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Source: *Journal of Vertebrate Paleontology*, Vol. 16, No. 3 (Sep. 19, 1996), pp. 522-530

Published by: The Society of Vertebrate Paleontology

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A NEW SPECIES OF *HOLOCHILUS* (RODENTIA: SIGMODONTINAE) FROM THE MIDDLE PLEISTOCENE OF BOLIVIA AND ITS PHYLOGENETIC SIGNIFICANCE

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ABSTRACT—A series of mandibles and maxillae from the Ensenadan (middle Pleistocene) sediments of the Tarija Basin of Bolivia are assigned to *Holochilus primigenus*, sp. nov. This marsh rat of the subfamily Sigmodontinae (=“South American cricetid”) is one of the few extinct muroids known from South America. A cladistic analysis indicates that this new species is the sister taxon to living species of *Holochilus* and possesses a morphology transitional between extant *Holochilus* and their closest living relative, *Lundomys*. The occlusal molar morphology of *H. primigenus* is virtually indistinguishable from that in extant *Lundomys*, but synapomorphic characters of the mandible and palate unite *M. primigenus* with the extant *Holochilus*. *Holochilus primigenus* is a potential ancestor to its living congeners because it possesses no known autapomorphies. The explicit hypothesis of phylogenetic position for this new species combined with its presumed geologic age of 0.7–1.0 Ma may provide a calibration point to estimate ages of divergence among lineages of sigmodontines.

INTRODUCTION

The predominantly South American muroid rodents of the subfamily Sigmodontinae (excluding neotomine-peromyscines; sensu Reig, 1984) form one of the largest mammalian subfamilies. The South American fossil record of this subfamily is poor, and all fossils date from the Pliocene or Pleistocene (Winge, 1887; Ameghino, 1889, 1908; Rovereto, 1914; Reig, 1978, 1980, 1987, 1994). Names of most of these fossil species have been synonymized with those of living species, and only a few fossil species have been studied in sufficient detail to demonstrate that they are distinct from living species. The few valid extinct species are often little differentiated from extant forms (Reig, 1980) and preserve too few characters to provide insights into phylogenetic relationships. In this paper, I describe a species of marsh rat of the genus *Holochilus* from the middle Pleistocene Tarija Formation of Bolivia and explicitly place this new species in a phylogenetic context. It has a transitional morphology within a lineage that has moved from sylvan to semi-aquatic habitats, and it lacks any autapomorphies that distinguish it from a possible ancestor of extant species of *Holochilus*.

Systematic studies of Neotropical sigmodontines (previously assigned to Cricetidae, more recently assigned to equal rank with Cricetidae in the family Muridae [Carleton and Musser, 1984; Musser and Carleton, 1993]) have until recently (Hershkovitz, 1962, 1966; Hooper and Musser, 1964; Gardner and Patton, 1976; Pearson and Patton, 1976; Reig, 1984) had limited success in achieving a consensus regarding several fundamental issues of phylogenetic relationships (Carleton and Musser, 1984; Czaplewski, 1987; Musser and Carleton, 1993; Voss, 1993). However, the situation has improved with recent phylogenetic studies building more robust hypotheses (Voss, 1988; Patton et al., 1989; Smith and Patton, 1993; Steppan, 1993, 1995b; Voss and Carleton, 1993). These recent advances facilitate the interpretation of the material described below.

In this paper, I shall focus on the fossil muroids of South America. Their fossil record is poor, and it is in that context that this paper is most significant. The oldest fossils attributed to Sigmodontinae are from southern North America, mainly dating from the Hemphillian and Blancan of the Pliocene (Baskin, 1978, 1986; Jacobs and Lindsay, 1984; Czaplewski, 1987).

The oldest South American sigmodontines date from the Montehermosan, about 3.5 Ma. Two common scenarios for the biogeographic origins of the Sigmodontinae place their original diversification in the late Miocene of North America, followed by dispersal into South America, either through island-hopping by one or two species (Savage, 1974; Marshall, 1979) or multiple colonizations after the formation of the Panamanian Isthmus (Baskin, 1978, 1986; Simpson, 1980; Jacobs and Lindsay, 1984; Czaplewski, 1987). Primary support for these scenarios comes from the North American fossils that predate the earliest South American fossils by 3–6 my. However, some workers have expressed doubts regarding the assignment of North American “cricetid” fossils to the Neotropical Sigmodontinae (Reig, 1980; Hershkovitz, 1993; Steppan, 1995b). For example, the North American Pliocene taxon *Bensonmysis* is conventionally considered to be a subgenus of the extant *Calomys*, a South American endemic genus in the Sigmodontine tribe Phyllotini. Many species of *Bensonmysis* are very similar to extant *Calomys* in molar occlusal morphology. However, early (Hemphillian) *Bensonmysis* species retain a distinct mesoloph, the absence of which is a synapomorphy for the tribe Phyllotini (Steppan, 1995b). This would make *Bensonmysis* paraphyletic with respect to the entire tribe, and unequivocally exclude the early forms from *Calomys* unless one hypothesizes multiple losses or reversals. Furthermore, the reduced number of molar roots in some early *Bensonmysis* (two or three on first molars; Baskin, 1978; Czaplewski, 1987) is derived relative to the plesiomorphic condition (four roots) in phyllotines and other tetralophodont genera (Steppan, 1995b). This argument does not preclude the possibility that *Bensonmysis* is a basal member of the tetralophodont tribal group (sensu Steppan, 1995b), but if so, then the similarity between *Bensonmysis* and extant *Calomys* in molar occlusal morphology may be convergent. Jacobs and Lindsay (1984) proposed that Phyllotini is the most basal sigmodontine tribe, on the assumption that *Bensonmysis* bears the plesiomorphic sigmodontine dentition because it is the oldest known sigmodontine. This contrasts sharply with the conclusions drawn from studies of extant sigmodontines, that the Phyllotini, including *Calomys*, possess a derived dentition and occupy a terminal branch on the sigmodontine tree (Hershkovitz, 1962; Hooper and Musser, 1964; Gardner and Patton, 1976; Reig, 1980, 1986; Sarich, 1985; Spotorno, 1986; Catzeffis et

al., 1993; Voss, 1993; Steppan, 1995b). Baskin (1978, 1986) has been a major proponent of the North American origins of the sigmodontines, but he also considered *Bensonmys* to possess derived dentitions and to occupy a side branch, not the root, of the sigmodontine tree.

Slaughter and Ubelaker (1984) also proposed a North American origin for the sigmodontines, but these authors derived the sigmodontines from the Old World cricetodontines, rather than from *Copemys*, as is more commonly hypothesized. Their scenario is supported principally by the occurrence of the lungworm *Parastrongylus*, an endoparasitic nematode, in some sigmodontines and a scattered array of Old World muroids (murines, gerbillines, and arvicolines), but not in neotomine-peromyscines. Baskin (1986) pointed out that the taxonomically dispersed distribution of *Parastrongylus*, and its occurrence in only three sigmodontines, *Sigmodon*, *Oryzomys*, and *Zygodontomys*, all of which occur in Central and North America, provided very weak support for their hypothesis. More extensive sampling of muroids, and especially sigmodontines, is needed before the parasite data can help resolve the relationships of sigmodontines.

The strongest evidence for early sigmodontines in North America comes from *Bensonmys*, *Sigmodon*, and the several species of *Prosigmodon*. *Prosigmodon* is reported from the Pliocene of Mexico and Arizona, possesses lophate molars lacking mesoloph(id)s, and is possibly ancestral to *Sigmodon* (Jacobs and Lindsay, 1981; Lindsay and Jacobs, 1985; Czaplewski, 1987). Two other sigmodontine tribes have been reported as present in North America: Akodontini, represented by *Symmetrodontomys* (Baskin, 1978, 1986; Jacobs and Lindsay, 1984); and Oryzomyini, represented by 'undescribed' material from New Mexico ('S. May, pers. comm. '; Jacobs and Lindsay, 1984; Czaplewski, 1987) and Florida (Webb et al., 1981; Jacobs and Lindsay, 1984). The Florida material has since been described by Baskin (1986) as *Abelmoschomys*, which he considered to be the oldest sigmodontine (late Miocene, approximately 9 Ma). Because of the age and primitive nature of *Abelmoschomys*, Baskin chose not place it in the Oryzomyini nor in any other tribe. He considered *Abelmoschomys* to be an early member of the sigmodontine radiation, possibly derived from *Copemys*. Czaplewski (1987) described the late Blancan *Jacobsonomys* as a basal member of the radiation of akodontines, oryzomyines, and *Zygodontomys*, but did not assign *Jacobsonomys* to any tribe. (Cladistic studies now indicate that *Zygodontomys* is an oryzomyine sensu stricto with simplified dentition [Voss and Carleton, 1993; Steppan, 1995b].) Unfortunately, the evidence and reasoning behind the systematic assignments of the material attributed to the akodontines and oryzomyines has not been presented formally. Therefore, at present, there is no direct evidence for either of those tribes in North America prior to the Great American Interchange.

The most thorough discussion of sigmodontine origins and diversification to date has been made by Baskin (1986), and the reader is referred there for more detail. My purpose in this review and discussion is to illustrate some of the diversity of interpretations regarding the North American fossil record. A major difficulty in resolving the issue of the biogeography of sigmodontine diversification is the small amount of phylogenetic information preserved in the fossils. However, any substantive critique of the North American model for sigmodontine diversification would be premature without a comprehensive review of both fossil and Recent material.

In contrast to North American muroids, few extinct muroid (=sigmodontine) species from South America are known. Most of the names applied originally to Pliocene and Quaternary sigmodontine fossils by Ameghino (1889, 1908) have been synonymized with extant species (Hershkovitz, 1962; Reig, 1978; Massoia and Pardiñas, 1993; Pardiñas, in press), as have many

of the names applied by Winge (Massoia, 1980; Voss and Myers, 1991; Voss and Carleton, 1993). For example, the Pleistocene rat *Hesperomys molitor* (Winge, 1887) is conspecific with the senior specific synonym for the extant *Holochilus mag-nus*, now *Lundomys molitor* (Voss and Carleton, 1993). Furthermore, most material from the late Pleistocene and Holocene can be assigned to extant species (e.g., Tonni et al., 1985, 1988).

Accurate phylogenetic placement of any of the New World fossil muroids is severely limited by the paucity of available material, and the absence of nearly any cranial, post-cranial, soft anatomical, or molecular data useful for examining relationships within the Sigmodontinae (Sarich, 1985; Voss, 1988; Patton et al., 1989; Smith and Patton, 1993; Voss and Carleton, 1993; Steppan, 1993, 1995a, 1995b). Even though the new material reported on here includes only a few non-dental characters, the highly distinctive nature of its dental morphology indicates that only the few species belonging to *Holochilus* and *Lundomys* need be directly considered in assessing the phylogenetic position of this new species.

The extant genus *Holochilus* has long been considered to be closely related to *Sigmodon* (named for the S-shaped enamel pattern in m3, produced by deeply interpenetrating folds). Hershkovitz (1955) defined a sigmodont group that included those two genera, as well as *Neotomys* and *Reithrodon*. The other New World genera with "sigmodont" molars are the extant phyllotine *Euneomys* and the extinct *Prosigmodon*. Subsequent studies of the phallus (Hooper and Musser, 1964) and chromosomes (Gardner and Patton, 1976; Baker et al., 1983) suggested that *Neotomys* and *Reithrodon* belonged to the tribe Phyllotini, while *Holochilus* may be related to Oryzomyini rather than to *Sigmodon*. The Oryzomyini, whether sensu Hershkovitz (1962) or sensu Reig (1984), are characterized by a complete mesoloph(-id) fused to the mesostyle(-id) (forming a mesolophostyle[id]; Hershkovitz, 1962), a condition absent from all the other genera discussed here. The suggestion that *Neotomys* and *Reithrodon* belong in Phyllotini generally has been followed since (Reig, 1984, 1986; Spotorno, 1986; Olds and Anderson, 1989; Ortells et al., 1989; Braun, 1993; Steppan, 1993), while *Holochilus* usually is maintained in the tribe Sigmodontini (Reig, 1984, 1986). Only recently, more comprehensive phylogenetic studies have allocated *Holochilus* to the Oryzomyini, considering it to be only distantly related to *Sigmodon* (Voss and Carleton, 1993; Steppan, 1995b).

The specimens described here were collected from two localities in the Tarija Basin (Tarija and Rio Turumoya), and are part of the extensive, mostly undescribed collections made by the Field Museum's Elmer S. Riggs in 1924 and 1927, in the Tarija and Padcaya basins, Department of Tarija, Bolivia (Padcaya is located 45 km south of the city of Tarija). The faunas from the Tarija and Padcaya basins are thought to be part of a single assemblage (Hoffstetter, 1963). Paleomagnetic analysis of the relevant beds of the Tarija Basin suggest correlation to magnetic polarity [chron] Clr.In to early Cln (Matuyama), zones that date to about 0.7–1.0 Ma (MacFadden et al., 1983; Flynn and Swisher, in press). Some portions of the basin may be younger. The Tarija Formation consists of fluvial sediments deposited in channel and floodplain regimes (MacFadden et al., 1983). Sigmodontine genera reported from the Tarija fauna include *Andinomys*, *Calomys*, *Kunsia*, *Nectomys*, *Oxymycterus*, and *Phyllotis* (Marshall et al., 1984, and references therein). Other sigmodontines in the Field Museum collections made by Riggs include at least one unidentified akodontin species (probably *Akodon* or *Bolomys*), and a probable *Calomys*.

Abbreviations—FMNH P, Field Museum of Natural History, Paleontology collections; FMNH PM, Field Museum of Natural History, Mammalian Paleontology collections.

Dental terminology follows Reig (1977).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowditch, 1821
 Superfamily MUROIDEA Miller and Gidley, 1918
 Family MURIDAE Illiger, 1815
 Subfamily SIGMODONTINAE Wagner, 1843
 Tribe ORYZOMYINI Vorontsov, 1959

HOLOCHILUS PRIMIGENUS, sp. nov.
 (Figs. 1, 2)

Holotype—FMNH PM 56940, right mandible with incisor, m1–3.

Hypodigm—Holotype plus FMNH PM 56941, 56942, 56949, right mandibles with m1–3; PM 56943, right mandible with m2–3; PM 56944, 56945, left mandibles with m1–3; PM 56946, left mandible with m2–3; PM 56948, left mandible with m1–2; PM 56947, left maxilla with M1–3; PM 56950, left maxilla with M1–2; PM 56951, left maxilla with M2–3; P 15081, M1; P 15080, M3; P 15086, m1; P 15084, 15085, m3.

Occurrence—Tarija Basin, Department of Tarija, Bolivia, Ensenadan Land Mammal Age (middle Pleistocene).

Diagnosis—Large rat of the sigmodontine tribe Oryzomyini (sensu Voss and Carleton, 1993) with lophate, sigmodont molars; distinguished from living species of *Holochilus* by labial and lingual folds overlapping but not deeply interpenetrating, cusps not alternate, very small mesolophs and short but distinct mesoflexus on unworn M1 and M2, protoflexus M2, mesoloph of M3 vestigial, M3 shorter and narrower than M2, small, bud-like mesolophids on unworn m1 and m2, entolophid on m3, and smaller tooth size; from *Lundomys* by labial root of M1, present smaller tooth size, robust mandible with steeply-angled coronoid process, incisive foramen not extending well between M1s, and mesopterygoid fossa extending nearly to M3 posterior alveolus; from *Sigmodon*, *Prosigmodon*, and the phyllotine “sigmodonts” by large enameled pit in anteroconid of m1 and small, bud-like, but distinct, mesolophs and mesolophids on all upper and lower molars. Measurements in Table 1.

Etymology—*primigenus* (Latin), meaning primitive.

Discussion—It is important to note that *Holochilus primigenus* would be likely be classified in *Lundomys*, and possibly not even recognized as distinct from *L. molitor*, if the only material available were isolated teeth. The dentitions of *H. primigenus* and *L. molitor* are virtually indistinguishable except by size (Fig 3). Teeth are the only material available for many fossil muroids. Three non-dental characters are shared by *H. primigenus* with living *Holochilus* and distinguish it from *Lundomys*: a robust mandible with steeply-angled coronoid process; incisive foramen not extending well past the margin of the anterior alveolus of M1; and mesopterygoid fossa extending nearly to the posterior alveolus of M3. The mandible is fully as robust in *H. primigenus* as it is in living species of *Holochilus*, including a long alveolus of the lower incisor and large capsular process, and the coronoid process is possibly even more nearly vertical than in living *Holochilus*. The incisive foramen in *Lundomys* usually extends past the margins of the anterior alveolus of M1. In living *Holochilus*, the foramen stops well short of the alveolus, except in some young individuals (Voss and Carleton, 1993). The condition in *H. primigenus* is intermediate, with the incisive foramen just reaching the anterior alveolus in the two specimens with intact anterior palates. The mesopterygoid fossa terminates well posterior to M3 in *Lundomys* and does not reach the posterior alveolus. The fossa extends to or between the molars in living *Holochilus*, although there is some individual and age-related variation (Voss and Carleton, 1993). In *H. primigenus*, the fossa extends to the posterior alveolus of M3 in the single specimen. Thus, the mesopterygoid of *H. primigenus* is either intermediate for this trait or this species shares the shorter palate condition with living *Holochilus*.

PHYLOGENETIC RELATIONSHIPS

Methods

Sufficient parts of the mandible, upper and lower molars, and palate are preserved in the available specimens of *Holochilus primigenus* to permit its inclusion in a limited cladistic analysis. In order to estimate the cladistic relationships of *H. primigenus*, I used the same data set that Voss and Carleton (1993) used to investigate the relationship of *Lundomys* and *Holochilus* with respect to *Sigmodon* and the oryzomyines. Character descriptions are listed in the Appendix and the data matrix is presented in Table 2. Characters 1–25 are from Voss and Carleton (1993) where more detailed discussion of these characters can be found. Characters 26 and 27 were added for this study.

Multistate characters were treated as ordered (following Voss and Carleton, 1993) and analyzed under Wagner parsimony, using PAUP version 3.1.1 (Swofford, 1993) with the exhaustive search option. In the principle analysis, as in the preferred phylogeny of Voss and Carleton (1993), the tribe Oryzomyini (*Holochilus*, *Lundomys*, *Oryzomys*, and *Pseudoryzomys*) was constrained to be a monophyletic group that excluded *Sigmodon*. The rationale for this assumption is that a disproportionate number of the characters included in the analysis are dental characters subject to convergence on a sigmodont pattern in adaptation to a fibrous diet shared by *Holochilus* (Oryzomyini) and *Sigmodon* (Sigmodontini) (Voss and Carleton, 1993). Additionally, a much more extensive phylogenetic analysis for the subfamily Sigmodontinae strongly supports the monophyly of Oryzomyini to the exclusion of *Sigmodon* (Steppan, 1995b). The characters and taxa in this study are not sufficient to demonstrate oryzomyine monophyly, but they may be sufficient to estimate relationships within the “sigmodont” genera of the Oryzomyini. Outgroups examined by Voss and Carleton (1993) to estimate a hypothetical ancestor included a selection of extant New World muroids: neotomines, peromyscines, and Central American tylomyines (a group of uncertain affinity to the North American neotomine-peromyscines or Neotropical sigmodontines).

Synapomorphies described in the Results and Discussion section are those unequivocally hypothesized by both accelerated and delayed transformation options for character optimization. Accelerated transformation favors reversals over parallel evolution of characters, while delayed transformation favors parallelisms.

Results and Discussion

The most parsimonious tree under the constraint of a monophyletic Oryzomyini is 58 steps long (CI = 0.57, RI = 0.57) and places *Holochilus primigenus* as the sister species to the extant members of *Holochilus*, with *Lundomys* as the sister group to all *Holochilus* (Fig. 4A). *Pseudoryzomys* is the sister group to the *Holochilus/Lundomys* clade. The most parsimonious trees overall, in an unconstrained analysis, are significantly shorter, at 52 steps (Fig. 4B). The strict consensus of those five trees shows extant *Holochilus* and *Sigmodon* to be sister taxa, together forming one branch in an unresolved polytomy that includes *Lundomys*, *Pseudoryzomys*, and *H. primigenus*. The general results of intergeneric relationships are nearly the same as those found by Voss and Carleton (1993). Voss and Carleton (1993) found two most parsimonious trees assuming a monophyletic Oryzomyini, one matching the tree in Fig. 4A (minus *H. primigenus*) and the other placing *Lundomys* as the sister group to *Holochilus* plus *Pseudoryzomys*. My inclusion of *H. primigenus* reduces the number of most parsimonious trees in the constrained analysis from two to one. Thus a result of including this fossil species in the analysis thus solidifies support

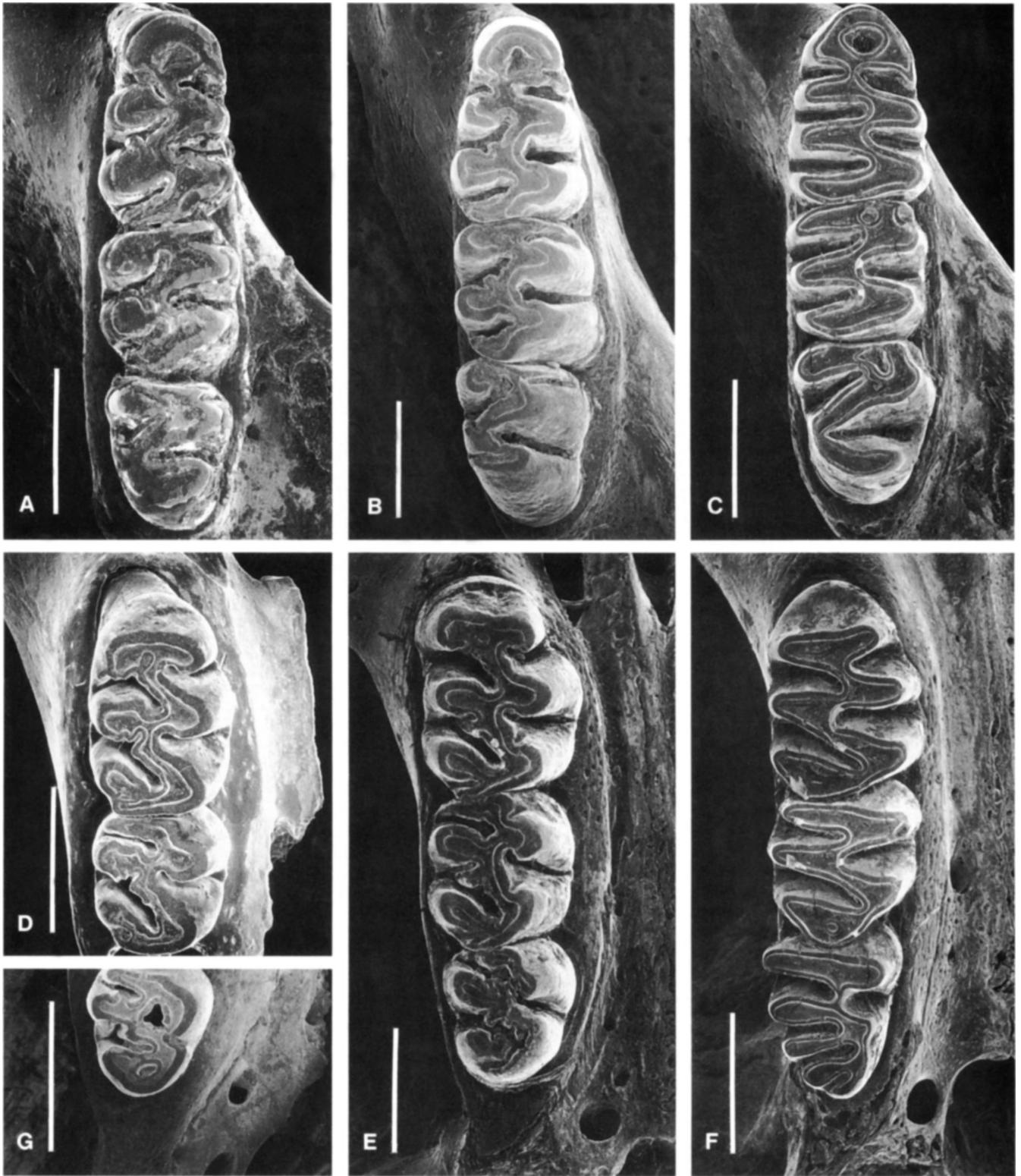


FIGURE 1. Lower (A–C) and upper (D–G) tooth rows of *Holochilus* and *Lundomys*. A, holotype of *Holochilus primigenus*, sp. nov., FMNH PM 56940; B and E, *Lundomys molitor*, FMNH 29255; C and F, *Holochilus brasiliensis*, FMNH 88914; D, *Holochilus primigenus* M1–M2, FMNH PM 56950; G, *Holochilus primigenus* M3, FMNH PM 56951. Scale bars = 2.0 mm.



FIGURE 2. Lateral views of mandibles. A, *Lundomys molitor*, FMNH 29263; B, holotype of *Holochilus primigenus*, sp. nov., FMNH PM 56940; C, *Holochilus brasiliensis*, FMNH 88913. Scale bar = 1.0 cm.

for the sister group relationship between *Holochilus* and *Lundomys*.

Monophyly of the extinct and living species of *Holochilus* is supported by the putative synapomorphies of a shortened incisive foramen and shorter palate (i.e., mesopterygoid fossa extending anteriorly nearly to the level of the posterior most alveolus of M3). A robust mandible with a steep coronoid process is also a synapomorphy under optimization with accelerated transformation. Three characters of the hindfeet that are not observable in *H. primigenus* support a clade containing extant *Holochilus* and *Lundomys*: unguis absent; natatory fringe present; and webbing extending between the digits. Characters supporting monophyly of extant *Holochilus*, to the exclusion of *H. primigenus*, are: cusps alternate, with lingual and labial folds deeply interpenetrating; mesoloph vestigial or absent from M1 and M2; anteroloph absent from M1; protoflexus absent from M2; and mesolophids absent from the lower molars. The placement of *Pseudoryzomys* outside the *Holochilus/Lundomys* clade means that complete loss of the mesolophid either occurred twice among these oryzomyines (in *Pseudoryzomys* and extant *Holochilus*) or a reversal occurred in *Lundomys*. There is no strong evidence for the evolution of a mesoloph or mesolophid from ancestors lacking these structures anywhere else among the sigmodontines (Steppan, 1995b). Reduction of the mesolophid may have occurred just once, leading to the common ancestor of *Holochilus*, *Lundomys*, and *Pseudoryzomys*.

The branch lengths in Figure 4A are proportional to the num-

TABLE 1. Measurements (in mm) of *Holochilus primigenus* from Tarija Basin, Bolivia. N = number of specimens.

Measurement	Mean	N	Observed range
Maxillary tooth row length		1	6.64
Length M1	2.67	2	2.63–2.70
Width M1	2.03	2	2.03
Length M2	1.97	3	1.86–2.11
Width M2	1.89	3	1.88–1.90
Length M3	1.65	2	1.61–1.68
Width M3	1.64	2	1.58–1.69
Mandibular tooth row length	7.28	8	6.79–7.58
Length m1	2.89	7	2.62–3.08
Width m1	1.85	7	1.75–1.93
Length m2	2.04	9	1.88–2.17
Width m2	1.94	9	1.84–1.99
Length m3	2.02	8	1.79–2.25
Width m3	1.74	8	1.65–1.81
Depth of ramus below m1	5.80	6	5.40–6.35

ber of character state changes, calculated using delayed transformation, which favors parallelisms over reversals. Of particular significance is that the branch leading to *Holochilus primigenus* is of zero length, independent of the character optimization used. In other words, *H. primigenus* shares at least two synapomorphies with extant *Holochilus* (shortened incisive foramen and palate), but this species possesses no known autapomorphies that can distinguish it from a potential ancestor. One possible autapomorphy for *H. primigenus*, given the available material, may be a short tooth row. There are two equally parsimonious reconstructions for tooth row length: parallel evolution of larger molars in *Lundomys* and in the lineage leading to extant *Holochilus* (*H. primigenus* retaining the plesiomorphic smaller size), or larger size leading to the *Holochilus/Lundomys* group, with an autapomorphic reversal to smaller size in *H. primigenus*. More detailed sampling of immediate outgroups to the *Holochilus/Lundomys* group is required to estimate the plesiomorphic size of the tooth row in this clade.

In summary, *Holochilus primigenus* appears to be a transi-

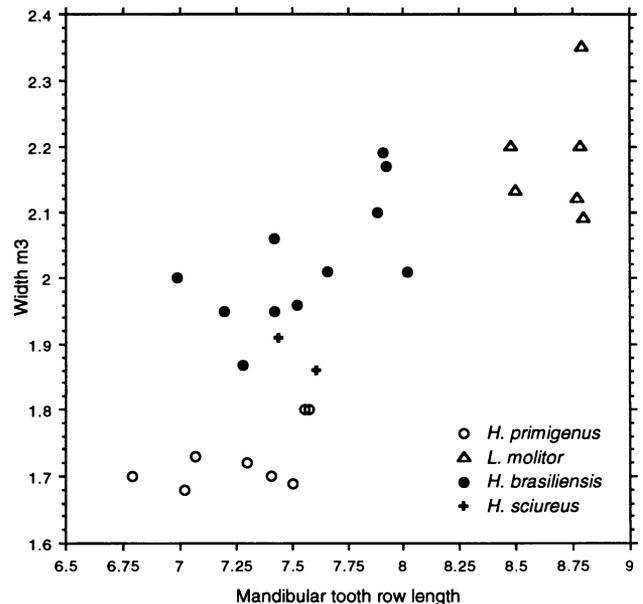


FIGURE 3. Scattergram of width of m3 plotted against mandibular tooth row length for the fossil *Holochilus primigenus*, sp. nov., and the extant *H. brasiliensis*, *H. sciureus*, and *Lundomys molitor*.

TABLE 2. Data matrix of morphological characters used in phylogenetic analysis. Data for characters 1–25 and all taxa except *Holochilus primigenus* are from Voss and Carleton (1993).

	Characters																										
	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	27
ancestor	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	?
<i>Holochilus brasiliensis</i>	1	1	1	2	0	1	1	1	0	0	1	1	1	1	1	1	0	2	1	1	2	1	1	1	1	2	0
<i>Holochilus sciureus</i>	1	1	1	2	0/1	1	1	1	0	0	1	1	1	1	1	2	2	0	2	1	1	2	1	1	1	1/2	0
<i>Lundomys molitor</i>	1	1	1	2	0	1	0	0	1	1	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	0	1
<i>Oryzomys subflavus</i>	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
<i>Pseudoryzomys simplex</i>	0	0	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	2	0	1	2	1	1	1	1	0	1
<i>Sigmodon hispidus</i>	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	2	1	2	1	0	2	1	1	0	1	0	0
<i>Sigmodon peruanus</i>	0	0	0	0	1	1	1	0	0	0	0	0	0	1	2	2	1	2	1	0	2	1	0	?	?	?	?
<i>Holochilus primigenus</i>	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	1	1	1	0	1	1	1	1	?	?	1	0

tional form. It retains the occlusal morphology that is plesiomorphic for the *Holochilus/Lundomys* clade and that it still shares with *Lundomys*, while having acquired the *Holochilus* synapomorphies of a robust mandible, steeply-angled coronoid, partially shortened incisive foramen, and shortened palate. The clade formed by living *Holochilus* species later evolved an even shorter incisive foramen and palate, and further reduced the mesoloph(-ids) until they became vestigial (*H. brasiliensis*,

M1–2) or were lost altogether (*H. sciureus*, M1–2 and m1–3; *H. brasiliensis*, m1–3). *Holochilus primigenus* is thus intermediate for those features. Therefore, it appears that major changes in the jaw and at least minor changes in the palate preceded final loss of the mesoloph(-id)s. Hershkovitz (1962, 1993) has maintained that loss of the complete mesolophostyle(id) (mesoloph[id] fused with mesostyle[id]) is preeminently important in sigmodontine evolution. It would be valuable to have good

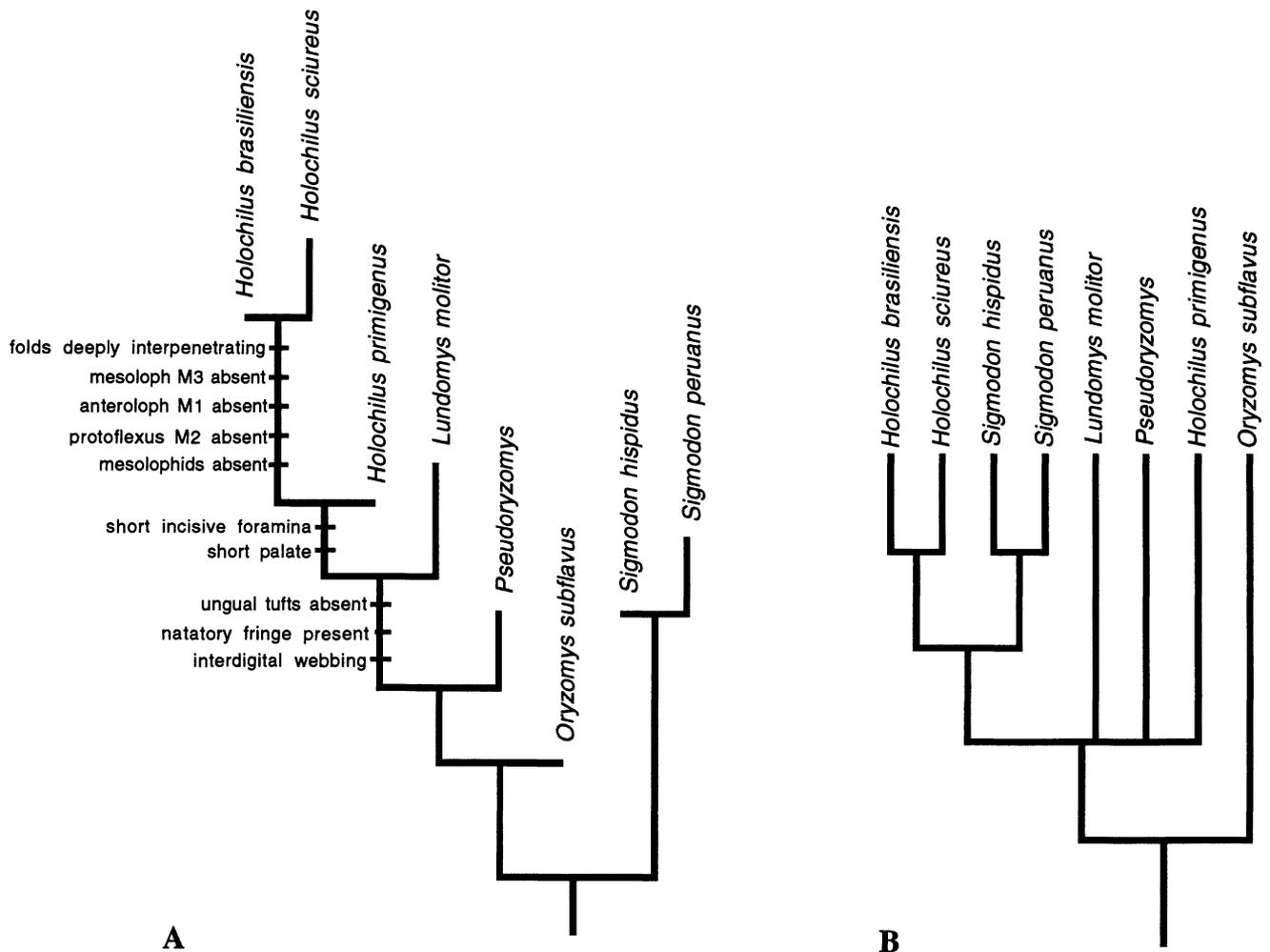


FIGURE 4. A, cladogram of most parsimonious tree under the constraint of a monophyletic Oryzomyini (sensu Voss and Carleton, 1993; Stepan, 1995b) that excludes *Sigmodon*. The single tree is 59 steps long (CI = 0.57); branch lengths are proportional to hypothesized character state changes assuming delayed transformation. Optimization by accelerated transformation differs primarily by lengthening branch leading to *Holochilus* and shortening branch to living *Holochilus*. Unambiguous synapomorphies for the *Holochilus/Lundomys* clade are indicated. B, strict consensus cladogram for the five most parsimonious trees overall, without constraints. Tree length is 52 steps.

dietary and ecological data on *Lundomys*, very little of which currently exists (Voss and Carleton, 1993), to compare with *Holochilus*, so that the possible adaptive significance of this evolutionary sequence can be examined.

It is possible that improved phylogenetic resolution of oryzomyine relationships could alter our estimate of the plesiomorphic condition for jaw and palatal morphology and molar size in the *Holochilus/Lundomys* clade. Reversal of the character polarities within the clade might shift the root into *Holochilus*, such that *H. primigenus* would be basal to both extant *Holochilus* and *Lundomys*. Taxonomy for the group would then need to be modified. However, given the available data, assigning *H. primigenus* to *Holochilus* is the best-supported hypothesis with the minimum nomenclatural impact.

The ability to place a fossil of known age onto a phylogenetic tree in, or close to, an ancestral position provides a constraint on divergence ages, the significance of which extends well beyond the "sigmodont" oryzomyines examined here. Attempts to use molecular data to estimate times of sigmodontine diversification have been hampered by the lack of calibration points (ages of phyletic branching points) and the likelihood of rate heterogeneity in mammals (Wu and Li, 1985; Baskin, 1986; Catzeflis et al., 1992), making the application of rates from other mammalian groups suspect. For example, Smith and Patton (1993) had only a single divergence date within sigmodontines with which to estimate molecular rates, and that was a minimum age with no associated maximum: the first appearance of *Bolomys* (= *Necromys*; Massoia and Pardiñas, 1993) in the fossil record (Reig, 1987). Those *Necromys* fossils do not record the time of the splitting of the *Necromys* lineage from the lineage leading to *Akodon*, but rather they are the first fossils found that possess some of the characters that distinguish *Necromys* from other genera. The actual splitting of lineages, which are the events estimated by DNA-based divergence estimates, surely predates those fossils by some significant, but unknown, time interval. As *H. primigenus* appears to be 0.7–1.0 million years old, the *Holochilus/Lundomys* split must have occurred prior to 700,000 years ago. Additionally, if *H. primigenus* is a direct ancestor to living *Holochilus*, or at least close to an ancestor both phyletically and temporally, then *H. brasiliensis* and *H. sciureus* may have split less than 1 Ma. This age information provides new data for calibrating molecular clock estimates of divergence times among sigmodontines, by providing an upper limit on divergence within *Holochilus* and a lower limit on the *Holochilus/Lundomys* split. DNA sequences from *Holochilus* and *Lundomys* are needed so that they can be combined with fossil dates (e.g., Reig, 1987) and sequences from other sigmodontines (e.g., Phillips et al., 1993; Smith and Patton, 1993; Stepan, 1995a) to help calibrate divergence age estimates among all sigmodontines. A calibrated "clock" would provide important information for evaluating biogeographic scenarios. However, even if *H. primigenus* is ancestral to living *Holochilus*, divergence times between these two groups will be underestimated if the former is a long-lived metaspecies (sensu Donoghue, 1985; Archibald, 1994) that persisted along with its daughter species for some time before examples of the latter were fossilized. Additionally, the geochronology and stratigraphy of the Tarija and Padcaya basins need to be refined to confirm the estimated age of *H. primigenus*.

ACKNOWLEDGMENTS

I thank John Flynn for his assistance with collections, access to his manuscripts currently in press, and for helpful discussions in formulating this manuscript. Curatorial assistance was provided by Bill Simpson. Jon Baskin, Robert Voss, Bruce Patterson, and John Flynn provided constructive criticisms on earlier drafts of this manuscript.

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Received 28 November 1994; accepted 9 August 1995.

APPENDIX. Characters and character states.

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1. Ungual tufts on hindfoot: 0, present; 1, absent.
 2. Natatory fringe on hindfoot: 0, absent; 1, present.
 3. Plantar pads on hindfoot: 0, thenar, hypothenar, and four interdigital pads well developed; 1, all pads very small and hypothenar usually absent.
 4. Interdigital webbing on hindfoot: 0, absent; 1, present, not extending to first interphalangeal joint of any digits; 2, present, extending to or beyond first interphalangeal joints of digits II, III, and IV.
 5. Mammary counts: 0, eight, thoracic teats absent; 1, ten, thoracic teats present.
 6. Anterodorsal margin of zygomatic plate: 0, smoothly rounded without sharp corner or spine; 1, with sharp corner or spine.
 7. Supraorbital margins: 0, without raised beads; 1, with raised beads, at least in older specimens.
 8. Postorbital ridge: 0, absent, postorbital wall without conspicuous relief; 1, present and concealing frontal-squamosal suture in most older specimens.
 9. Incisive foramen: 0, short, not extending posteriorly to or between anterior M1 alveoli in adults; 1, long, extending to or between alveoli.
 10. Alisphenoid strut: 0, present; 1, absent.
 11. Carotid circulation: 0, complete stapedial contribution to the facial supply; 1, without any stapedial contribution to the facial supply.
 12. Bullar suspension: 0, posterior suspensory process of squamosal present and connected to the tegmen tympani; 1, process absent, tegmen tympani not touching or barely in contact with squamosal.
 13. Enamel band of upper incisors: 0, smoothly rounded or flattened, but without labial bevel; 1, flattened medially, with distinct labial bevel.
 14. Molar occlusal topography: 0, bunodont; 1, flat crowned.
 15. Molar occlusal design: 0, cusps essentially opposite, lingual and labial folds not interpenetrating, rounded margins; 1, cusps slightly alternating, some lingual and labial folds deeply interpenetrating, more acute outer margins; 2, cusps alternating, some lingual and labial folds deeply interpenetrating, acute margins (prismatic).
 16. Mesoloph on M1 and M2: 0, mesoloph large, extending to labial cingulum, fused with mesostyle; 1, small, not extending to labial cingulum nor fused with mesostyle; 2, absent.
 17. Mesoloph on M3: 0, usually present and well developed; 1, absent or vestigial.
 18. Anteroloph on M1: 0, present and well developed, extending to labial cingulum; 1, small, not extending to cingulum; 2, absent.
 19. Protoflexus of M2: 0, present as a shallow indentation, at least in unworn teeth; 1, absent.
 20. Internal enameled pit of m1 procingulum: 0, absent; 1, present.
 21. Mesolophids on lower molars: 0, present and well developed, extending to lingual cingulum; 1, present in unworn teeth, small, not extending to lingual cingulum; 2, absent.
 22. Labial accessory root of M1: 0, absent; 1, present.
 23. Accessory roots of m1: 0, only labial accessory root usually present (three roots total); 1, labial and lingual accessory roots usually present (four roots total).
 24. Gastric glandular epithelium: 0, restricted to antrum (hemiglandular); 1, extends beyond esophagus, into corpus.
 25. Gall bladder: 0, present; 1, absent.
 26. Mesopterygoid: 0, not extending closer than $\frac{1}{3}$ length of M3 from posterior margins of M3s; 1, extending to less than $\frac{1}{3}$ length of M3 from posterior margins M3s; 2, extending between M3s.
 27. Coronoid angle: 0, anterior margin of coronoid process rising nearly perpendicular to body of ramus; 1, forming an angle of less than 60° with body of ramus.
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