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ABSTRACT

New material shows that *Nonomys simplicidens* has the dental formula, and some of the dental characters, of the Cricetidae. These are combined with an hystricomorphous zygomasseteric structure like that in Dipodoidea, i.e., the enlarged foramen for the medial masseter is separated by a lamina of bone from a smaller foramen which transmits the infraorbital nerve and blood vessels, and there is virtually no development of a zygomatic plate. This ambiguous combination of characters is seen also in the late Eocene *Simimys*, which has been classified as a dipodoid and as a muroid. *Nonomys* and *Simimys* are interpreted as members of an early radiation of myodont rodents, with derived characters that place them in the Muroidea rather than Dipodoidea, but with a combination of characters that excludes them from any presently defined family.

INTRODUCTION

Knowledge of the early Oligocene rodent *Nonomys simplicidens* has heretofore been very limited; no information has been published since Emry and Dawson (1972) described the lower dentition and partial dentary. Additional material recovered since that time includes skull fragments with maxillary dentitions, which provide new information about the anatomy of *Nonomys* and shed additional light on its relationships.

Abbreviations used in the text to denote institutional collections are as follows: F:AM, Frick Collection, American Museum of Natural History, New York; LACM:CIT, California Institute of Technology collection, now in Los Angeles County Museum of Natural History; TMM, Texas Memorial Museum, University of Texas, Austin; USNM, National Museum of Natural History, Washington, D.C.

[1] Research Associate, Department of Vertebrate Paleontology, the American Museum of Natural History; Curator of Tertiary Mammals, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution.

ACKNOWLEDGMENTS

SYSTEMATIC PALEONTOLOGY

SUPERFAMILY MUROIDEA

FAMILY *INCERTAE SEDIS*

GENUS *NONOMYS* EMRY AND DAWSON, 1973

Nanomys Emry and Dawson, 1972, not *Nanomys* Marsh, 1889.
Nonomys Emry and Dawson, 1973.
Subsumus Wood, 1974.[1]

Nonomys simplicidens (Emry and Dawson, 1972)

TYPE: F:AM 79304, right mandibular ramus with M_{1-3}.

[1] While this was in press, two papers appeared which require comment: Wood (1980) synonymized his genus *Subsumus* with *Nonomys*, as I had done here, but he placed it in the Geomyoidea, cf. Geomyidae, an assignment with which I do not agree. Martin (1980) created a new cricetid subfamily, the Nonomyinae, to include *Nonomys* and *Subsumus,* in my view an incorrect familial assignment for an unnecessary subfamily.

HYPODIGM: Type and; USNM 175368, left M_2; USNM 256764, right maxillary with M^{1-2} and palatine; USNM 256766, left maxillary with M^2; USNM 256763, right M^2; USNM 256765, left dentary, edentulous; USNM 256767, left dentary with I_1; USNM 256761, right M_1; USNM 256762, right M_1; TMM 40504-244, left dentary fragment with M_{1-2} (type of *Subsumus candelariae*).

EMENDED DIAGNOSIS: Small rodent, hystricomorphous, sciurognathous, foramen that carries the infraorbital nerve and blood vessels separated by bony lamina from the enlarged infraorbital foramen for the medial masseter, cheek teeth reduced to three molars, M_1^1 largest of molars, M_3^3 smallest, teeth low crowned, cuspate with indistinct connecting crests, well-developed lingual cingula on upper molars, buccal cingula on lowers, M^1 with large anterocone, M_1 with anteroconid, distinct hypoconulids on M_1 and M_2, entoconid of M_3 absent or barely indicated.

KNOWN DISTRIBUTION: Except for the type and TMM 40504-244, all specimens are from a single rich concentration of vertebrate remains at about 96 m. (315 ft.) above the base of the White River Formation in the Flagstaff Rim area of central Wyoming. The section is shown by Emry (1973, p. 29); detailed location of this concentration as well as the detailed locality of the type are given by Emry and Dawson (1972, p. 3). TMM 40504-244 is from the Airstrip Local Fauna of the Capote Mountain Tuff, Vieja Group, Trans-Pecos Texas (Wood, 1974, p. 101). *Nonomys* is known only from these two localities, the Flagstaff Rim area of Wyoming and the Big Bend area of Texas. Within the Flagstaff Rim area, *Nonomys* is known from only two stratigraphic levels, which are separated by only 4.5 m. (15 ft.). The type is at about 300 ft. and the remaining specimens at about 315 ft. on the zonation section (Emry, 1973, p. 29).

DESCRIPTION: The two mandibular rami (USNM 256765 and 256767, fig. 1A–C) are edentulous except for an incisor in the latter, but can nevertheless be confidently referred to *Nonomys*. Both are from the same concentration of small- and medium-sized mammals that produced the four isolated teeth
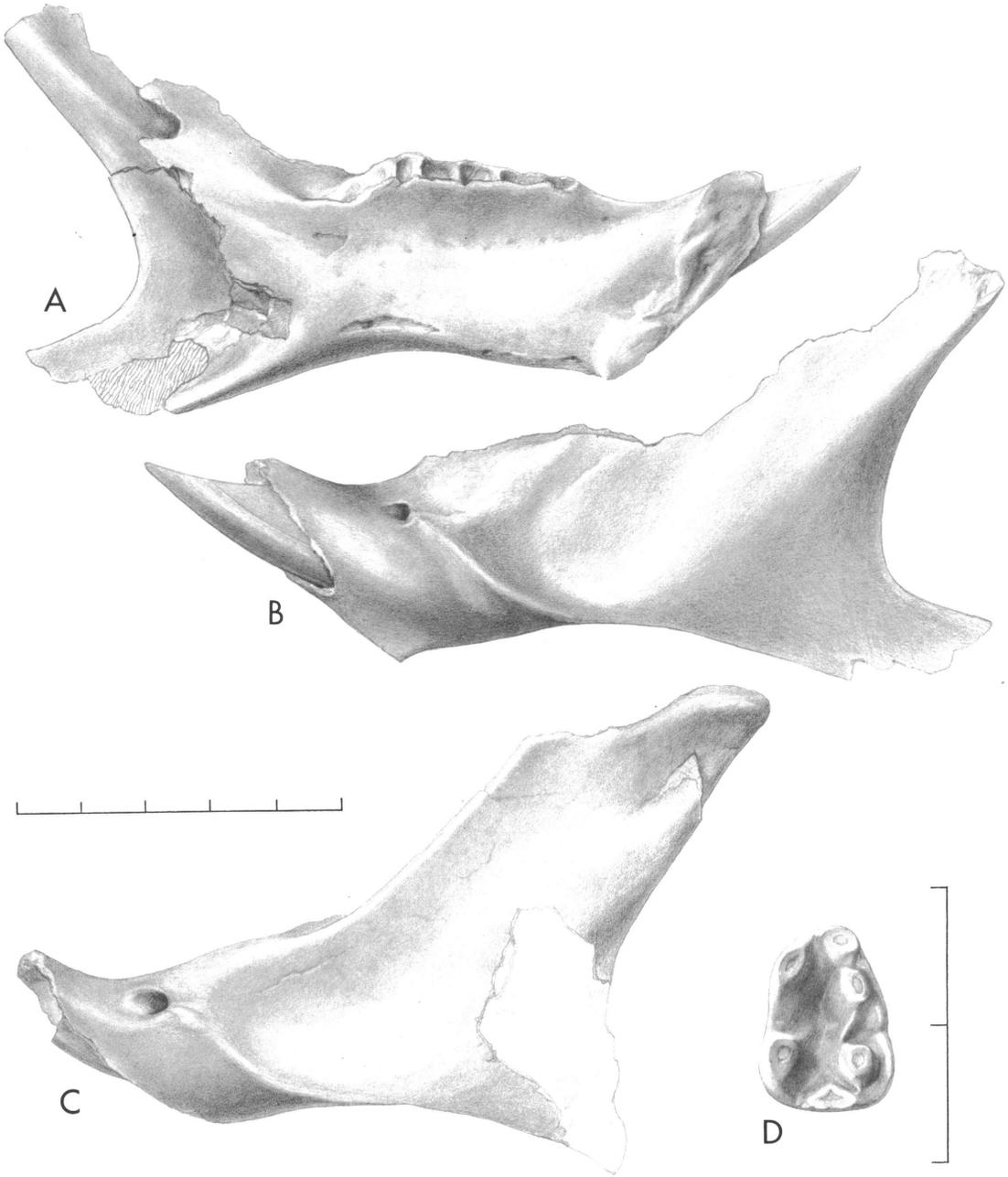
FIG. 1. *Nonomys simplicidens*. A. Medial view of left dentary, USNM 256767. B. Lateral view of same. C. Lateral view of left dentary, USNM 256765. D. Occlusal view of right M_1, USNM 256761. A–C approx. ×9.5, D approx. ×20; scales in mm.

and two maxillaries referred herein to *Non-omys*. The alveoli indicate three cheek teeth were present; the incisor shape, and the size

and other features of the dentary are like those of the type. These anatomical similar-ities, in conjunction with the absence of any

FIG. 2. Reconstruction of lower jaw of *Nonomys simplicidens,* based on USNM 256765 and 256767 and the type, F:AM 79304. Approx. ×5.

other rodent in these deposits to which the dentaries could be referred, leaves little doubt that they belong to *Nonomys simplicidens*. Each of the two dentaries has some parts preserved that are not present in the type, and together with the type they allow a nearly complete reconstruction of the lower jaw (fig. 2).

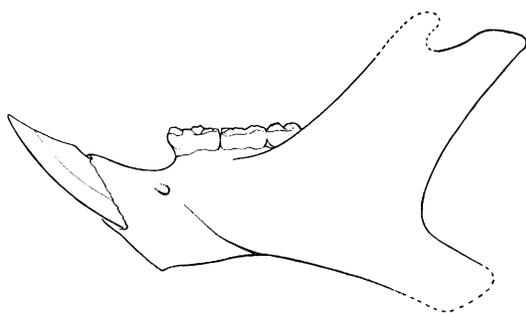USNM 256767 is complete anteriorly, and shows that the posteroventral edge of the symphysis ends beneath the middle of the diastema and protrudes ventrally in a distinct symphyseal process reminiscent of that in *Eumys*. The anterior end of the masseteric fossa is well preserved in both of the jaws referred herein. The main part of the fossa extends anteriorly as far as the middle of M_1; anterior to this, a distinct shelflike scar is presumed to be for insertion of the M. masseter medialis pars anterior. The lower edge of the masseteric fossa is defined by a rather sharp crest much like that of *Eumys* and other cricetids. This conflicts with the statement by Emry and Dawson (1972, p. 3) that the sharp crest is lacking in the type. I now believe the rounded nature of this crest in the type is a result of air-abrasive preparation. The upper border of the masseteric fossa is rounded and less distinct. The leading edge of the ascending ramus passes the alveolar border at about the middle of M_3.

In both specimens, a small linear muscle insertion is suggested by a slight shelf within the masseteric fossa, somewhat below, and parallel to, its upper border (see fig. 1B–C). This may be for some particular division of

the more posterior part of M. masseter medialis pars anterior.

The condyle is elevated somewhat above the level of the cheek teeth. Enough of the base of the coronoid process remains in USNM 256765 to indicate that it was an independent projection. In neither specimen is the angular process complete, but it can be determined that it was rather thin, extended posteroventrally at least as far back as the condyle and well below the main body of the jaw, and was slightly infected.

The dental foramen is well behind and somewhat above the level of the cheek teeth (fig. 1A). The other features of the mandible are as described in the type (Emry and Dawson, 1972). Figure 2 shows the general shape of the dentary of *Nonomys* in a composite reconstruction.

The two isolated lower first molars (USNM 256761 and 256762) are from the same concentration as the two edentulous lower jaws and the maxillaries referred herein. The better preserved of the two is shown in figure 1D. It is very similar to M_1 of the type, differing principally in the slightly larger anteroconid and in the heavier buccal cingulum, which is continuous from the anteroconid to the hypoconulid; in the type the cingulum is very faintly developed buccal to the protoconid. Each of the lower cheek teeth has two roots; the posterior root of M_1 is stouter than the anterior, whereas the opposite is true of M_2 and M_3.

Wood (1974, p. 100) gave the name *Subsumus candelariae* to a small fragment of jaw with M_{1-2} from the early Oligocene of the Big Bend area of Texas. He referred the new genus and species to cf. Cricetidae, though he considered this assignment "exceedingly tentative and probably incorrect." He did not compare the specimen with *Nonomys,* though comparable parts are preserved. I have done so and can find no significant differences. The morphology, as far as can be determined, is extremely similar to that of the type of *N. simplicidens,* and the size is also nearly identical (see table 1). I therefore have placed *Subsumus candelariae* in the synonymy of *Nonomys simplicidens*.

From the same site that produced the man-

TABLE 1

Measurements (AP = anteroposterior, TR = transverse) in Millimeters of the teeth of
Nonomys simplicidens

	M^1		M^2		M_1		M_2		M_3	
	AP	TR	AP	TR	AP	TR	AP	TR	AP	TR
USNM 256764	1.49	1.28	1.24	1.29	—	—	—	—	—	—
USNM 256763	—	—	1.25	1.23	—	—	—	—	—	—
USNM 256766	—	—	1.12	1.30	—	—	—	—	—	—
F:AM 79304[a]	—	—	—	—	1.33	1.06	1.23	1.13	1.06	0.96
TMM 40504-244[b]	—	—	—	—	1.34	1.05	1.30	1.20	—	—
USNM 175638[a]	—	—	—	—	—	—	1.21	1.14	—	—
USNM 256761	—	—	—	—	1.37	0.99	—	—	—	—
USNM 256762	—	—	—	—	1.30	0.97	—	—	—	—

[a] From Emry and Dawson, 1972, p. 8.

[b] From Wood, 1974, p. 102.

dibles and lower dentitions described above, two maxillaries have also been recovered, one (USNM 256764) with M^{1-2} and most of the palatine attached (fig. 3) and the other (USNM 256766) with M^2 and more of the ventral root of the zygomatic process (fig. 4). An additional isolated M^2 was also recovered. M^3 of *Nonomys* is still not known.

As in most muroids, M^1 is the largest of the cheek teeth, and, judging from the size of its alveolus, M^3 the smallest. The upper dentition, like the lower, is generally cuspate with connecting crests much lower than the cusp apices and with strong lingual cingula.

M^1 has a prominent anterocone lobe, buccally placed, and connected by a low curving crest to the anterior end of the paracone. On this crest, buccal to the anterocone, are two additional minute cuspules. Except for this low connection to the anterocone, the paracone is isolated. A mure connects the posterobuccal edge of the protocone with the anterobuccal edge of the hypocone. A low crest from the metacone joins the mure near the posterobuccal corner of the protocone. A small mesostyle is present at the buccal end of the valley between paracone and matacone. Lingual to the protocone and hypocone is a broad cingulum which is continuous posteriorly with the posterior cingulum. Opposite the protocone and hypocone the cingulum is developed into distinct cusps which, at the wear stage represented, are

higher than the protocone and hypocone. However, the width of dentine exposed by wear of the protocone and hypocone suggests that they were higher than the cingular cusps when the teeth were unworn. The posterior cingulum merges with the posterior surface of the metacone. M^1 has three roots (see alveoli in fig. 4B); the anterior root and lingual of the two posterior roots are about equal in size, while the posterobuccal is somewhat smaller.

The anteroposterior and transverse dimensions of M^2 are nearly equal. A low anterior cingulum connects the anterior surfaces of the paracone and protocone. As in M^1, the paracone is otherwise isolated. The relationships of the other major cusps are much as they are in M^1, with metacone connected by a low crest to the mure, which joins protocone and hypocone; the broad lingual cingulum is developed into cusps opposite the protocone and hypocone. M^2 has three roots; the two buccal roots, beneath paracone and metacone, are about equal in size, while the single lingual root is much stouter.

M^3 is not yet known, and both maxillaries are damaged in this region so that the number of roots borne by M^3 cannot be determined from alveoli.

In USNM 256764 the palatine bone extends between the maxillaries as far anteriorly as the protocone of M^1. The posterior palatine foramen is opposite M^2, the com-
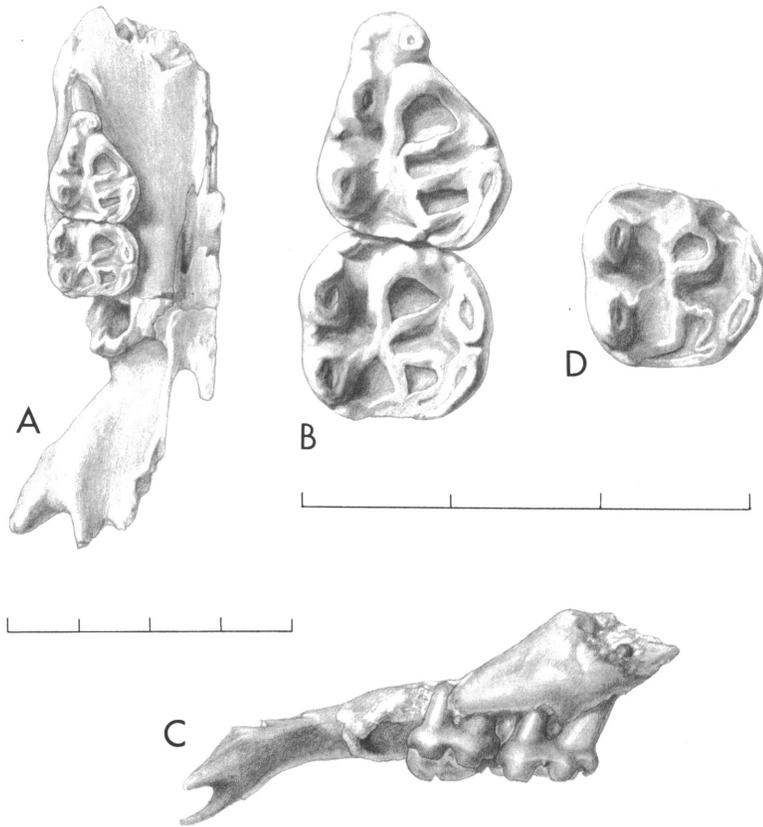
FIG. 3. *Nonomys simplicidens*. A. Palatal view of right maxillary and palatine, USNM 256764. B. Occlusal view of M^{1-2} of same. C. Lateral view of same. D. Occlusal view of right M^2, USNM 256763. A and C approx. ×9.5, B and D approx. ×20; scales in mm.

mon dipodoid-muroid position, and is entirely within the palatine, the primitive rodent condition retained in some myomorphs. The posterior narial opening is behind a transverse line drawn at the posterior edge of M^3. The palatine is broad and quite flat posteriorly, with short pterygoid processes and apparently a very shallow pterygoid fossa. The anterior end of the palate as preserved in USNM 256764 is a broken edge, so the posterior limit of the incisive foramina cannot be determined; the foramina did not extend as far posteriorly as in some modern muroids and dipodoids. With the cheek teeth oriented horizontally, the palate slopes upward anteriorly.

Although the superior zygomatic root of the maxillary is not preserved, enough remains of the inferior root in USNM 256766 to show that it is dipodoid in character. The inferior root is narrow and only slightly inclined beneath a large infraorbital foramen that is broad ventrally as in dipodoids, rather than narrow ventrally as in most cricetids. On the ventral surface of the inferior root, near its base, is a distinct depression, which, if a natural feature rather than a breakage artifact, may have been for the origin of a distinct anterior head of the M. masseter superficialis. The posterior margin of the inferior root of the zygoma (or anterior limit of the temporal opening) is slightly ahead of M^1.

A thin plate of bone forms the ventromedial edge of the large foramen for the medial
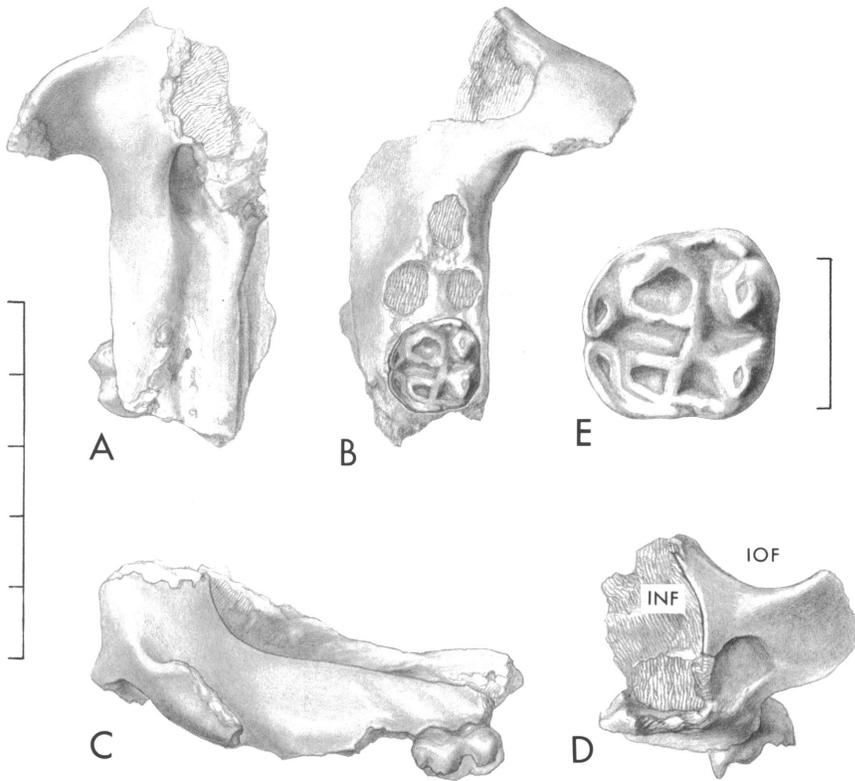
FIG. 4. *Nonomys simplicidens,* USNM 256766, left maxillary with M². A. Dorsal view. B. Palatal view. C. Lateral view. D. Anterior view, IOF indicates enlarged infraorbital foramen for masseter, INF indicates separate neurovascular infraorbital foramen. E. Occlusal view of M². A–D approx. ×9.5, E approx. ×20; scales in mm.

masseter and separates it from the smaller ventromedial foramen, as in *Simimys* and the dipodoids. Tullberg (1899) found that the smaller separate foramen in dipodoids transmits the infraorbital nerve, and Klingener (personal commun.) has determined that it carries the infraorbital blood vessels as well. The bone separating the two foramina is relatively thicker in *Nonomys* than in modern dipodoids, and appears to be most like the condition seen in *Simimys.* In dorsal view (fig. 4A) a shallow trough can be seen in the upper surface of the maxillary, above the molar roots, leading forward into the smaller separate foramen. The similarity of these features to those of modern dipodoids suggests that *Nonomys* was like dipodoids in having the large foramen for the medial masseter separated by bone from the neurovascular infraorbital foramen.

DISCUSSION

Emry and Dawson (1972) interpreted *Nonomys* as an early product of the myomorph radiation, and placed it in the Cricetidae, not so much because it was manifestly a cricetid, but because it fit less comfortably in any other family. They remarked (1972, p. 8) that the lower cheek teeth of *Nonomys* are so simple in character and lacking in most special features usually used in determining relationships, that its phylogenetic position is difficult to interpret. The problem was compounded by the absence of upper jaws and teeth. Upper jaws and teeth now being known, a reassessment is in order.

It is now clear that *Nonomys* has the typical cricetid dental formula, I_1^1, M_3^3. It is equally clear that *Nonomys* is hystricomorphous and sciurognathous and, furthermore, that it is hystricomorphous in the same way that dipodoids are, i.e., the foramen for the medial masseter is broad ventrally rather than compressed as in cricetids, there is virtually no development of a zygomatic plate, and a smaller separate foramen for the infraorbital nerve and blood vessels is present ventromedial to the enlarged muscular foramen. *Nonomys* has, with its cricetid dental formula and dipodoid hystricomorphy, the same ambiguous combination of characters that makes the late Eocene rodent *Simimys* so taxonomically fickle.

Wilson (1935) originally placed *Simimys* in the Cricetidae, and later (1949a) viewed it as representing a stock ancestral to cricetids and dipodoids, but with sufficient progress in skull structure and dental formula to make it a muroid rather than dipodoid rodent. Wood (1937, 1955) and Stehlin and Schaub (1951) pointed out similarities with *Plesiosminthus* and favored referral to the Zapodidae. Klingener first considered it a dipodoid (1963) and later a muroid (1964). Dawson (1966), Vianey-Liaud (1972), and Wood (1974) pointed out its ambiguous nature. Lindsay (1968) considered it a muroid, Lillegraven and Wilson (1975) favored referring it to the Zapodidae, and Lindsay (1977) argued that *Simimys* belongs at the base of the Cricetidae.

Emry and Dawson (1972) pointed out that the cuspate lower teeth of *Nonomys* are very different from the more lophate teeth of *Simimys,* and concluded that the two were probably not closely related. However, the derived features of the zygoma shared by the two genera, in conjunction with their common dental formula, suggests a closer relationship than previously thought.

The zygomasseteric structure of *Simimys* is known from a single specimen, LACM:CIT 3529, the type and only specimen representing *Simimys ? murinus* Wilson, 1949a. This specimen, a rostrum with palate, contains only one tooth, an M^1, which was so different from all other first molars of *Simimys*

then known that Wilson was unsure of its referral to the genus *Simimys.* However, Lillegraven and Wilson (1975, p. 871) found that the morphology of this M^1 can be matched very nearly exactly with variants seen in samples that also include morphologies characteristic of *S. vetus* and *S. simplex.* They concluded that all represent the same species, with *S. simplex* the surviving senior synonym. There is no longer any doubt therefore that the zygomasseteric structure of *Simimys* is represented by LACM:CIT 3529.

In the presence, relative size, and position of the separate neurovascular and muscular infraorbital foramina, *Nonomys* and *Simimys* are very similar. The only apparent difference in the zygomasseteric region is in the more distinct area of origin of the lateral masseter in *Simimys.* In *Nonomys* the inferior root of the zygomatic process is convex on its anteroventral surface and has no distinctly defined area of origin of the lateral masseter. In this respect, *Nonomys* is more like modern Zapodidae; it is specifically more like *Sicista,* in which the origin of the lateral masseter is even less distinct than in zapodine zapodids. In *Simimys,* on the other hand, the inferior root of the zygomatic process is concave on its anteroventral surface, with distinctly defined area of origin of the lateral masseter. This surface is inclined upward anteriorly, suggesting incipient development of a zygomatic plate, though it is not comparable to the development of this feature in typical cricetids. Actually, some of the larger modern dipodids, such as *Jaculus,* have a distinct origin of the lateral masseter, and development similar to that of *Simimys* is seen even in some protrogomorphous rodents (e.g., *Sciuravus,* particularly *S. powayensis,* and some *Ischyromys*). This feature of *Simimys* is not sufficiently advanced to be indicative of cricetid affinities.

Wilson (1949) noted the presence of a small foramen just below the infraorbital foramen in *Simimys* (LACM:CIT 3529). Lillegraven and Wilson (1975, p. 874) recalled Wilson's statement and added that "such an opening is present but larger in *Zapus.*" I cannot reconcile this with my own observa-

tions; the separate neurovascular foramen (NF) in *Simimys* is relatively as large as, perhaps larger than, it is in *Zapus,* and is certainly larger absolutely. This discrepancy in observations might be explained by the presence in *Simimys* of a very small foramen just below the NF, which is ventromedial to the very large infraorbital masseter foramen (MF) (see fig. 5C). Lillegraven and Wilson may have interpreted this very small foramen as the NF, the NF as the MF, and the much enlarged MF as the anterior edge of the orbit. Such an interpretation by Lillegraven and Wilson seems unlikely, but their observation on the size of the NF relative to that of *Zapus* is otherwise inexplicable.

Lindsay (1977) discussed the infraorbital foramina of *Simimys,* and though he regarded the separate small foramen as the most significant dipodoid character of *Simimys* (1977, p. 601), it is apparent from his discussion (and confirmed by personal commun.) that he has indeed interpreted the minute foramen previously mentioned as the separate neurovascular foramen. What I have called the smaller separate neurovascular foramen (NF of fig. 5), Lindsay interprets as the enlarged masseter foramen, and what I have called the enlarged masseter foramen (MF of fig. 5) Lindsay interprets as the orbit. There are a number of reasons why Lindsay's interpretation cannot be correct.

If Lindsay's interpretation were correct, then the orbit of *Simimys* would be extremely small for a rodent, and would be situated entirely above the anterior root of the zygoma, facing forward (see fig. 5). The small ascending process on the maxillary that I interpret as the posteroventral limit of the enlarged masseteric foramen (MF of fig. 5) is interpreted by Lindsay (personal commun.) as a "process posterior to the orbit for attachment of fascia that circle the eye," and he believes it is the same as the postorbital process which is better developed in the fossil cricetid *Cricetops* and in modern zapodids and cricetids. I call attention to the position of this process in *Simimys*; it is even with the middle part of the inferior zygomatic root, well ahead of the front edge of M^1 (fig. 5A and 5C are anterolateral oblique views,

so the process may appear to be more posteriorly placed; fig. 5B and Wilson's, 1949, pl. 2, fig. 1 are full lateral views). This is where the posteroventral edge of the enlarged masseter infraorbital foramen is situated in dipodoids (fig. 6A), and in many histricomorphs the posterior edge of the infraorbital foramen is even further back relative to the root of the zygoma. But in no rodent is the posterior edge of the orbit situated above the anterior root of the zygoma, ahead of M^1. And perhaps more important than position is the fact that in *Simimys* this small process is on the maxillary bone, whereas the postorbital process of *Cricetops* (fig. 6B) is on the jugal bone, as it is in all rodents (so far as I can determine, in all mammals) that have a postorbital process developed on the zygomatic arch. The postorbital process on the jugal of *Cricetops,* and the many other rodents that have low postorbital processes on the arch, is well behind the anterior root of the zygoma, usually opposite the posterior part of the palate, and often even farther back. The orbits of rodents are generally large, occupying more than half the temporal opening, and facing upward and outward.

In most rodents the jugal extends forward and upward to contact the lacrimal so that no part of the orbital rim is formed of maxillary bone. This is the condition found in most mammals and is almost certainly the primitive conditions for rodents. It is seen for example in protrogomorphs including paramyids (*Paramys, Leptotomus, Thisbemys, Reithroparamys, Ischyrotomus*), sciuravids (*Sciuravus*), cylindrodonts (*Cylindrodon, Ardynomys*), and in *Aplodontia.* It is also the condition found in most sciuromorphs (all sciurids, castorids, and eomyids), and in all dipodoids. Even in such forms as *Alactagulus,* where the bone between the orbit and the large masseteric foramen is reduced to a very slender bar, the jugal still has a thin dorsal process reaching up to the lacrimal and forming the anterior orbital rim. The maxillary bone forms part of the orbital rim in some of the more advanced rodent groups such as modern geomyoids (as far as can be determined in fossil heteromyids and
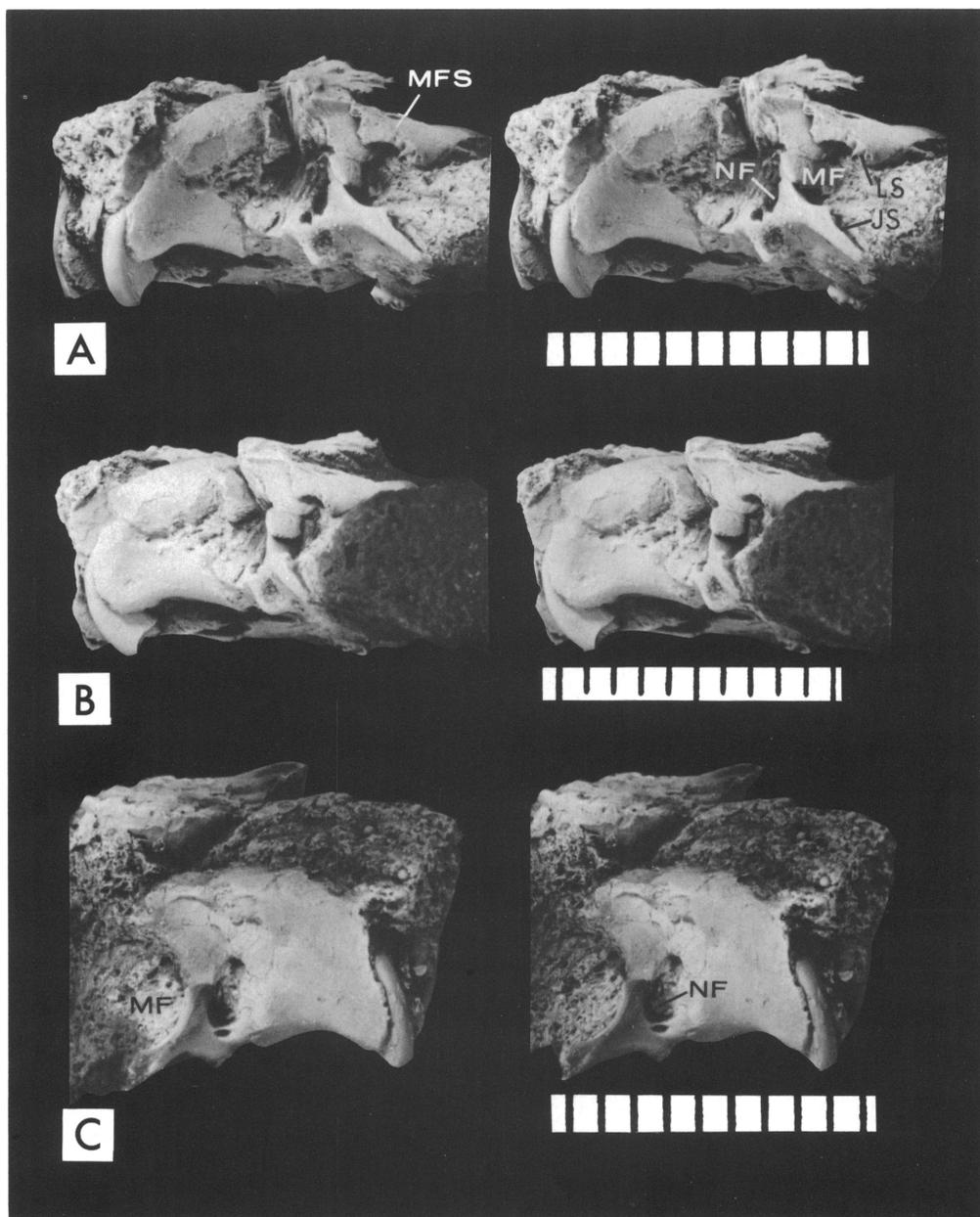
FIG. 5. Rostrum of *Simimys simplex,* LACM:CIT 3529 (type of *S.* ? *murinus* Wilson, 1949), stereograms. A. Left anterolateral oblique view. B. Left lateral view. C. Right anterolateral oblique view. MFS = maxillary-frontal suture, NF = neurovascular infraorbital foramen, MF = masseteric infraorbital foramen, LS = suture on frontal for lacrimal, JS = suture on maxillary for jugal. Scales in mm.

geomyids as well), cricetids, and murids, and at least some of the hystricomorphs. But even in these, the maximum extent of the maxillary contribution to the orbital rim is from about the anteriormost to ventralmost part of the orbit; the posteroventral part of

the orbit is bounded by jugal, and where a postorbital process is formed on the zygoma it is invariably on the jugal.

The left side of the *Simimys* specimen is more informative than the right side, even though a wide, plaster-filled crack separates the zygomatic area from the rostrum, adding some confusion to the illustration (fig. 5A–B). The relationships of the masseteric and neurovascular foramina and the very small additional foramen are best interpreted on the right side (fig. 5C), but the relationships of these to other parts of the skull can best be seen on the left (fig. 5A–B). On the left side the bone separating the neurovascular and muscular foramina appears to be composed of two overlapping lamina, one extending upward and inward from the root of the zygoma and the other outward and downward from the side of the rostrum (fig. 5A–B); that this is more likely a break than a suture is suggested by the right side which appears to have a solid bar of bone. The overall size and shape of the enlarged masseteric foramen is also best seen on the left side, where all the parts preserved are bounded by maxillary bone; the jugal suture can be clearly seen (JS of fig. 5) just posterior to the small dorsal process that marks the posteroventral limit of the large foramen, the suture for the lacrimal (LS of fig. 5) can be seen on the frontal, and the maxillary-frontal suture is distinct on the specimen (its position indicated by MFS in fig. 5).

If the large opening above the inferior zygomatic root of the maxillary of *Simimys* is interpreted as the orbit, then *Simimys* is not only a unique rodent, but a unique mammal. If it is interpreted as the enlarged opening for the masseter, then *Simimys* has typical dipodoid hystricomorphy, closely comparable to that of modern dipodoids.

Some features of *Simimys* suggest that dipodoid hystricomorphy, at least as developed in *Simimys*, was not the result of invasion of the infraorbital foramen by the medial masseter, but that the medial masseter may have penetrated the maxillary lateral to the infraorbital foramen, possibly at the maxillary-jugal suture. There is no clear evidence that the enlarged masseteric foramen
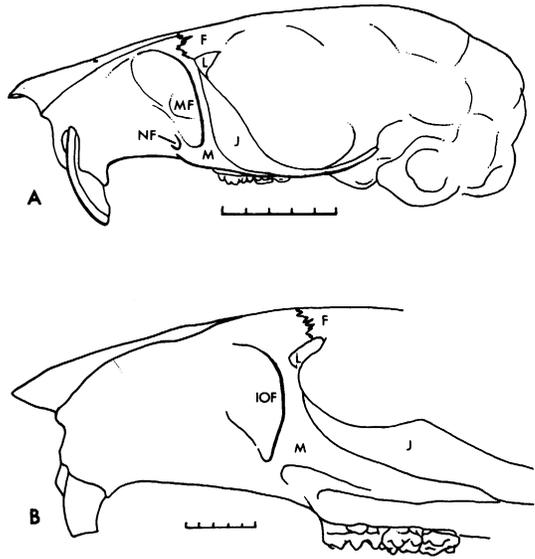

FIG. 6. Dipodoid and cricetid skulls. A. *Zapus hudsonius,* drawn from USNM 46827 (modern mammal series). B. *Cricetops dormitor,* drawn from AMNH 19054, right side reversed. F = frontal bone, L = lacrimal bone, J = jugal bone, M = maxillary bone, MF = masseteric infraorbital foramen, NF = neurovascular infraorbital foramen, IOF = combined neurovascular and masseteric infraorbital foramen. Scales in mm.

in *Simimys* was bounded posteriorly by maxillary bone. The small process on the maxillary that marks the posteroventral limit of this large foramen is not definitely broken on either left or right side of the specimen. The jugal suture is immediately posterior to this process, most clearly observed on the left side of the specimen. It may have been that in *Simimys* the posterior margin of this large foramen was bounded by jugal bone, rather than by a slender bar of maxillary bone as it is in modern dipodoids (fig. 6A). It is the smaller separate neurovascular foramen in dipodoids that has the functions of the primitive infraorbital foramen. It is in *Simimys* and *Nonomys,* which of the known fossil material must most closely represent the condition of the muroid-dipodoid common ancestor, that the bone separating the neurovascular and muscular foramina is thick-

est. These morphologic details raise the question of whether dipodoid hystricomorphy might not have developed by the medial masseter penetrating the maxillary-jugal suture and migrating onto the side of the rostrum, while remaining completely separated from the infraorbital foramen. This hypothesis is admittedly speculative, but is an alternative suggested by, and consistent with, the evidence, and at present cannot be falsified.

Wilson (1949b, p. 123), primarily on the basis of fossil evidence, suggested that the myomorphous masseter was derived from the dipodoid (hystricomorphous) type. Klingener (1964, p. 76) noted that the myomorphous type could have been derived from protrogomorphous, sciuromorphous, or hystricomorphous types, but considered the first two very unlikely, and strongly favored derivation from the hystricomorphous type by "upgrowth of the lateral masseter on a zygomatic plate and consequent ventral compression of the infraorbital foramen" (meaning lateral compression of the ventral part of the IOF). Klingener cited supporting evidence from living and fossil myomorphs, including *Cricetops* and *Simimys*. Lindsay (1977) also favored this hypothesis, adding considerable evidence from other fossil rodents that either support the hypothesis or are consistent with it. *Nonomys* lends additional support.

Wilson (1949b, p. 124) pointed out the similarity of the dental pattern of *Simimys* to that of the dipodoid *Pliesosminthus*, and suggested that this indicates that *Simimys* is close to the common ancestor of muroids and dipodoids. I agree fully with this interpretation and believe *Nonomys*, with its combination of muroid and dipodoid characters, occupies a similar position. Present evidence best supports the hypothesis that the common ancestor of muroids and dipodoids had dipodoid hystricomorphy (i.e., with separate neurovascular and muscular infraorbital foramina), or, in other terms, that this is the primitive condition of the Infraorder Myodonta, erected by Schaub (1958) to include the Dipodoidea and Muroidea. Separation of the neurovascular and

muscular foramina is retained to some degree by all modern dipodoids and by all fossil ones for which the zygomasseteric region is known. I qualify this with "to some degree" because in some dipodoids the lamina of bone separating the two foramina extends upward and inward from the inferior zygomatic root but does not quite contact the side of the rostrum; the separation of the two foramina is therefore not complete, even though the neurovascular passage is effectively separated from the muscular passage. The separation is complete for example in *Jaculus, Dipus, Allactaga,* and *Zapus,* and incomplete in *Stylodipus, Alactagulus, Sicista, Eozapus,* and *Napaeozapus.* Few fossil taxa are preserved well enough to allow a determination; *Megasminthus,* for example, is known from many specimens, and it appears that the lamina of bone has a free border, not joined to the side of the rostrum, but in most specimens it also appears to have been abraded by stream action so the determination is inconclusive.

The strong lingual cingula of the upper molars and buccal cingula of lower molars in *Nonomys* are not particularly reminiscent of either dipodoids or muroids. Emry and Dawson (1972) called attention to the buccal cingula of the lower molars by suggesting that these, along with the essentially cuspate character of the teeth might be suggestive of relationships to the Muridae. In the absence of more compelling evidence, this relationship was not considered very likely.

Among the hypotheses on the origin of the murid dental pattern (for example see Petter, 1966; Vandebroek, 1966; Lavocat, 1967), the most promising suggests that the third anteroposterior row of cusps on murid molars was derived from lingual cingula. Jacobs (1978) reviewed the various hypotheses and argued convincingly, on the basis of considerable fossil evidence, that the third row of cusps is indeed derived from lingual cingula. The cingular cusps of the molars of *Nonomys* (figs. 3 and 4) cannot be reconciled exactly with the murid cusp homologies suggested by Jacobs (1978), and, if he is correct in his assertion that a single pattern of cusp connections and associations is diagnostic

for the Muridae, then a close relationship between *Nonomys* and murids is ruled out.

Among the cricetids are a few forms that also have one or more extra lingual cusps on the upper molars, apparently convergent to murids in this respect. *Cricetomys* for example, usually has two lingual cusps, which seem to be associated most closely with the protocone and hypocone, and *Petromyscus, Dendromus,* and *Myocricetodon* also have one or more lingual cusps on the upper first molar. The lingual cingular cusps of *Nonomys* might also be suggestive of affinities to these European cricetids, but convergence is equally likely.

Nonomys shares some similarities with fossil geomyoids. The enigmatic medial Oligocene *Diplolophus,* for example, has the cricetid dental formula, and relatively low-crowned, cuspate dentition. The cusp pattern in *Diplolophus* is, however, more consistent with geomyoids, being organized into two transverse lophs (as its name suggests), with no anteroposterior connections between them. Comparisons between the teeth of *Nonomys* and *Diplolophus* break down when carried beyond the superficial level.

The morphology of the dentary of *Nonomys* is similar to that of some fossil geomyoids, particularly to the early heteromyid *Heliscomys.* Here the position of the mental foramen, position of the anterior limit of the masseteric fossa, and the indistinct dorsal border of the masseteric fossa are points of resemblance. Forward migration of the origin of the medial masseter in both *Nonomys* and the geomyoids apparently produced similar results in the morphology of the dentary. The similarities are certainly convergent, the forward migration of the medial masseter in *Nonomys* being accomplished through hystricomorphy, and that of geomyoids through sciuromorphy.

SUMMARY

Nonomys, Simimys, and the Dipodoidea all share the derived condition of dipodoid hystricomorphy (i.e., a smaller foramen for the infraorbital nerve and blood vessels sep-arate from the enlarged foramen for the medial masseter). Evidence from both fossil and modern rodents indicates that the myomorphous masseter of cricetids and murids was derived from this hystricomorphous condition, which is present in some early muroids. This condition unites the Muroidea and Dipodoidea into the Myodonta. *Nonomys* and *Simimys* both have the teeth reduced to three in each maxillary, a derived character of the Muroidea, excluding them from the Dipodoidea which retains P^4 (except in one modern genus). *Nonomys* shares other dental characters with the muroids, the most important of which are probably the large anterocone of M^1 and anteroconid of M_1. The dental pattern of *Simimys* is more reminiscent of that of the zapodid dipodoids. *Nonomys* and *Simimys* differ in degree of distinctness of the origin of the lateral masseter, *Nonomys* more nearly retaining the primitive dipodoid condition, and *Simimys* showing incipient development of a zygomatic plate, which is not sufficiently derived to be called typically muroid. Although *Nonomys* and *Simimys* have derived characters placing them in the Muroidea, they are combined with dipodoid characters that suggest both genera are close to the common ancestry of the two superfamilies. This returns essentially to Wilson's (1949, p. 23) interpretation of *Simimys* as representing "a stalk which was ancestral to both cricetids and Dipodoidea, but in which enough progress had been made in skull structure and dental formula so that it is a muroid rather than a dipodoid rodent." The subsequent confusing taxonomic history of *Simimys* resulted from attempts to place the genus into one or another of the modern families by emphasizing only certain of its characters. The same conflicts would be encountered in trying to place *Nonomys* in any modern family. Both *Simimys* and *Nonomys* are best interpreted as members of an early radiation of hystricomorphous muroid rodents, neither being in any presently defined family, and probably neither being in the direct ancestry of any modern rodent. Until much more is known about them, they are best retained in Muroidea, Family *incertae sedis.*

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