ART. VIII—*Oligocene Rodents of the Genus Ischyromys*;
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A great diversity of form is shown in the rodents of the Early Tertiary period; some of these have lived even to the present time, others became extinct long ago and are only remotely connected with existing genera.

Leidy in 1856¹ first described the squirrel-like rodent which he called *Ischyromys typus*, and in 1889² published a detailed morphology of the skull and teeth, having not only a full appreciation of the relationship to the modern *Sciurus* but also a realization that the one was not ancestral to the other.

Cope in 1873³ and 1881⁴ added new points of interest concerning the skeleton, and further emphasized the relationship of this genus to the squirrels in the nature of the teeth, but to other genera, *Arctomys*, *Castor*, etc., in skull and skeletal features, and he agreed with Alston that there should be a separate family, the Ischyromyidæ. Several new genera and species were made by Cope, which he afterward concluded were synonyms of *Ischyromys typus* Leidy or belonged to entirely different groups.⁵ *Colotaxis cristatus* and *Gymnoptychus chrysodon* are equivalent to Leidy's genus and species; they are based on what one finds to be moderate-sized specimens with or without the variable tubercles between the lobes of the lower molars.

Matthew⁶ has worked out the interrelation of the early rodents and discusses in full the family Ischyromyidæ. His new species and subgenus *Ischyromys* (*Titanotheriomys*) *veterior* was based on the narrow heel of M_3 , the narrow incisors, and the earlier geological age, i. e. Titanotherium beds. He places the following genera under Ischyromyidæ Alston: *Ischyromys*, *Paramys*, *Sciuravus*,

¹ Joseph Leidy, Proc. Acad. Nat. Sci. Phila., 8, 89.

² Joseph Leidy, Jour. Acad. Nat. Sci. Phila. (2), 7, 335, pl. 26, figs. 1-6.

³ E. D. Cope, Pal. Bull. No. 15, p. 1; *ibid.*, No. 16, p. 5.

⁴ E. D. Cope, Bull. U. S. Geol. and Geog. Survey Terr., vol. 6, 366-368.

⁵ See O. P. Hay, Science (2), 10, p. 253, 1899.

⁶ W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 28, 43-72.

Mysops, and *Prosciurus*, and comes to the conclusion that the genus *Ischyromys* reached extinction in Oligocene time. In the present paper, however, the suggestion is offered that they may have developed into the modern prairie-dog of the genus *Cynomys*.

DESCRIPTION OF NEW SPECIES.

Ischyromys pliacus, sp. nov.

(FIG. 1.)

Holotype, Cat. No. 12511, Y. P. M. Middle Oligocene, Cherry Creek, Colorado.

FIG. 1.—*Ischyromys pliacus*, sp. nov. Lower right dentition of the largest species of the genus. Note the many small cusps on teeth. Holotype, Cat. No. 12511, Y. P. M. $\times 2$.

This specimen, consisting of the right lower jaw, is notable for its large size and for the great number of tubercles and deep pits on both premolar and molars. The posterior cross crests do not arise directly from the external tubercle but from its union with the central longitudinal ridge, thus forming a "Y". This cross crest is made up of two distinct minute cusps, but only on P_4 and M_2 are they still unworn. Small additional tubercles are to be seen on the posterior side of the anterior cross crests on all the teeth and conspicuous cusps occupy the wide openings of the external grooves.

Measurements are given in a table further on.

Ischyromys typus nanus, subsp. nov.

(FIGS. 2, 3.)

Holotype, Cat. No. 12519, Y. P. M. Oligocene (lower Oreodon beds), Warbonnet ranch, 12 miles north of Harrison, Nebraska. Paratype, Cat. No. 12555. Gerry's Ranch, Weld Co., Colo.

The specimens here described consist of the small lower jaws with the molar teeth. The holotype was a part of a young animal in which the last molar was just being cut. Besides the fact that this is the smallest subspecies of *Ischyromys*, it is further distinguished by the very nar-

row M_2 and by the general absence of secondary tubercles, external basal cusps, etc. In the ratios given in the table beyond, it is seen that *I. pliacus* is over 50 per cent larger in certain dimensions and averages about 30 per cent greater.

FIG. 2

FIG. 3

FIG. 2.—*Ischyromys typus nanus*, subsp. nov. Holotype. Cat. No. 12519, Y. P. M. Three molars from right lower jaw. M^1_2 very narrow. $\times 2$.

FIG. 3.—*Ischyromys typus nanus*, subsp. nov. Paratype. Cat. No. 12555, Y. P. M. Left lower molars, to show results of wear. $\times 2$.

Ischyromys typus lloydi, subsp. nov.

(FIGS. 4, 5, 7.)

Holotype, Cat. No. 12521, Y. P. M. Oligocene (lower Oreodon beds), from the ranch of Mr. Paul Zerbst, 10 miles north of Harrison, Nebraska.

This new subspecies is based upon an unusually complete skull and jaws, together with certain portions of the skeleton. These were found in 1915 by the writer who takes pleasure in adding them to the collections of Peabody Museum. The new name is given in honor of Dean Lloyd of the University of Michigan, in appreciation of a delightful friendship.

FIG. 4.—*Ischyromys typus lloydi*, subsp. nov. Holotype. Cat. No. 12521, Y. P. M. $\times 2$. A, molars and premolar of lower right side, and single deciduous premolar, Dp_1 , from opposite side. B, left upper molars and premolars; the latter were drawn from a vertical position, and the skull was then rotated inward in order to get the crown view of the molars.

The specimen is moderate in size and corresponds in general to the dimensions of *I. typus* Leidy. The upper molars, unlike those in most specimens, do not decrease in size toward the rear, for the last molar is actually greater than the premolar or M^1_1 . The third permanent premolar, the first of the cheek series, is just coming into view; it was actually hidden beneath the conical deciduous predecessor when first worked out of the matrix. A single tubercle with a crescentic ridge on the postero-internal

corner forms the crown of this tooth, which in shape and size resembles the lead of a pencil, an elongated cylinder.

P⁴ is distinctly molariform, but small and nearly round. Unlike the molars, it has no internal groove and the cross crests extend more than halfway across the crown. This tooth now stands vertical in the maxillary, but had it grown to its normal position, it would have turned outward, following the curve of the large interior root, to face more nearly like the molars.

M¹ and M² are alike in general form. In each, the posterior groove, after slight wear, becomes a pit near the center of the posterior side. M³ seems to be slightly rotated backward and inward, giving the cross crests an oblique direction; it is elongated fore and aft. The triangular area about the posterior pit is small.

The lower molars have the two simple outer cusps with the two main, parallel cross crests leading from them. The crowns are higher and the teeth are larger and wider than in *I. typus nanus* just described. The last molar is the widest; the first is narrowest and the total length of the three molars is 10 per cent greater than that of *I. nanus*. In all the subspecies of *I. typus* there is a notable absence of small secondary cusps.

The first premolar was just appearing in the lower jaw to take the place of the single deciduous tooth which had been serving the young animal. Dp₄ is elongated but narrow and has a low crown. The anterior cusps are not paired transversely, for the inner one is placed far anterior. (See fig. 4 A.)

The lower jaws are short and relatively deep; the ventral border forms a broad curve backward to a point beneath M₃; here there begins a reverse curve and the thin edge is folded inward to lend support to the pointed angle. The coronoid extends as far above the condyle as the angle does below; the two together give a vertical measurement of about 26 mm. to the posterior part of the ramus. On the upper side of the ridge leading to the condyle opens the mandibular foramen; this passage then leads down and forward, following along the upper surface of the incisor root within the ramus, and finally emerges in the mental foramen just in front of P₄. Except for the greater height of the ascending ramus, the extended angle, and the lack of a distinct muscle scar on

the outer surface, this mandible resembles that of *Sciurus*, cf. *S. carolinensis*.

Additional distinctive features in the present subspecies may be noted in the vascular impressions on the supra-occipital and the slight overhanging of this bone, the large otic bullæ, slightly crushed down, the flat triangle formed by the sagittal crest where it joins theinion, and the absence of a deep groove on the zygomatic pedicle near the maxillary.

FIG. 5.—*Ischyromys typus lloydi*, subsp. nov. Holotype. Cat. No. 12521, Y. P. M. Side view of skull and jaws. Premolars just coming into view. Skull slightly bent downward by crushing. Nat. size.

Measurements of Holotypes.

	<i>I. nanus</i> mm.	Ratio	<i>I. pliacus</i> mm.	Ratio	<i>I. lloydi</i> mm.
Length of three lower molars....	9.8	124	12.2	113	11.1
Length of M_1	3.2	116	3.7	113	3.6
Width of M_1	2.7	137	3.7	119	3.2
Length of M_2	3.2	125	4.0	116	3.7
Width of M_2	2.7	152	4.1	126	3.4
Length of M_3	3.2	131	4.2	119	3.8
Width of M_3	3.0	123	3.7	110	3.3

INTERPRETATION OF ISCHYROMYS.

Wear of the teeth.—The long transverse ridges or crests and the corresponding grooves led Leidy to observe that the upper teeth were like the lower ones reversed; this is true, however, only in a general sense. In addition to the transverse crests of enamel, the teeth show series

of ridges clearly the result of lateral wear; furthermore, the upper teeth are often worn to the roots on the inner side while the outer borders still stand high. This gives evidence that the movement of the jaws was transverse rather than longitudinal as in the case of many rodents where the grinding surface as a unit is worn to one smooth plane (cf. the water hog, *Hydrochærus capybara*).

FIG. 6.—Upper milk teeth of *Ischyromys typus* Leidy, Cat. No. 12508, Y. P. M. *Dp*³ is very much like the premolar which succeeds it. *Dp*⁴ is short-crowned, but elongated fore and aft. Note that the first molar faces outward. $\times 2$.

The third superior molar is set in the maxillary facing downward and outward at an angle of more than 40°, but the deviation from the vertical is progressively less toward the anterior teeth; the lower teeth correspondingly face upward and inward. In the action of chewing, therefore, the first contact is formed by the vertically placed premolars, then, as the lower teeth move inward, the molars from front to rear successively come into use.

Taking each tooth separately, its action may be analyzed into a chopping process with the first contact of the sharp grooves and crests; this becomes secondarily a tearing or grinding where two teeth are fully opposed; at that phase the inner tubercles of the upper tooth and the outer cusps of the lower tooth resist further lateral movement, thus causing additional grinding of the food particles.

The milk teeth, like the premolars in their early stages, stand vertical both above and below, but the wear of these teeth indicates that the immature individual has already learned the transverse movement of the jaws. There are two milk teeth above and one below in the young animal.

Relationship and adaptations.—A most interesting comparison may be made between *Ischyromys*, the fossil, and *Cynomys*, the prairie dog, and although certain features stand out sharply separating the two genera, yet they show a fundamental similarity which tells of close relationship. The skull of *Cynomys* (Cat. No. 01228,

Y. P. M.) is about the same length but broader, especially across the temporal portion of the zygomatic arch; there are strong postorbital processes which are entirely absent in the fossil. Further distinctions of *Cynomys* are the narrower antero-posterior dimension of the teeth, the large P^3 and $M^3_{\frac{2}{3}}$, the anterior position of the infraorbital foramen resulting from the large groove anterior to and beneath the zygomatic projection of the maxillary, the large angle of the lower jaw with numerous additional projections for muscle insertions, the decrease in the size of the coronoid, the longer segments of the hind limbs with the cnemial crest of the tibia and the third trochanter of the femur far up on the shaft, the single groove (instead of double as in the fossil) on the distal end of the tibia for the tendon of the deep digital flexor running to the sole of the foot, and the large, longer claws.

Important similarities, on the other hand, may be noted in the structure of the teeth with the cross crests of enamel, the shape of the occipital region of the skull and the sagittal crest, the form of the nasals and premaxillaries, the peculiar supra-auditory foramen, and the same dental formula. There is a remarkable agreement in the size and form of the humerus and of the distal end of the femur in each genus, both being distinct from those of the squirrel, *Sciurus*. In the humerus there is a strong deltoid crest, a wide condyloid crest on the outer side, and a supracondylar foramen on the inner side distally. This foramen, according to Flower, is a departure from the general rodent humerus, but is seen in the wombat and in certain carnivores. It is thought probable that the spiral condylar grooves on the humerus permit a freer movement of the ulna and allow its rotation for swimming or burrowing as in the beaver, while the large deltoid prominence and the lateral condyloid crest, again like those of the beaver, tell of the strong muscles which manipulated the front limb.

An objection which may be offered to any theory attempting to derive *Cynomys* from *Ischyromys* is the presence of the very small third premolar in the latter. This resolves itself into the question whether P^3 of the fossil is reduced to a vestigial state and therefore much advanced in evolution, or whether it is small and yet undeveloped but has within it the potential molariform tooth of *Cynomys*.

The prairie dog now occupies the same Great Plains region where once scurried the small ischyromyds, but the conditions are greatly changed: the former is a burrowing animal in a semi-arid climate; the latter lived where the Oligocene streams from the young Rocky

FIG. 7.—*Ischyromys typus lloydi*, subsp. nov. Holotype. Cat. No. 12521, Y. P. M. Nat. size. *A*, front and back views of humerus; note broad distal end, supracondylar foramen on posterior side, spiral condylar grooves, and large deltoid crest on one side. *B*, front and rear of distal end of the heavy femur. *C*, right tibia viewed from inner side, showing deep double groove for tendons to the foot. (See also figs. 4 and 5.)

Mountains spread widely their flood waters, just as the rivers from the east slope of the Andes do to-day. This probably necessitated burrowing in the dry seasons and at other times called for the ability to cope with the rising flood.