A New Species of Heteromyid Rodent from the Middle Oligocene of Northeast Colorado with Remarks on the Skull

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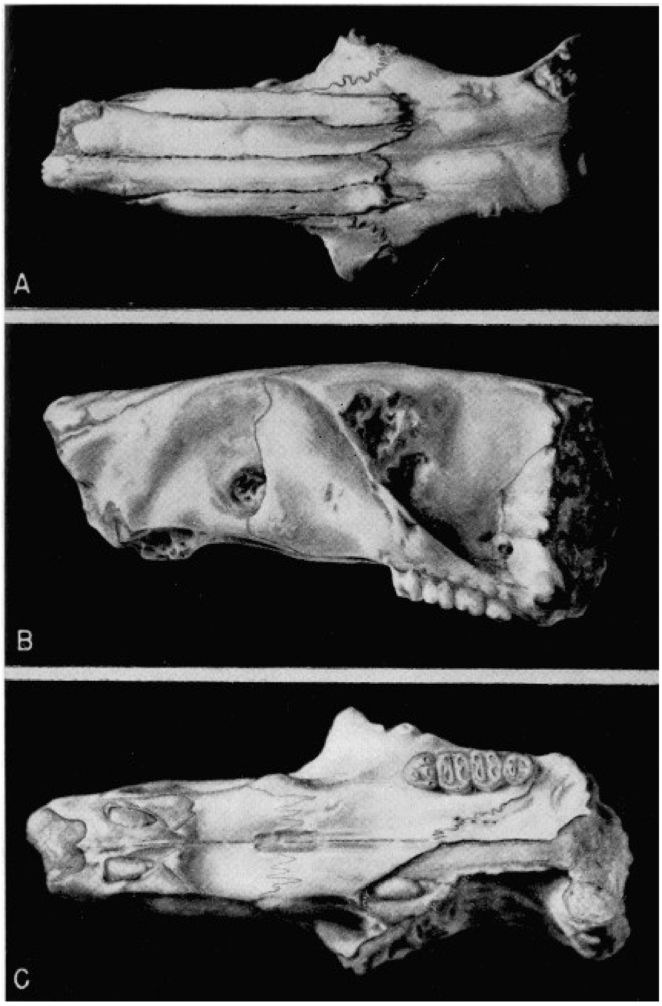

Plate 2. Heliscomys tenuiceps. Univ. Kans. Mus. Nat. Hist., Vert. Paleo. Coll. No. 7702. A, dorsal view; B, lateral view; C, ventral view. All views approximately × 5.

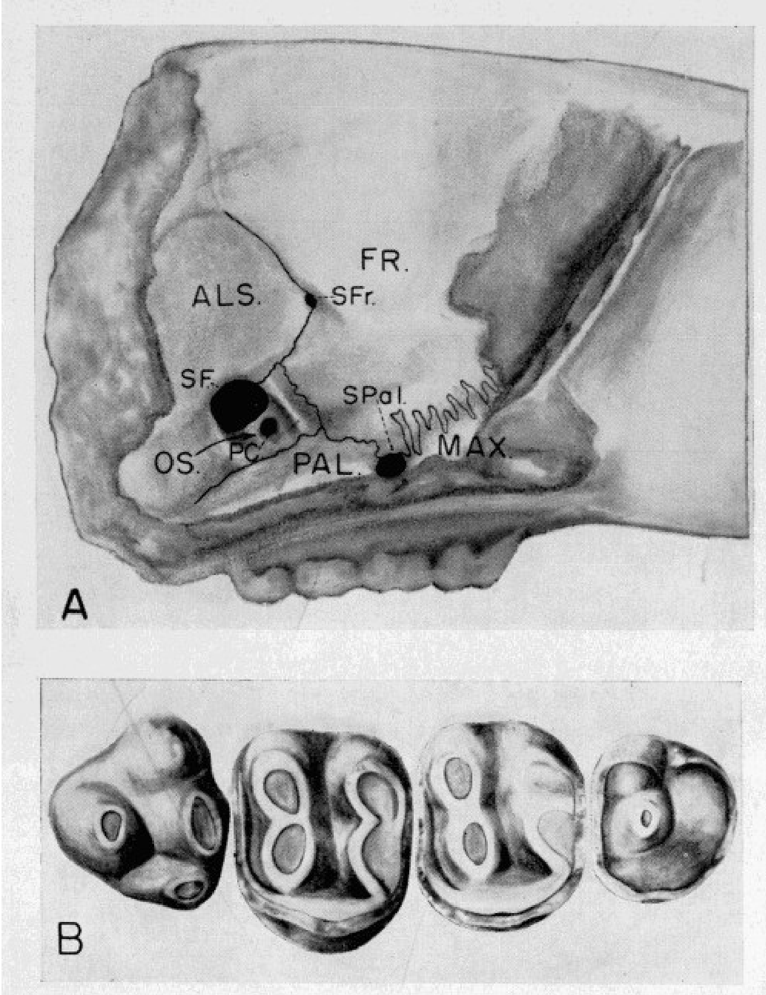

Plate 3. Heliscomys tenuiceps. Univ. Kans. Mus. Nat. Hist., Vert. Paleo. Coll. No. 7702. A, lateral view of right side of skull showing structures in orbital area. ALS, alisphenoid. FR, frontal. MAX, maxillary. OS, orbitosphenoid. PAL, palatine. PC, presphenoid canal. SF, sphenoidal fissure. SFr, sphenofrontal foramen. SPal, sphenopalatine foramen. Approximately × 9.3; B, occlusal view of P4-M3. Approximately × 23.4.

New Species of Heteromyid Rodent from the Middle Oligocene of Northeast Colorado with Remarks on the Skull

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Heretofore our knowledge of the osteology of *Heliscomys* Cope has been extremely limited; this genus previously was known by its teeth, fragmental maxillaries, incomplete palatine bone and mandible, and part of one forelimb. In the summer of 1946 the writer, as a member of the University of Kansas Museum of Natural History field party, discovered the anterior part of a skull of *Heliscomys* in the middle Oligocene deposits of Logan County, Colorado. This specimen, representing a new species, yields a welcome, and greatly desired addition to our fund of information about the genus.

The writer is indebted to Dr. Robert W. Wilson for advice and helpful criticism in the course of this study, and to Mr. Bryan Patterson of the Chicago Natural History Museum for the loan of comparative material. Mrs. Bernita Mansfield of the Geology Department, University of Kansas, prepared the plates.

Family HETEROMYIDAE

Heliscomys tenuiceps, new species

Holotype.—Anterior part of a skull with left P4-M3, No. 7702, Vertebrate Paleontological

Collection, Museum of Natural History, University of Kansas.

Geological Age and locality.—Silts of Orellan age in the Cedar Creek facies of the Brule formation in "Chimney Canyon," Sec. 3, T. 11 N, R. 54 W, Logan County, Colorado.

Diagnosis.—Size larger than any known species; P4 with posteroexternal cusp (metacone) anterior to central (hypocone) and lingual (entostyle) cusps, which are connected by a cingulum; internal cingula of molars undivided, and as high as paracone and metacone; style of each cingulum opposite the straight median valley; rostrum deep and laterally compressed.

Description.—The type consists of the preorbital and interorbital parts of a skull. Its size is comparable to that of the Recent heteromyid, *Liomys pictus* Merriam. *L. pictus* is the species referred to in the comparisons below when only the generic name *Liomys* is mentioned. Both incisors have been broken off. The right tooth-row is missing, but the left row is complete, and its orientation indicates that the tooth rows were parallel. The zygomata are broken off close to the rostrum, which is relatively narrow in comparison with its length and depth. In this narrowness, the specimen resembles *Florentiamys* Wood more than it does such Recent heteromyids as *Liomys* or *Heteromys*, where the rostrum is much wider at the dorsal surface than at the ventral [Pg 290] surface (correlating with the wide interorbital dimension). In No. 7702 the rostrum is not appreciably expanded on the dorsal surface. The wide interorbital dimension also gives a tapering appearance to the rostrum of the Recent heteromyids, when viewed dorsally, which is not seen in the fossil specimen. Like those of most heteromyids, the nasals and premaxillaries project forward beyond the incisors.

H. tenuiceps has a distinctly heteromyidlike appearance, and it is obvious that the features of the anterior part of the skull, which characterize the heteromyids, had been established by middle Oligocene time.

The nasal bone extends caudad as far as does the premaxillary; they terminate at the anterior border of the orbit. The nasal is widest anteriorly where it curves downward on the side to meet the anterior projection of the premaxillary bone beyond the incisor. Posteriorly, the two nasals have practically parallel lateral borders much as in *Liomys*.

The frontal bone dorsally is relatively narrower than in any Recent heteromyid, and closely resembles that of the geomyids. There is a slight depression in the midline of the skull where the two frontals unite, but no evidence of a ridge for the attachment of the temporal muscle. In lateral view, the ledge seen in *Liomys* at the dorsal surface is absent, nor is this surface rounded as in *Geomys*. Preservation around the nasolacrimal canal is poor, but traces of sutures indicate that the frontal bone is not involved in the posteromedial wall of that canal. The orbital plate is broad, comparatively flat, and extends farther ventrad than in *Liomys*, and enters into the composition of the sphenopalatine foramina. Ventrally the frontal bone meets the orbital processes of the palatine and maxillary bones, and posterolaterally meets the orbitosphenoid.

In the anterodorsal angle of the rim of the orbit the lacrimal bone rests against the frontal and maxillary bones, where the body of the lacrimal contributes to the formation of the posteromedial wall of the nasolacrimal canal. Only a slight part of the maxillary process of the lacrimal remains on each side.

The premaxillary bone, which constitutes most of the anterior part of the rostrum, is typically heteromyid in shape. The frontal process is long and slender. On the side of the rostrum the premaxillary forms the anterointernal border of the infraorbital foramen. The ventrolateral border of the bone is expanded slightly and aids in the formation of the tuberosity made by the maxillary bone at the ventroposterior border of the foramen. Ventrally the premaxillary makes up the anterior two-thirds of the lateral wall of the incisive (anterior palatine) foramen. It is not possible to establish what part of the median septum between the foramina is made up of premaxillary bones. The incisor arches through the premaxillary in a manner similar to that in *Liomys*, with the upper wall of the root canal being formed by the upper surface of the bone. Due to the narrowness of the rostrum, the root of the incisor is prominently outlined on the side of the rostrum, both in the premaxillary and maxillary bones. With this modeling of the side of the rostrum because of the incisor root canal, and the flaring of the posterior and ventral edges of the infraorbital foramen, the side wall of the premaxillary appears as a depressed area. Anterior to the incisor root the tip of the premaxillary projects forward, and parallels its opposite, laterally, instead of turning inward as in *Liomys*. This condition, together with the prominence of [Pg 291] the root canal, makes the anterior tip project as a flange. The premaxillary extends downward as a plate of bone, and embraces the posterior and lateral sides of the incisor as in Recent heteromyids. The interpremaxillary foramen, if present, is obscure. However, there appears to be a foramen posterior to the incisor, which possibly has taken over the function of the interpremaxillary foramen.

Both maxillary bones are incomplete, and lack the zygomatic processes. The rostral part of the maxillary is compressed laterally, as is the premaxillary. The anterior border of the maxillary contributes to the formation of the border of the anterior opening of the infraorbital canal where, at the posteroventral border of the opening, the bone is produced into a prominent tuberosity which projects laterally approximately one millimeter on each side. The infraorbital foramen (anterior opening of the infraorbital canal) lies about midway between the anterior end of the skull and the root of the zygoma. High on each side of the rostrum, and beneath the dorsal edge of the masseteric plate, is an area containing small foramina. The zygomasseteric plate is inclined forward at the dorsal end, and extends anteriorly almost to the highest part of the arch of the canal for the root of the incisor. The posterior end of the infraorbital canal lies on the median side of the zygomatic root as it does in *H. hatcheri* Wood. Ventrally the zygomatic root rises above the fourth premolar as in *H. gregoryi* Wood, *H. hatcheri*, and in Recent heteromyids. The ventral part of the orbit, containing the sphenopalatine foramen, presphenoid foramen, and the sphenoidal fissure, is not constricted as in *Liomys*, but is open like that of the squirrels. This condition is emphasized by the narrowness of the interorbital part of the skull and the more vertical position of the orbital plate.

The alisphenoid bone is large and forms part of the posteromedial wall of the orbit. The sphenofrontal foramen lies in the suture between the extreme anterior margin of this bone and the frontal bone.

The orbitosphenoid bone makes up little of the orbital wall. It occupies the posterior area of the orbit between the alisphenoid and palatine, and is in contact with these bones and the frontal. The presphenoid canal between the orbits is large, and the entrance at each end is well separated from the sphenoidal fissure. Damage to the sphenoidal fissure, which occurred prior to preservation, obscures its relationship to the optic foramen. No bar was found that would indicate that the two openings were widely separate. Anteroventrally the sphenoidal fissure is bounded by the orbitosphenoid bone, and dorsolaterally by the alisphenoid bone. Between the presphenoid foramen and the orbitosphenoid-frontal suture there is a distinct ridge, and the suture between the two bones lies in an elongate pit or trough formed by the anterior sloping side of the ridge and the impressed lateral wall of the frontal bone.

The palatine bone is represented by fragments joined to other bones of the skull. The maxillary process of the left palatine bone is united to the maxillary by a highly sinuous suture. The union of the palatines to the maxillaries make a suture in the shape of a "V" with the base forward and somewhat blunt. The canal for the palatine artery and nerve has a multiple opening on the palate. One major foramen opens on each side of the palatomaxillary suture, and two or possibly three smaller foramina open posteriorly on the palatine bone. Prominent on the palatine bone, posteromedial to the third molar, is the foramen (palatine pit) for the palatine vein. Collectively, [Pg 292]
this complex of foramina is often known as the posterior palatine foramina. Wood (1933) states that *H. gregoryi* has two posterior palatine foramina as in Recent genera, the anterior one opening opposite the posterior end of M1, and the posterior one opposite the median part of M3. The orbital process of the left palatine bone lies inside (medial to) the palatine process of the maxillary. Anteriorly this orbital process meets the orbital process of the maxillary bone, and the sphenopalatine foramen is found in the suture between these two bones and the frontal.

As previously mentioned, the preserved dentition of this specimen consists of the complete left row of cheek teeth and roots of the incisors.

The incisor is compressed laterally, more so than in any Recent heteromyid. The anterior face is rounded, asulcate, and covered with a heavy band of enamel, whereas the posterior side, due to lateral compression, is drawn out into a thin blade. The root of the incisor is at the lateral border of the premaxillary, so it is obvious that the two incisors converged on each other at the midline to form a cutting surface. The writer has not examined the asulcate, laterally compressed incisors of *H. hatcheri*, and cannot say how they compare with this specimen.

The most significant features of the cheek teeth are their size, and the undivided internal cingulum. The molars are well worn, but the pattern, as a whole, is easily discernable.

P4 has an anterior cusp and three posterior cusps as in other members of the genus. However, the buccal cusp (metacone) of the metaloph is considerably anterior to the central (hypocone) and lingual (entostyle) cusps, and the three cusps do not form a curve as in other species. In size the central cusp is largest, the buccal cusp is practically as large, and the lingual cusp is small. A cingulum connects the lingual and central cusps at the posterior margin of the tooth. In the Pipestone Springs specimen of *Heliscomys* reported by McGrew (1941) the central and buccal cusps were connected by a cingulum, and some *H. hatcheri* specimens have all three cusps connected in a similar manner. A low arm or ridge extends from the lingual cusp forward to the lingual side of the base of the anterior cusp. The valleys between the posterior cusps are shallow. There is no sign of the small cuspule on the anteroexternal base of the anterior cusp seen in *H. gregoryi*, *H. hatcheri*, and the Pipestone Springs specimen. However, when one sees the variability of the cuspules on P4 of *H. hatcheri*, the presence of a minor cuspule does not seem to be of taxonomic importance.

M1 deviates from the pattern typical of *Heliscomys* more than do any of the other molar teeth. However, it must be kept in mind that some of the differences may be due to wear. For example, the protocone and paracone, and the hypocone and metacone are united to form protoloph and metaloph respectively. If the height of the external border of the paracone and metacone is taken into account and compared with the worn inner parts of these two cusps and the equally well-worn protocone and hypocone, it appears that these cusps formed no more of a true bilophodont tooth than do the cusps in other species of *Heliscomys*; in each of the species the cusps generally are separate entities. *H. gregoryi* is reported to have an "incipient tendency to form lophs," and [Pg 293]
H. hatcheri does the same when worn, but by union with the anterior cingulum. If cusps in *H. tenuiceps* do form lophs, the process is definitely not by union of the cusps with the anterior cingulum. The transverse median valley is deep and divides the tooth on the buccal side. The anteroposterior valleys are shallow and hanging, and can be said to exist only as indentations between the two sets of cusps. The paracone and metacone are much higher than the other two cusps, but much of this disparity in height may be the result of greater wear on the protocone

and hypocone; *H. gregoryi* agrees with *H. tenuiceps* in these respects. Possibly the protocone and hypocone were much larger than the paracone and metacone. The internal cingulum of M1 exhibits only one large cusp opposite the medial end of the transverse valley, and shows no evidence of having been divided into two cusps. It is barely possible that there may have been two cusps and that wear makes it appear that there was only one. I doubt that there were two cusps because the cingulum is still so high (as high as the outer edges of the paracone and metacone) as to suggest that it is only slightly worn. Posteriorly this single cusp in the cingulum is united with the hypocone. Anteriorly the cusp is confluent with an anterior cingulum that is small, but, nevertheless, plainly visible as it crosses the occlusal face of the tooth to the paracone. There is some reason to believe that there was a posterior cingulum, but wear, which has obliterated even the posterior wall of the hypocone, prevents my being certain about this. This cingulum is absent in *H. gregoryi* and present in *H. hatcheri*.

M2 compares favorably with M1 except for the following differences: The protocone and hypocone are equal to the paracone and metacone in area, but not in height; although the internal cingulum is undivided, there is no evidence of a cusp as in M1. Here, too, the cingulum is as high as the paracone and metacone. Possibly the cingulum was confluent with the hypocone. The internal cingulum continues around the margin of the tooth to the paracone as an anterior cingulum which is sharper and plainer than the anterior cingulum on M1. There is no evidence of a posterior cingulum.

M3 shows a great amount of wear, and the occlusal pattern is not too clear. The median transverse valley is reduced almost to a pit, and the paracone and metacone are divided by a small notch. The protocone and paracone, the latter being much higher, are larger than the metacone which is reduced in size, and not all this difference in size can be the result of wear. The hypocone is absent. The internal cingulum is as high as the paracone and shows no evidence of division into two cusps, but in M3 this character is apparently variable for *H. gregoryi* does not have the internal cingulum divided and *H. hatcheri* has it markedly so. A slight anterior arm of the internal cingulum may have reached forward to the anterior face of the protocone. Wear prevents knowing whether a crest surrounds the tooth completely, or only on three sides.

In size the teeth of *H. tenuiceps* average twenty per cent larger than any of the upper teeth of *H. gregoryi*, *H. hatcheri*, or the Pipestone Springs specimen, and exceed any of the known lower teeth including those of *H. vetus* and *H. senex* by twenty-five per cent or more. Inasmuch as the upper teeth rarely exceed the lower in length in all the related genera of heteromyids, it is assumed that a similar relationship existed between the upper and lower molars of *H. tenuiceps* [Pg 294] and, therefore, that this species can be distinguished by its large size. The relative size of the premolars and molars is the same in *H. tenuiceps* as in other species of *Heliscomys*. However, within the framework of this similar relationship there are two differences. P4 of *H. tenuiceps* is relatively larger than the P4 of *H. gregoryi*, and relatively smaller than the P4 of *H. hatcheri*. The width of the molars is relatively greater in *H. tenuiceps* and *H. gregoryi* than in *H. hatcheri*.

Measurements

(In millimeters)

	U. K. M. N. H. (Vert. Paleo.) No. 7702
Height of skull at M2	7.48
Length from anterior end of nasals to rear of M3	15.41
Length of nasal bones	10.50
Width of rostrum at highest point of root canal	3.97
Interorbital width	4.39
Estimated length of skull	25.00
I, anteroposterior length	1.56
I, transverse width	0.63
P4-M3 crown length	3.75
P4-M3 alveolar length	3.80
P4, anteroposterior length[A]	1.05
P4, transverse width	1.08
M1, anteroposterior length	0.93
M1, transverse width	1.17
M2, anteroposterior length	0.93
M2, transverse width	1.14
M3, anteroposterior length	0.78
M3, transverse width	0.93

[Note A: This and the following measurements at occlusal surface.]

Discussion.—Heliscomys tenuiceps shows beyond any doubt that the heteromyid pattern of skull was developed by mid-Oligocene times, and in this species was already undergoing lateral compression. The major change later made in heteromyid skulls is broadening of the dorsal surface of the skull in the interorbital area.

The complete confirmation of Wood's (1939) statement that the "sciuromorph" zygomasseteric structure had been developed by this time in the heteromyid rodents as it had been in the early Eomyids is demonstrated in this specimen. Further, it is to be noted that the infraorbital canal is not sciuridlike, but has been forced forward on the rostrum, as in the Geomyoidea.

In some ways this skull shows similarities to *Florentiamys loomisi* Wood, of the early Miocene, which aid in determining the relationship of that unusual genus to *Heliscomys* and to the heteromyids in general. When Wood described *Florentiamys* the peculiar combination of characters found in this animal prompted him to speculate that: (1) It was a typical heteromyid which had secondarily developed cingula; (2) its cheek teeth were nearer the primitive pattern than were those of any other known fossil heteromyid, and that *Heliscomys* represented a simplification in the reduction of the cingula; or (3) it was not a heteromyid, but a parallel development from the "Paramys" stock. Wood favored the second possibility. Now that a part of the skull of one species of *Heliscomys* is known, the undivided internal cingulum that is confluent with the hypocone, the lateral compression of the deep rostrum, and the general similarity to the heteromyids appear as points in common between the two skulls, and demonstrate the closeness of *Florentiamys* to the heteromyids. However, the specimen does not contribute anything new to use in choosing between Wood's first two postulates. In the writer's opinion the undivided internal cingulum is a primitive condition that has survived in *Florentiamys* and *Heliscomys tenuiceps*. This common character together with the laterally compressed rostrum leads me to think that structurally, *H. tenuiceps* is a link between *Florentiamys* and the ancestral form of *Heliscomys*. Admittedly P4 of *Florentiamys* seems far from the *Heliscomys* pattern, but I think that this highly specialized structure could have been derived from *Heliscomys* or a common ancestor. [Pg 295]

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