question the definitions and diagnoses of hystricognathous rodent clades. Considerable attention has been devoted recently to phylogenetic taxonomy and the meaning (and difference) of definitions and diagnoses (de Queiroz and Gauthier, 1990, 1992; de Queiroz, 1994; Bryant, 1994). Tullberg (1899: 69) defined Hystricognathi on the basis of a single character, the hystricognathous jaw, and supported this character-based definition with other character states that are not all uniquely restricted to Hystricognathi. This type of definition is what de Queiroz (1994) terms "essentialistic," in which the definition is in the form of a description of characters. If a phylogenetic definition is adopted for the name "Hystricog-

nathi," then the problem reduces to defining "Hystricognathi" in terms of ancestry. Furthermore, for nomenclatural stability the name "Hystricognathi" should, to retain priority, apply to the clade conceptually recognized by Tullberg (1899). Tullberg included in his "Tribus Hystricognathi" all of the living hystricognathous rodents known at that time, corresponding to all hystricognathous rodents considered in this analysis except *Tsaganomys*. On the basis of taxa included in Tullberg's (1899) concept of Hystricognathi and our phylogenetic results (fig. 15), Hystricognathi is defined phylogenetically as the most recent common ancestor of Erethizontidae, Hystricidae, Thryonomyidae, Batherygidae, Octodontoidea, Chinchillioidea, and Cavioidea, plus all of its descendants. This follows a crown group definition as advocated by Patterson and Rosen (1977), de Queiroz and Gauthier (1990, 1992) and de Queiroz (1994), which is argued to improve stability in the phylogenetic hierarchy and provide unambiguous statements regarding inclusiveness of the taxon. This definition avoids use of the word "living" so that the "extinction criterion" (Lucas, 1992) is not a consideration, although effectively the definition of Hystricognathi proposed here refers to all living hystricognathous rodents. Hystricognathi, as currently perceived, is diagnosed (fig. 15) as hystricognathous rodents with perforated pterygoid fossa, reduced alisphenoid, and mesolophule on the molars. Although the mesolophule or any other character may later be shown to diagnose a more-or less-inclusive taxon (for example, members of "Chapattimyidae" have a mesolophule but are not strictly considered in this analysis), the diagnosis is distinct from the definition and the name Hystricognathi will remain stable.

Tsaganomys, as the nearest outgroup of all other hystricognathous rodents considered in this analysis, is not a member of Hystricognathi. The definition of Hystricognathi excludes a taxon (*Tsaganomys*) that has the important character upon which Hystricognathi was originally diagnosed *and named* (hystricognathy) and is, therefore, not *diagnostically* equivalent to the original concept of Hystricognathi as proposed by Tullberg (1899). The problem is not in the definition but in the name applied to the group: Hystricognathi as

defined here does not include all hystricognathous rodents and, therefore, the name has a misleading connotation which some taxonomists may find objectionable. This is not considered problematic in phylogenetic taxonomy. De Queiroz (1994: 507) specifically considered this problem for the definition of "Mammalia," and pointed out that the name "Mammalia" was proposed for a crown clade, "in spite of its less than perfect correspondance with the group of organisms possessing mammae." De Queiroz (1994: 507) went on to argue, "This is not to say that taxonomists adopting a nominalistic perspective treat the designation of taxon names as completely arbitrary; however, they grant more importance to such things as usage, usefulness, and nomenclatural conventions (e.g., priority) than to descriptive accuracy." On this basis the name "Hystricognathi" certainly has primacy for the crown group.

The non-erethizontid "caviomorphs" (Octodontoidea, Chinchillioidea, Cavioidea) form a monophyletic clade. "Caviomorpha" was first used by Wood (1955: 180), who stated, "These rodents have been separated as a distinct suborder almost exclusively on the basis of phylogenetic and paleogeographic grounds." Clearly the name is most widely used in a biogeographic context because phylogenetic differences between erethizontids and other "caviomorphs" are widely recognized. If "Caviomorpha" is adopted as a name with a phylogenetic definition and is as inclusive as Wood's (1955) concept, then it may be synonymous with Hystricognathi as defined here (depending on how the polytomy of Erethizontidae, Hystricidae, plus other Hystricognathi is resolved). Although "Caviomorpha" would have chronological priority if defined synonymously with Hystricognathi, it is most widely used in reference to a group of rodents recognized on the basis of geography rather than ancestry. Therefore it is best to suppress "Caviomorpha" in favor of a less inclusive, phylogenetically defined name. We define Caviida (new taxon) as the most recent common ancestor of Octodontoidea, Chinchillioidea, and Cavioidea, plus all of its descendents. Caviida is diagnosed as hystricognathous rodents having a horizontally positioned fenestra ovalis, enlarged fenestra rotunda, and optic foramina confluent between the orbits. It is not clear if early South American rodents such as *Branisamys, Incamys, Sallamys*, and *Platypittamys* are members of Caviida as defined here. Although these taxa are often forced into one of the three groups nested within Caviida, a detailed cladistic analysis has not been completed to test their relationships.

The next step in redefining hystricognathous rodent taxonomy within a phylogenetic framework is to define a name for the more inclusive clade containing *Tsaganomys* and Hystricognathi. We define Hystricognathiformes (new taxon) as the clade consisting of *Tsaganomys* and Hystricognathi, plus all rodents more closely related to them than to Ctenodactylidae. This follows a stem group definition as advocated by de Queiroz and Gauthier (1990, 1992). Hystricognathiformes may include, in addition to *Tsaganomys* and Hystricognathi, taxa often more closely allied with them than with any other crown group, such as *Phiomys, Metaphiomys, Gaudeamus*, possibly the "Chapattimyidae," and *Platypittamys*, as well as *Branisamys, Incamys*, and *Sallamys* (possibly members of the more elusive Caviida). This demonstrates one advantage of phylogenetic definitions: even if any of these taxa are later shown to be more closely related to another crown group, or if their phylogenetic position along a stem changes relative to other members of Hystricognathiformes, the name and definition of Hystricognathiformes remains stable.

CTENODACTYLIDAE AND HYSTRICOGNATHIFORMES

The sister taxon of Hystricognathiformes in this analysis is the living Ctenodactylidae (fig. 15). In addition to the morphological characters from our analysis, this relationship is supported by embryological (Luckett, 1985), reproductive and chromosomal (George, 1985), and dental characters (Hussain et al., 1978; Jaeger et al., 1985; Flynn et al., 1986). The "Ctenodactyloidea" and Ctenodactylidae have a contentious history. Dawson et al. (1984) and Wang (1994) included *Cocomys* in the "Ctenodactyloidea" but did not consider ctenodactylids to be closely related to any other modern rodents.

Flynn et al. (1986) excluded *Cocomys* from the "Ctenodactyloidea," which they considered to include the Ctenodactylidae and the extinct families Yuomyidae and "Chapattimyidae." Flynn et al. (1986) considered the "Ctenodactyloidea" to be the sister taxon of Hystricognathi. On the other hand, Wood (1977) argued that ctenodactylids had nothing to do with hystricognathous rodents and considered all of their shared characters to be convergent.

Our results and those of Martin (1992) necessitate a reconsideration of "Ctenodactyloidea." Martin (1992) found that the incisor enamel microstructure among the "Ctenodactyloidea" varies from pauciserial to multiserial. The three Eocene "ctenodactyloids" that Martin (1992) analyzed (*Cocomys*, an unidentified early chapattimyid, and cf. *Birbalomys*) are pauciserial. The Oligocene and younger "ctenodactyloids" (Baluchimyinae and living Ctenodactylidae) are multiserial. Multiserial enamel is a derived character shared by Pedetidae, Ctenodactylidae, and Hystricognathiformes. *Cocomys* does not have a close cladistic relationship with the Ctenodactylidae (fig. 15). The broad concepts of "Ctenodactyloidea" used by Dawson et al. (1984) and Flynn et al. (1986) and the "Chapattimyidae" are, therefore, not monophyletic groups if multiserial enamel evolved once and the cladistic relationships suggested by our analysis are correct. Only the living Ctenodactylidae are, therefore, explicitly included in this analysis. The Ctenodactylidae certainly have a long independent history (Wood, 1977). Although it is likely that Ctenodactylidae as diagnosed by Dawson et al. (1984) is monophyletic, this remains to be tested. Flynn et al. (1986) pointed out several dental similarities between "thryonomyoids" and baluchimyines. Our phylogeny is consistent with Flynn et al.'s (1986) proposal that the crown group Ctenodactylidae is the sister taxon of Hystricognathi and that Baluchimyinae may be a member of Hystricognathiformes.

CONCLUSIONS

The Mongolian-American expeditions to Mongolia have recovered new material of *Tsaganomys altaicus* Matthew and Granger, 1923a, the oldest hystricognathous rodent known from complete skulls. The fossils are preserved in carbonate-cemented sandstone and mudstone, which allows acid preparation. Minute details of the ear region can be discerned from dissected, acid-prepared bullae. No meaningful characters could be identified to distinguish "*Cyclomylus lohensis*" Matthew and Granger, 1923a from *Tsaganomys altaicus*. *Sepulkomys eboretus* Shevyreva, 1972, *Beatomus bisus* Shevyreva, 1972, and *Tsaganomys minutus* (Kowalski, 1974) were originally diagnosed in part by the presence or absence of a "P3," which is demonstrated to be a dP3 lost in very early wear and not replaced in *Tsaganomys altaicus*. All of these taxa, as well as *Pseudotsaganomys* Vinogradov and Gambaryan, 1952, are considered junior synonyms of *Tsaganomys altaicus* Matthew and Granger, 1923a.

Tsaganomys has usually been considered a cylindrodont; Patterson and Wood (1982) argued that bathyergids were derived from *Tsaganomys*, which in turn was derived from a cylindrodont such as *Ardynomys occidentale*. Characters that align *Tsaganomys* with *Ardynomys* are adaptive and shared with other fossorial rodents; no synapomorphies in the auditory region or other cranial features could be identified. The dental patterns are similar but cannot be supported as well as the auditory characters. Rather, *Tsaganomys* is the sister taxon to all other hystricognathous rodents. *Tsaganomys* lacks the fused malleus and incus, expanded head of the malleus, perforated pterygoid fossa, and reduced alisphenoid that are characteristic of Hystricognathi, but has the hystricognathous jaw, has lost the internal carotid artery system, has multiserial enamel, and has a reduced lacrimal. *Tsaganomys* and bathyergids share no synapomorphies implying a closer relationship to each other than to other hystricognathous rodents; rather, bathyergids have synapomorphies that diagnose Hystricognathi.

The skull of *Tsaganomys* does much to improve our knowledge of the origin and early diversification of hystricognathous rodents. *Tsaganomys* is the sister taxon of all living hystricognathous rodents, which are included in a phylogenetic definition of Hystricognathi. Non-monophyly of the "Caviomorpha," "Phiomorpha," and "Frani-

morpha" is confirmed by this analysis. The "Ctenodactyloidea" is certainly not monophyletic, but living Ctenodactylidae probably is. Ctenodactylidae is the sister taxon to Hystricognathiformes, the clade including *Tsaganomys*, Hystricognathi, and other rodents more closely related to them than to the crown group Ctenodactylidae.

The appearance of *Tsaganomys* in the early Oligocene of Asia is close in time to the appearance of hystricognathous rodents in the latest Eocene or earliest Oligocene of North Africa (Wood, 1968; Gagnon, 1982; Gingerich, 1993) and South America (Wyss et al., 1993, 1994). A rather complex picture of diversity among early hystricognathous rodents is emerging. The Erethizontidae is often considered to be the most plesiomorphic hystricognathous rodent taxon because an internal carotid artery is present. *Tsaganomys* has lost the internal carotid artery system but retains other plesiomorphic characters such as unexpanded and unfused ear ossicles, imperforate ptyergoid fossa, and large alisphenoid. The Hystricidae, on the other hand, have a loose bulla-petrosal contact and uniformly coiled cochlea, a different set of plesiomorphous characters than found in either erethizontids or *Tsaganomys*. The fossil record of Hystricidae and Erethizontidae is very inadequate, and there is evidently a considerable amount of unknown diversity in the very early history of Hystricognathi and Hystricognathiformes. This initial diversity must have preceeded the earliest Oligocene, because the most recent common ancestor of *Tsaganomys* and Hystricognathi must predate the oldest member of the clade (Norell, 1993).

Our phylogenetic results clearly point to an Asian origin for the Hystricognathi. The paraphyletic "Ctenodactyloidea" (generally considered the sister taxon to Hystricognathiformes [Flynn et al., 1986]) and *Tsaganomys* are abundant in the early Tertiary of Asia (Li and Ting, 1983; Wang, 1994). The initial diversification of hystricognathous rodents, therefore, likely occurred in Asia and is rep-

resented by *Tsaganomys* (although *Tsaganomys* is not the ancestral form). A second diversification phase is represented by "phiomorphs" in Africa (Wood, 1968). "Caviomorphs" represent two ancestral stocks, one for Erethizontidae and one for Caviida. This precludes derivation of "caviomorphs" from a single transatlantic dispersal event of an exclusively African clade. There were at least two separate rodent dispersal events from the Old World to South America. Because of the possibility that Erethizontidae may share a common ancestor with other Hystricognathi in Asia (because the basal node of Hystricognathi is not fully resolved), the possibility exists that the dispersal of porcupines to the New World was not from an African ancestor.

ACKNOWLEDGMENTS

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