Zoology

A New Central Brazilian Genus and Species of Sigmodontine Rodent (Sigmodontinae): Transitional between Akodonts and Oryzomyines, with a Discussion of Muroid Molar Morphology and Evolution

Philip Horsham

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A New Central Brazilian Genus and Species of Sigmodontine Rodent (Sigmodontinae) Transitional between Akodonts and Oryzomyines, with a Discussion of Muroid Molar Morphology and Evolution

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Abstract

Monotypic Microakodontomys, a long-tailed sigmodontine rodent, inhabits the fringe zone between open grassland and bordering scrubland of the Brazilian cerrado. It most nearly resembles the oryzomyine Oligoryzomys but differs by pointed, blackish striped muzzle, cranial proportions, absence of stapedial and sphenofrontal foramina, and loss of mesoloph (id) in all molars. Whereas the derived dental character is an adaptation for a harsh pastoral diet, as in vole-like akodontines, the primitive oryzomyine-like long tail and feet are adaptations for climbing and better suited for sylvan life. The character mosaic marks a transition from the sylvan to pastoral habitus within an ecological fringe zone. The generic description is followed by a discussion of muroid molar crown morphology and its evolution from the primitive pentalophodont pattern characteristic of sylvan mice, to the derived tetrалophodont pattern characteristic of pastoral mice, and the phylogenetic implications.

Introduction

The heretofore undescribed long-tailed mouse discovered in the Brazilian cerrado resembles small species of the widespread sigmodontine Oligoryzomys. Its molars, however, each with mesoloph (id) absent, are unlike those of Oligoryzomys or any oryzomyine. In contrast, sigmodontines with mesoloph-less, brachyodont, tuberculate molars are, as a rule, short-tailed, terrestrial herbivores of open or scrub country.

The sylvan-pastoral phenotype parallels that of certain other oryzomyine–thomatomyine-like sigmodontines such as Pseudoryzomys and Wiedomys with reduced or absent mesolophs (ids) and habitat in a fringe zone between retreating forests and advancing savannas. Those mice also appear to be transitional between their hypothetical sylvan ancestral morphs characterized by complex pentalophodont molars and their ultimate derived pastoral morphs with simplified tetrалophodont molars.

Material and Methods

The holotype of the new form was taken in a snap trap, its skull damaged with zygoma and right half of braincase lost during hand cleaning and its prepared study skin in poor condition. Direct comparisons were made with 18 individuals of an undescribed species of Oligoryzomys taken in the same fringe zone, 4 in the same trapline. Also used in comparison were representatives of other small sigmodontines, including Oligoryzo-
Classification

South American mice are here regarded as forming a monophyletic group of the subfamily Sigmodontinae. Unresolved is the family to which the subfamily belongs. Some assign the taxon to the Muridae, others to the Cricetidae. In any case, it is generally accepted that these and all other families of mice and rats constitute the superfamily Muroidae.

In their arrangement of the major components of the Muroidae, Carleton and Musser (1984, p. 294) placed the Sigmodontinae, Cricetinae, Murinae, and others with the Muridae, but with some equivocation. They asked, “Should rats and mice, be assigned to just one family, to the two families Muridae and Cricetidae, or to more than two?” Their answer, “We don’t know” (p. 299). The “arrangement of the groups as equivalent subfamilies of Muridae,” they explained, “reflects not our conviction that this is the preferred nomenclature, but rather our uncertainty of the hierarchical pattern and our design to focus upon the distinctive and richly varied geographic and biological properties of the groups comprising the Muroidae.”

The following description of a new genus with a new species focuses on the environmental factors and processes involved, primarily those related to the designs of the molars, in sigmodontine radiation. As for the family designation, it is generally held that the “Cricetidae” appeared in upper Eocene, the “Muridae” much later, in Middle Miocene. There is no consensus, however, regarding lineal relationship, and none regarding origin of

Mys nigripes, of the same region and elsewhere, and the two known species of Andean Microryzomys.

The material collected in Brasília, D.F., in 1986 by the author and associates of the Field Museum of Natural History (FMNH), are registered in the Museu Nacional, Rio de Janeiro (MNR). Comparative material, collected in 1988 in Iporanga, São Paulo, by the same personnel, are entered in the registry of the Museu de Zoologia, Universidade de São Paulo (USPZ).

Cranial measurements (in mm) and terminology for evolutionary stages of cricetid molar crown topography are described elsewhere (Hershkovitz, 1990b, pp. 27, 33).

Microakodontomys, New Genus
(Superfamily Muroidae)

Genotype—Microakodontomys transitorius, new species.

Diagnosis—One of smallest sigmodontines with most external and cranial characters as in comparably small, long-tailed, pentalophodont oryzomyines but all molars without mesoloph (tetralophodont), snout pointed, each side of rostrum with blackish stripe, stapedial and sphenofrontal foramina absent.

Remarks—The genus combines the tetralophodont molar crown pattern characteristic of pastoral rodents such as akodonts and phyllostines with most external and cranial characters of such pentalophodont sylvan rodents as oryzomyines. Overall resemblance to Microryzomys and Oligoryzomys suggests differentiation from an oryzomyine stock in a scrub brush habitat transitional between forest and savanna.

The following detailed description and comparisons combine those of the genus with its genotype and only species.

Microakodontomys transitorius,
New Species

Holotype (frontispiece)—Young adult male, skin and skull, MNR, no. 25986, collected 14 July 1986, by Philip Hershkovitz and Scott Morrow Lindbergh, original no. PH 9515. Skull with right half of braincase, zygomatic arches, and posterior half of each mandible missing.

Type Locality—Parque Nacional de Brasília, D.F., about 20 km NW of Brasília, D.F. (15°47′S, 47°55′W); taken on edge of campo limpo (wet valley side grassland), cerrado biome, at about 1100 m altitude where Akodon lindberghi, Thalpomy cerradensis, and Oligoryzomys sp. near flavescens were captured during the same period.

Distribution—Known from the type locality only. Judged by the single capture during 5 weeks of intensive trapping, the species is probably rare. The Parque Nacional had been continuously.
trapped for small mammals during the last quarter century by other investigators, mainly ecologists, without indication in their reports that another specimen of *Microakodontomys* had been taken or observed.

**Description**

**EXTERNAL** (frontispiece)—Size small; pelage soft, somewhat lax, upper parts ochraceous-buff lined with blackish, more satureate on head, the cover hairs dark brown basally, broadly banded buffly subterminally, narrowly tipped blackish; projecting guard hairs blackish; eyes rimmed blackish; muzzle with narrow blackish band on each side from tip of snout to corner of eye; sides of trunk paler than dorsum, the guard hairs shorter and fewer; underparts and inner surface of limbs washed with ochraceous; tail longer (133%) than combined head and body length, dark above, terminal two-thirds beneath paler; mystacial vibrissae short, the longest extending back to ears; hindfeet long, narrowly palmate basally, inunigulate pedal digit I extending to base of phalanx of digit II, digits II and IV nearly as long as longest digit III, digit V extending to base of phalanx 3 of digit IV; entire plantar surface coarsely scutulated, the interdigital and hypothenar plantar tubercles small, padded thenar tubercle elongate; claws thin, moderately long, not concealed by sparse whitish digital vibrissae, the manual slightly longer than the pedal, the middle claw longest.

**CRANIAL** (figs. 1–2)—Rostrum moderately long, slender; nasals about 34% greatest skull length, tapered with pointed tip not projecting beyond incisors; facial lamina of lachrymal bone slightly inflated; interorbital region narrow, smooth, slightly constricted medially, comparatively little divergent posteriorly, fragmented zygomatic arches with only anterior upright plates preserved, the flaring right suggesting widespread nearly parallel-sided zygomatica; zygomatic plate slightly projecting, anteroposterior diameter of superior notch of infraorbital foramen about 0.87 mm, or length of m1; capsule of incisor root partially overlapped by anterior margin of zygomatic plate; dorsal contour of braincase flat above, moderately curved behind; interparietal bone long, wide; inflated portion of supraoccipital bone visible dorsally; incisive foramina narrowly ovate and extending to anterior margin of first molars; palatal bridge produced beyond plane of last molars the border with large posterolateral pits; mesopterygoid fossa at anterior base of pterygoids wider than either parapterygoid fossa at same transverse plane; length of auditory bulla slightly greater than length of upper molar row; stapedial and sphenofrontal foramina absent, squamosal-alisphenoid groove absent.

Fragmentary mandible (fig. 2) with angular notch deep, angular process extending posteriadi to posterior rim of condylar process; incisor root capsule little projecting.

**DENTAL** (fig. 3)—Upper incisors opisthodont, the outer enamel orange; upper molar brachyodont, tuberculate; outer and inner upper cusps opposing, the outer slightly higher than inner; mesoloph (id) absent in all molars. (Numbers in parentheses are of elements shown in figs. 4–8.)

**M1**—Anterocone with well-defined anteroand posterolingual conules, anteromedian style not distinct or fused with anterolabial conule; anterolabial conule, anterolophule, plesiostyle, and parastyle fused isolating paraflexus (3) from margin; paraflexule, metalophule, and ill-defined mesoloph fused isolating metaflexus (5) from margin; anterior fossette absent; median fossette opening into mesoflexus (4); posterior fossette coalesced with metaflexus; low entoloph extending to margin fused with entostyle in left molar, absent in right; posteroflexus (6) obsolete; posterostyle and posteroabsent; protoflexus (8) and hypoflexus (10) broad, deep; enterostyle present; distoflexus not indicated.

**M2**—Paraflexus (3) isolated from margin by fusion of mesofolhule with anteroloph and parastyle; median fossette discrete; posterior fossette indicated; posteroflexus (6) present; mesostyle present; enterostyle present; short protoflexus (8) present; hypoflexus (10) broad, deep; enterostyle present.

**M3**—Outline subtriangular, less than half bulk m2; cusps low; isolated paraflexus (3) and metaflexus (5) extremely short; median fossette greatly enlarged; protoflexus (8) weakly defined; hypoflexus (10) short, compressed.

Lower molars subhyopsodont, terraced, the inner cusps crested, the outer plane, cusps of each side alternating; protoflexid (8) well defined in all 3 molars, hypoflexid (10) broad, deep, median fossette confluent with mesoflexid (4), posterior fossete confluent with posteroflexid (6).

**M4**—Well-defined anterolingual and anterolabial conules subequal; anterolophid absent, anterostyloid fused with metaconid isolating antero-
flexid (2) from margin; posterolophulid absent; mesostylid and posterostylid present, each isolating mesoflexid (4) and posteroflexid (6), respectively, from margin; median and posterior fossettes each coalesced with corresponding mesoflexid and posteroflexid; ectolophid and styliids between outer cusps absent.

M₁—Mesoflexid and posteroflexid isolated; mesostylid well developed; each fossettid probably coalesced with corresponding flexid; ectolophid absent, ectostylid present; hypoflexid (10) broad, deep.

M₃—Subtrapezoidal, about two-thirds bulk of m₃; hypoconid flat like protoconid; lingual flexids isolated.

Comparisons (figs. 1–3)

The comparisons apply to the genus and lone species of Microakodontomys.

Microakodontomys transitorius is hardly distinguishable externally from Microrzomyx minutus Tomes or Microrzomyx altissimus Osgood except for smaller ears and blackish rostral stripes. It also resembles the slightly larger sympatric Oligoryzomys sp. with ears the same size but rostral stripes absent. A series of the latter was taken in the same habitat. The larger Oligoryzomys nigripes was taken during the same trapping period in other nearby more humid localities.

Cranially the holotype is grossly similar to Microrzomyx spp. and Oligoryzomys spp. except diastema shorter, rostrum narrower, interorbital region more nearly parallel-sided, less divergent behind, braincase narrower, the parietals not globe, nasals tapered proximally, the tips bluntly pointed, not rounded and not overhanging the incisors. The partially damaged left half of braincase (right half missing) resembles that of Oligoryzomys spp. by absence of sphenofrontal foramen and associated squamosal-alisphenoid groove. It differs from those of Microrzomyx spp. and most Oligoryzomys spp. by absence of stapedial foramen.

Dentally, complete absence of mesoloph (id) in all molars separates M. transitorius from oryzomyines, thomasyines, and all other pentalophodont rodents and from all tetralophodont rodents with mesoloph short or vestigial.

The tetralophodont molar pattern combined with the cranial characters may seem to align the holotype with akodont rodents, particularly the smaller species of Akodon including the syntopic A. lindberghi (Hershkovitz, 1990a, p. 16). It is distinguished from like-sized akodonts, however, by one or more characters such as tail longer than length of head and body combined, hindfeet long and narrow, claws unspecialized, upper molars brachyodont, tuberculate, interorbital region smooth and parallel-sided with little divergence behind, incisive foramina short, bullae small. Morphometric comparisons with small species of Akodon appear in Table 1. Additional measurements and characterizations of larger akodonts and related forms are given by Hershkovitz (1990b, p. 4) and by Myers et al. (1990). Compared with like-sized phylloptines such as Calomys spp., tail considerably longer than combined head and body length, hindfeet longer, zygomatic plate less projecting, interorbital region narrower, mesopterygoid fossa wider incisive foramina shorter. In no way could Microakodontomys be derived from any phylloptine with molars like those of Calomys (sensu stricto) or its molariform parallel, the North American Blancan Bensonomyx Gazin. For characters and dimensions of Calomys, see Hershkovitz (1962, pp. 124, 189).

The blackish rostral stripes of Microakodontomys transitorius recalls facial patterns of the long-clawed sigmodontine Geoxus valdivianus and many didelphoids (Marsupialia). Oxymycterus paramensis nigirfons also shows the blackish midrostral stripe with extensions to outer corner of each eye in a few individuals.

SUMMARY—Judged only by the fragmented skull and damaged skin, M. transitorius could be taken for a well-differentiated species of Oligoryzomys most nearly related to O. flavescens, or O. fornesi, or the larger O. nigripes. Absence of mesoloph (id) in all molars, blackish rostral bands, and tail length more than 110% of combined head and body length, however, distinguishes Microakodontomys transitorius not only from oryzomyines but from all other sigmodontines of comparable or other body size.

Systematic Affinity

Microakodontomys, like eastern Brazilian Wie- domys, Pseudoryzomys, and Rhagomys, retains the long tail, long foot, scansorial proclivities, and general appearance of its postulated sylvan oryzomyine-thomasyine origin. No intimate relationship, however, is inferred between any of the genera. Each appears to be too widely divergent
dentally and cranially for alignment with other genera or generic groups derived from either the oryzomyine or thomasomyine branch.

In his assessment of the Sigmodontinae, Reig (1980, p. 263) disposed of the eastern Brazilian Rhagomys and Pseudoryzomys, the Peruvian altiplano Punomys, and the intercontinental lowland Zygodontomys as “Sigmodontinae incertae sedis.” As for Wiedomys, Reig (1980, p. 265) combined it with his newly described Colomys from the Argentine Pleistocene to form the new tribe Wiedomyini. Other sigmodontine tribes recognized were the Recent Oryzomyini, Akodontini, Phyllotini, Sigmodontini, Scapteromyini, and Ichthyomyini. To these may be added the distinctive Thomasomyini and Oxymycterini. Pending further study, Microakodontomys, perhaps an independent offshoot of an oryzomyine branch of the presumed monophyletic sigmodontine tree, is tentatively cast as Sigmodontinae incertae sedis.

**Fringe Zone Faunas**

*Microakodontomys transitorius* is phenotypically and functionally transitional between sylvan and pastoral sigmodontines. Its habitat is the *cerrado* fringe or broad, intergrading zone between sylvan and pastoral environments. The bordering forests are isolated Amazonian outliers at the headwaters of the Rio Tocantins. Mice of these gallery forests are sylvan. Those of the *cerrado* are pastoral. Fringe faunas, on the other hand, include sylvan, pastoral, and transitional species. Most
abundant and adaptive fringe zone mice are the wide-ranging species of *Oligoryzomys*.

The *cerrado* grades from wet *campo limpo* or grassland, to *campo sujo* or mixed grassland, shrub, and low, widely scattered trees. *Campo sujo*, in turn, merges into *campo cerrado* with its thick cover of brush, bushes, and low trees. *Microakodontomys transitorius* was taken in the fringe between *campo limpo* and *campo sujo* in the same trapline as a large series of a superficially similar species of *Oligoryzomys* and the larger, short-tailed *Akodon lindberghi* Hershkovitz (1990b) and *Thalpomys cerradensis* Hershkovitz (1990a, pp. 763 et seq. for habitats and sigmodontine fauna).

The tetralophodont molar pattern of *M. transitorius* is primarily adapted for mastication and

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**Fig. 3.** Upper and lower right molars of specimens shown in Figure 1 (greatest length of tooth rows in mm in parentheses). A, *Microakodontomys transitorius* (3.1/3.2); B, *Oligoryzomys* sp. (3.1/3.2); C, *Oligoryzomys nigripes* (3.6/3.8); D, *Microryzomys minutus* (3.1/3.2).
Table 1. External and cranial measurements (in mm) of *Microakodontomys transitorius* and some like-sized Sigmodontinae (Oryzomyines and Akodonts).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>Head and body length</th>
<th>Tail length</th>
<th>Tail: head and body length ratio</th>
<th>Hind foot length with claw</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Microakodontomys transitorius</em></td>
<td>Brazil: Brasilia</td>
<td>70</td>
<td>93</td>
<td>133</td>
<td>21</td>
</tr>
<tr>
<td><em>Micoryzomys altissimus</em></td>
<td>Peru</td>
<td>74.6(62-84)22</td>
<td>108(95-122)22</td>
<td>144†</td>
<td>21(18-23)22</td>
</tr>
<tr>
<td><em>Oligoryzomys sp. &amp;</em></td>
<td>Brazil: Brasilia</td>
<td>79(70-86)10</td>
<td>105(97-111)10</td>
<td>133(117-149)10</td>
<td>22(21-23)10</td>
</tr>
<tr>
<td><em>Oligoryzomys sp. &amp;</em></td>
<td>Brazil: Brasilia</td>
<td>82(75-87)5</td>
<td>102(95-111)5</td>
<td>125(114-137)5</td>
<td>21.6(21-22)5</td>
</tr>
<tr>
<td><em>Oligoryzomys nigripes &amp;</em></td>
<td>Brazil: Iporanga</td>
<td>96(83-105)16</td>
<td>122(113-146)16</td>
<td>127(107-145)16</td>
<td>24(23-25)16</td>
</tr>
<tr>
<td><em>Oligoryzomys nigripes &amp;</em></td>
<td>Brazil: Iporanga</td>
<td>99(93-107)5</td>
<td>125(113-129)5</td>
<td>125(119-130)5</td>
<td>24(21-26)5</td>
</tr>
<tr>
<td>Akodon lutescens§</td>
<td>Peru: Arequipa</td>
<td>78(76-81)5</td>
<td>60(57-64)5</td>
<td>76(70-84)5</td>
<td>19.4(19-20)5</td>
</tr>
<tr>
<td>Akodon caenosus§</td>
<td>Argentina: Jujuy</td>
<td>98(85-103)9</td>
<td>60(56-64)9</td>
<td>61(55-66)9</td>
<td>19(18.5-19.5)9</td>
</tr>
<tr>
<td>Akodon dolichonyx</td>
<td>Chile: Atacama</td>
<td>87(77-94)14</td>
<td>55(47-66)14</td>
<td>63(52-78)9</td>
<td>20.3(19-22)14</td>
</tr>
<tr>
<td>Akodon alterus§</td>
<td>Argentina: Catamarca</td>
<td>91, 89, 100</td>
<td>63, 61, 78</td>
<td>69, 68, 78</td>
<td>19, 19, 20</td>
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<tr>
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<td>Bolivia: Cochabamba</td>
<td>84(75-94)5</td>
<td>71(70-75)5</td>
<td>85(80-93)5</td>
<td>18(15-21)5</td>
</tr>
<tr>
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<td>Peru: Puno</td>
<td>99(90-115)11</td>
<td>62(55-66)11</td>
<td>63(52-72)11</td>
<td>21(20-22)11</td>
</tr>
</tbody>
</table>

* Data from Carleton and Musser (1989, p. 81) except as noted with †.
† Mean tail: mean head and body length, and other measurements.
‡ FMNH, Peru (La Quinua).
§ According to Myers et al. (1990, p. 62), *A. lutescens* and *A. caenosus* are each subspecies of *A. puer*; *A. pacificus* is a synonym of *A. boliviensis*, whereas *A. spegazzini* is distinct from *tucumanensis*, a synonym.

Table 1. Continued.

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<th>Taxon</th>
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<th>Rostral width</th>
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<td>1.8(1.7-2.0)5†</td>
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<td>7.6(7.1-8.1)5</td>
<td>3.9(3.8-4.0)5</td>
<td>2.2(2.1-2.3)5</td>
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<td>8.8(7.8-9.2)13</td>
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<td>13</td>
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### Table 1. Continued.

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<th>M1-3 length</th>
<th>M1-3 across</th>
<th>M1 width</th>
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<td>0.98(0.92–1.0)9</td>
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<td>1.1(1.0–1.2)5</td>
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<td>5.0(4.8–5.3)10</td>
<td>1.1(1.0–1.3)11</td>
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</tbody>
</table>
Table 2. Frequency of fused mesolophid and mesostylid (= mesolophostylid) in lower molars of Oligoryzomys sp. (N = 18) from Parque Nacional, Brasilia D.F.; R = right, L = left. Fused mesoloph and mesostyle (= mesolophostyle) is present in all upper molars.

<table>
<thead>
<tr>
<th>M</th>
<th>Present</th>
<th>Absent</th>
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<tr>
<td></td>
<td>R</td>
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<tr>
<td>M₁</td>
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<tr>
<td>M₂</td>
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<td>16</td>
<td>16</td>
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<tr>
<td>Totals</td>
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secondarily for grinding harsh forage. The long tail and moderately long feet are suited both for terrestrial and scansional locomotion and for gaining nesting sites above ground level. In open grassland, a long tail on a small mouse could be disadvantageous.

Molar differentiation of Microakodonomys must have occurred during a long dry period when erstwhile extensive humid forests shrank to moist banks of streams or into tracts isolated by surrounding savannas. A syntopic species in transit from pentalophodonty to tetratophodonty is the undescribed fringe zone Oligoryzomys sp. mentioned above. All 18 specimens captured in the same trappine as the holotype of M. transitorius retain the sylvan externalities including long tail, long foot, and general oryzomyine appearance as in M. transitorius. Upper molars of the series are entirely pentalophodont, the mesolophystyle intact in each tooth. Lower molars, however, are about equally pentalophodont and tetratophodont. Those most frequently tetratophodont are the second lower molars, at the center of masticatory impact. Least tetratophodont are the third lower molars, the smallest and least functional of the suite judged by wear. Patterns of M₁, largest of the molars, are mixed (table 2).

Pace of Sigmodontine Evolution

Emergence of the semipastoral Microakodonomys with a clear stamp of oryzomyine origin, and discovery of the syntopic Oligoryzomys sp. in partial transition to the pastoral habitus, suggests rapid speciation, perhaps less than a millenial pace. The fossil record indicates, however, that many living sigmodontines had already attained present generic and perhaps species grade, no more recently than late Pliocene or early Pleistocene. The common sigmodontine ancestral form, likely near living thomamyine, remains to be discovered, perhaps in South America, possibly in Eurasia or Africa.

Molar Crown Patterns: A Review (figs. 4-8)

The morphology, terminology, and functional and ecological significance of pentalophodont and derived tetratophodont molar crown patterns, basic to an understanding of sigmodontine and other rodent radiations, have been described by Hershkowitz (1944, 1955, 1960, 1962). They are summarized here.

The ancestral complex or pentalophodont cricetid molar is characterized by five primary transverse crests (Hershkowitz, 1962, p. 76). Those of the upper molars are I, procinculid; II, paracone; III, mesoloph fused with mesostyle, or mesolophostyle; IV, metacone; and V, postcinculid. Those of the lower molars are I, procinculid; II, metaconid; III, mesoloph fused with mesostylid, or mesolophostylid; IV, entoconid; and V, postcinculid. All molars of oryzomyine, thomamyine, and the North American peromysceine Ochrotomys, Megadontomys, Aporodon, and Isthomomys are pentalophodont. Mice with pentalophodont molars are primarily sylvan. In most deforested environments, sylvan forms may find refuge in gallery forests, wooded ravines, shrub-covered hillsides, banks of brush-lined streams, and the fringe zones between strictly sylvan and pastoral habitats.

The derived or simplified tetratophodont molar is marked by the same primary transverse crests except that crest III, the primitively fused mesoloph-mesostyle (id), is disjunct, with either or both elements reduced or absent. Sometimes the mesostyle (id) alone becomes hypertrophied in absence of the mesoloph (id).

The evolutionary process of molar crown simplification, beginning with the breakup of crest III, proceeds with reduction and elimination of transverse crests IV and I (the order sometimes reversed), followed by merger of II and IV (Hershkowitz, 1962, fig. on p. 77, pp. 82-101). Modifications commence with the lower molars, the second usually earliest. Mice with tetratophodont molars are all New and Old World living muroids not mentioned above. Old World mu-

FIELDIANA: ZOOLOGY
ines lack even a vestige of the mesoloph. Tetralophodont sigmodontines are primarily pastoral; their habitats include deserts, savannas such as tundras, punas, scrublands, cerradoss, and caatingas, and palm, bamboo, and coniferous forests. These mice may also occur as intrusive, isolated, or fringe elements in relict or refuge bogs, meadows, rocky situations, and partially cleared or cultivated fields and along grassy or brush-lined banks of streams cutting through broad-leaf forests. The mesoloph is lost in transition from the ancestral sylvan pentalophodonty of sylvan forms to derived tetralophodonty of pastoral forms. Reversibility of the process, mentioned in a review by Voss (1991, p. 37), is improbable. An element once lost is never regained.

The narrow, fluctuating fringe between forest or thick shrub and open grassland may be foraged by rodents natural to either pastoral or sylvan habitats or transient between them. Seasonally changing diets in fringe zones, however, include harsh fiber plant foods selective for a tetralophodont mol- lar pattern.

**Pseudomesolophs (ids)**—Paralophules or metalophules are evaginations of corresponding upper cusps; metalophulids or entolophulids are equivalent extrusions of corresponding lower cusps. The lophules (ids) may appear singly or in combination in one or more of the pentalophodont or tetralophodont molars of a suite. A lophule (id), particularly of the tetralophodont molar, may simulate the mesoloph (id), often by fusion with it, the mesostyle (id), or both. Any one or combination of these protrusions and fusions of lophules (ids) are the pseudomesolophs (ids) described by Hershkovitz (1962, p. 80). The true mesoloph (id) is a lateral protrusion or evagination of the mid-sagittal spine or mure (id) of the molar and no other part of the tooth. It may fuse partially or completely with any or all enamel elements between paracone and metacone (metaconid and entoconid) as well as with the cones (ids) themselves (fig. 7B).

Failure to recognize the distinction between true mesoloph (id) as an evagination or development of the mure only, and its relationship with the mesostyle (id), on the one hand, and the various lophules (ids), on the other, obscures phylogenetic relationships between species, genera, and higher categories of sigmodontines. Vorontsov (1979) and Hooper (1957) adopted the molar enamel pattern introduced by Hershkovitz (1944, 1955) but never fully comprehended the taxonomic, much less phylogenetic, significance of the true mesoloph (id) or mesolophostyle (id). Others before and since have confused this element with pseudomesoloph (id) variables of little or no significance in the transition from pentalophodonty to tetralophodonty (cf. Lindsay & Jacobs, 1985, p. 24, fig. 8e, pls. 2i,j).

Hooper (1957, p. 9, fig. 1 on p. 14) provided an excellent description of the mesoloph (id), but the exposition exceeds the limitations of the subject. In his figure, the true mesoloph (id) is shown protruding directly and correctly from the mure in upper and lower second molars. The inset enlargements of various secondary positions of purported mesolophs (ids), however, are misleading. His inset figures 1–4, and possibly 5 of m^3^ are paralophules; the same numbered figures of m^2^ are entolophulids. Not shown are the equivalent metalophules and metalophulids. All may be categorized as pseudomesolophs (ids), but the correct term for the single element is lophule (id). The true mesoloph (id; fig. 7B) may fuse with any or all lophules (ids) or with the principal cones (ids) themselves.

**The Mesoloph (id): Evolutionary Significance**

The passage from pentalophodonty to tetralophodonty with reduced to absent mesoloph is as significant in murid evolution as is the transition from tritubercly to quadriverticle in earliest rodents, primates, and other mammalian orders. It compares with the gradual loss of digits in ungulate evolution from woodland browser to pastoral grazer.

The eight sigmodontine dental characters enumerated by Jacobs and Lindsay (1984, p. 269, table 2) as primitive include no. "4 short mesoloph (and mesolophid)." Molars with reduced or absent mesolophs (ids) are derived. They are almost the only kinds preserved as fossil in former pastoral or fringe habitats. Their characters were the ones considered by Jacobs and Lindsay (1984, p. 269) in their construction of sigmodontine phylogeny. Their putative ancestor, the middle Miocene *Megalricetodon* with mesoloph of m^1^ reduced, as in many living and extant muroids, was already too derived to have given rise to the Sigmodontinac, contra Jacobs and Lindsay (1984, p. 269, fig. 1b). On the other hand, Jacobs and Lindsay (1984, p. 269) were correct in rejecting *Leidymys* as a likely ancestor of sigmodontines. They were wrong in attributing this postulate of ancestry to Hershkovitz.
Fig. 4. Diagram of occlusal surface of a first right upper molar showing basic elements of the enamel pattern in muroid rodents.
Explanation for symbols of Figures 4–7 (a–i inclusive = procingulum or loph I; s, t, z = postcingulum of loph V); the fold terminology (1–11) is from Hershkovitz (1962, p. 70).

a. anteromedian style (may be fused with b, c, or both)
b. anterolabial lophule
c. anterolingual lophule
d. anterolophule (may be fused with f)
e. anterior fossette
f. plesiostyle (may be fused with d, h, or j)
g. protostyle (may be fused with i)
h. anteroloph (may be fused with f, j, or both)
i. protoloph (may be fused with g, u, or both)
j. paraastyle (may be fused with f, h, k, or a combination)
k. mesolophule (may be fused with h, j, or both)
l. paracone
m. paralophule (may be fused with n, o, or both); element may be multiplied
n. mesoloph (when fused with o = mesolophostyle)
o. mesostyle (may be fused with m, p, or both; when fused with n = mesolophostyle)
p. metalophule (may be fused with o, n, or both)
q. metacone
r. posterolophule (may be fused with s)
s. posterostyle (may be fused with r, t, or both)
t. posteroloph
t'. posteroconule (usually not differentiated from posteroloph, t)
u. protolophostyle (may be fused with i)
v. protocone
w. enteroloph (may be fused with x)

(continued)
Fig. 6. Some enamel patterns of the tetralophodont upper and lower molars formed by lamination and involution: A, crown pattern formed by lamination (3–8; 5–10), and involution (6), of right m2 of the South American caviomorph *Dinomys brannichi* Peters; B, pattern by lamination (5–10), and involution (3, 6), of right m2 of the South American caviomorph *Dactylomys dactylinus* Desmarest; C, formation of an epsilon pattern by involution (3, 5, 10) of left m2 of the South American sigmodontine *Phyllotis micropus*; D, formation of modified S or sigmoid pattern by involution (10) and elimination (5) of left m3 in *Phyllotis micropus*; E, formation of S or sigmoid pattern by involution (10, 3) and elimination (8) of left m2 in the South American sigmodontine *Euneomys chinchilloides*. For explanation of symbols, see pages 13–14, 17. Figure modified from Hershkovitz (1962, p. 96).

- **x. enterostyle** (may be fused with w)
- **y. hypocone**
- **z. distostyle**
- **a’. median fossette** (may be coalesced with 3, or unite with 4)
- **b’. posterior fossette** (may be coalesced with 5, or unite with 6)
- **c’. protolophule**
- **d’. hypolophule**
- **e’. mure** (border between lingual and labial cusps and lophs)
- **1. preflexus** (anterior median fold)
- **2. anteroflexus** (anterior secondary fold)
- **3. paraflexus** (first primary fold)
- **4. mesoflexus** (first secondary fold)
- **5. metaflexus** (in absence of mesoloph coalesced with 4 or first secondary fold)
- **6. posteroflexus** (second secondary fold)
- **7. supraflexus** (anterior lingual fold; in absence of protoloph coalesced with 8 or first minor fold)
- **8. protoflexus** (first minor fold)
- **9. entoflexus** (major fold)
- **10. hypoflexus** (in absence of enteroloph coalesced with 9 or major fold)
- **11. distoflexus** (second minor fold)
Fig. 7. Transition of enamel pattern of an upper second cricetid molar from pentalophodont (A) to tetralophodont through modifications of shaded portions shown in enlargement (B) after disjunction of mesoloph (n) and mesostyle (o) (loph III). All elements shaded may be lost in the tetralophodont molar, or some to all may be present individually or fused or coalesced in various combinations except with mesoloph (n). For explanation of symbols, see pages 13–14.
Fig. 8. Diagram of occlusal surface of a first right lower molar showing basic elements of the enamel pattern in muroid rodents.
Explanation for symbols of Figure 8 (a–h inclusive = procingulum or loph I; a’, 14, 16 = postcingulum or loph I); terminology (1–11) is from Hershkovitz (1962, p. 70).

a. anteromedian stylid (may be fused with b, c, or both)
b. anterolabial conulid (may be fused with c)
c. anterolingual conulid (may be fused with b)
d. labiobasalidul (may be fused with g)
e. anterior fossette
f. anterolophid (may be fused with h, i, or both)
g. protostylid (may be fused with d)
h. anterolophid (may be fused with f, i, s, or combination)
i. anterostylid (may be fused with f, h, s, or combination)
j. protoculid (may be fused with g)
k. protoconid
l. paralophid (may be fused with m, n, or both)
m. ectostylid (may be fused with l, n, o, or combination)
n. ectolophid (may be fused with l, m, o, or combination)
o. hypoconulid (may be fused with m or n)
p. hypoconid
q. posteroconulid (may be fused with r)
r. posteroconulid (may be fused with q)
r’. posteroconulid (usually not differentiated from posteroconulid, r)
s. mesolophulid (may be fused with h)
t. metaconid
u. metalophulid (may be fused with v, w, or both)
v. mesolophid (when fused with w = mesolophostylid)
w. mesostylyl (when fused with v = mesolophostylid)
x. entolophulid (may be fused with v, w, or both)
y. entoconid
z. distolophulid (may be fused with a’)
a’. posterostylid
b’. median fossetid
c’. posterior fossetid
d’. protolophid
e’. hypolophulid
f’. murid (zone between lingual and labial lophs and cusp)

1. prefixid (anterior median fold)
2. anteroflexid (anterior labial fold; in absence of anterolophid coalesced with 3)
3. metaflexid (first secondary fold)
4. mesoflexid (first primary fold)
5. entoflexid (second secondary fold; in absence of mesolophid, coalesced with 4)
6. posteroflexid (second primary fold)
7. supraflexid (anterior labial fold; in absence of labiobasalidul coalesced with 8)
8. protoflexid (first minor fold)
9. ectoflexid (major fold)
10. hypoflexid (in absence of ectolophid [n] coalesced with 9)
11. distoflexid (second minor fold)

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