American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2418 JUNE 23, 1970

The Early Oligocene Rodent *Ardynomys* (Family Cylindrodontidae) from Mongolia and Montana

BY ALBERT E. WOOD[1]

INTRODUCTION

Matthew and Granger (1925) described the genus *Ardynomys,* with two species, *A. olseni* and *A. chihi,* from the early Oligocene Ardyn Obo Formation of Mongolia, on the basis of material collected by the American Museum Third Asiatic Expedition in 1923. They referred the genus to the Ischyromyidae, a term used at that time to include all North American Eocene rodents. The genus was reported from North America, and a new species, *A. occidentalis,* was described by Burke (1936). An additional species, *A. kazachstanicus,* was described from Kazakstan by Vinogradov and Gambarian (1952). The genus was transferred to the Cylindrodontidae, where it is still placed, by Wood (1937). Very little additional attention has been paid to the genus, although it has been included in such standard works as Stehlin and Schaub (1951, p. 281); Schaub (1958, p. 754); and Gromov (1962, pp. 137–138, figs. 97, 98).

During my study of the rodents of the Vieja Group of Trans-Pecos Texas, specimens similar to Burke's material were discovered, and it has been necessary for me to review all the available material of the genus. Although the illustrations given by Matthew and Granger (1925, figs. 8, 9) are excellent, there are additional specimens in the American Museum

[1] Professor of Biology, Amherst College, Amherst, Massachusetts.

of Natural History not figured by them, and the increase in our knowledge of rodent paleontology during the last 40 years makes a re-evaluation of the material advisable. Newly found specimens of *Ardynomys occidentalis* from McCarty's Mountain, Montana, in the Carnegie Museum, show interesting features not previously observed.

I am grateful to Dr. Malcolm C. McKenna for permission to study the material in the American Museum of Natural History, and for arranging to have the present paper published. Dr. C. C. Black kindly lent me the Carnegie Museum material. The present study was assisted by National Science Foundation Grant GB-6075, and Grant No. 145 from the Marsh Fund of the National Academy of Science.

Abbreviations

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History
A.M.N.H. (M.), Department of Mammalogy, the American Museum of Natural History
A.N.K., Institute of Zoology, Akademii Nauk, Kazakstan S.S.R.
Carn. Mus., Carnegie Museum
F.M.N.H., Field Museum of Natural History
P.I.N., Paleontological Institute, Akademii Nauk, U.S.S.R.
U.M., Museum of Paleontology, University of Montana at Missoula
U.T.B.E.G., University of Texas, Bureau of Economic Geology

ARDYNOMYS MATTHEW AND GRANGER, 1925

Type: *Ardynomys olseni* Matthew and Granger, 1925.

Referred Species: *Ardynomys occidentalis* Burke, 1936, and perhaps *A. kazachstanicus* Vinogradov and Gambarian, 1952.

Revised Diagnosis: Cylindrodont rodent with brachydont to mesodont cheek teeth; interdental wear cuts through enamel on ends of teeth only after extensive use; P^3 present but small; P^4 and upper molars with protoloph and metaloph converging on protocone; hypocone small or absent; lower cheek teeth with hypoconid hypsodonty; hypolophid of P_4 variable in size, but usually close to posterolophid, and less well developed than other crests; metalophid of molars directed into buccal side of metaconid; incisors with flat or slightly rounded anterior faces; maxillary-premaxillary suture crosses diastema at rear of incisive foramina; lacrimal large; prominent bulge into ventral part of orbit formed by root of upper incisor leaving a very compressed passage for the infraorbital artery, vein, and nerve across the floor of the orbit; normally one mental foramen; massive, corrugated symphysis; prominent chin process; angle somewhat inflected.

DISTRIBUTION: Early Oligocene of Mongolia, Montana, and Trans-Pecos Texas; middle Oligocene of Kazakstan. Restudy of all of the material from the Ardyn Obo Formation (A.M.N.H.), together with that from McCarty's Mountain, Montana (Carn. Mus.) has left me with considerable doubt as to whether the Montana material, discussed below as *A. occidentalis,* is correctly referable to *Ardynomys.* The differences evident in *A. olseni* include flat incisors, a heavier chin process, and an apparently more pronounced angle. Similarities are the equivalent development of hypsodonty; the backward shifting of the hypolophid of P_4; the diagonal metalophids of the lower molars, which run from the protoconid anterolaterad rather than laterad as in *Pseudocylindrodon* (Black, 1965, fig. 2c–e); the usual presence of a single mental foramen in front of P_4 (but, for a possible exception, see Vinogradov and Gambarian, 1952, fig. 3); and the heavy symphysis. The extension of the base of the incisor of *Tsaganomys* into the orbit suggests relationship to *A. occidentalis* and hence implies that *A. olseni* and *A. occidentalis* are congeneric.

The best material of *A. occidentalis* is a series of skulls, but unfortunately nothing is known of *A. olseni* except lower jaws and one isolated upper incisor. Hence, it has seemed best to leave the species in the same genus until skull material of the Asiatic form becomes available and demonstrates either that the two are the same genus or that their separation is justified.

Ardynomys olseni Matthew and Granger, 1925

Figures 1, 2

PUBLISHED FIGURES: Matthew and Granger, 1925, figures 8, 9; Vinogradov and Gambarian, 1952, figures 2, 4.

SYNONYM: *Ardynomys chihi* Matthew and Granger, 1925.

TYPE: A.M.N.H. No. 20368, right lower jaw with P_4–M_2 and parts of M_3, and the incisor.

HYPODIGM: Type and A.M.N.H. No. 20369, left lower jaw with all the cheek teeth; A.M.N.H. No. 20370, associated right and left jaws with all the cheek teeth (type of *A. chihi*); A.M.N.H. No. 20371, juvenile jaw with RdP_4 and P_4–M_3; A.M.N.H. No. 20372, left lower dentition; and A.M.N.H. No. 20361, isolated left upper incisor.

DISTRIBUTION: Early Oligocene Ardyn Obo Formation of Mongolia.

REVISED DIAGNOSIS: Large species; hypolophid of P_4 variable in size and position, sometimes originating from ectolophid and sometimes from hypoconid; anterior cingulum of molars usually incomplete in unworn teeth; central valley opens freely linguad; posterior basin closed after wear; both upper and lower incisors with flat anterior faces; tooth

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF ASIATIC SPECIMENS OF *Ardynomys*

		Type A.M.N.H. No. 20368	A.M.N.H. No. 20369	*A. olseni* Type of *A. chihi* A.M.N.H. No. 20370 R	*A. olseni* Type of *A. chihi* A.M.N.H. No. 20370 L	A.M.N.H. No. 20372	A.M.N.H. No. 20371 Permanent	A.M.N.H. No. 20371 Deciduous	P.I.N. No. 473–106[a]	$\overline{X}$	*A. kazachstanicus* Type A.N.K. No. 451/47–1[a]	cf. *Ardynomys* sp. P.I.N. No. 473–111 (*A. chihi* of Vinogradov and Gambarian)[a]
P_4–M_3		15.25	14.2	13.8	14.1	14.0	*ca.* 12.9		14.5	14.1	11.5	9.0
P_4	anteroposterior	3.26	3.47	3.04	2.88	3.58	*ca.* 3.2	2.91	3.5	3.28	3.0	2.5
	width, metalophid	3.66	2.83	2.35	2.22	3.26	*ca.* 2.8	1.96	3.6	2.96	2.6	1.8
	width, hypolophid	4.47	4.30	3.60	3.58	4.93	*ca.* 3.4	2.32	4.4	4.10	3.2	2.3
M_1	anteroposterior	3.46	3.20	3.08	3.11	2.90	3.25		3.5	3.21	2.7	2.3
	width, metalophid	3.79	3.50	3.23	3.10	3.74	3.15		—	3.42	2.4	1.9
	width, hypolophid	4.25	5.10	3.50	3.47	4.4	3.50		4.6	4.11	2.8	2.1
M_2	anteroposterior	3.46	3.48	3.20	3.13	3.11	3.22		3.5	3.30	2.8	2.3
	width, metalophid	4.12	4.01	3.53	3.72	3.72	3.50		4.1	3.81	2.5	2.1
	width, hypolophid	4.39	4.93	4.02	4.00	4.62	3.70		4.3	4.28	2.7	2.4
M_3	anteroposterior	—	4.10	3.90	3.93	3.95	3.66		4.1	3.94	3.1	2.0
	width, metalophid	—	3.45	3.68	3.60	3.62	3.37		3.8	3.59	2.4	1.9
	width, hypolophid	—	3.52	3.67	3.53	3.25	3.31		3.6	3.48	2.9	1.7
I_1	anteroposterior	5.85	4.65	4.57	—	—	3.39		over 5.2	—	—	3.2
	transverse	4.20	3.63	3.27	—	—	2.91		—	—	—	—
	ratio	.72	.78	.72	—	—	.86		—	—	—	—

[a] The lengths of P_4–M_3 for these specimens were given by Vinogradov and Gambarian (1952). This permitted determination of the magnification of their illustrations, from which the other values given here were calculated.

measurements as given in table 1.

Matthew and Granger (1925, p. 7) separated *Ardynomys chihi* from the genotype *A. olseni* by stating, "size one-tenth less than the preceding, molars less robust, central inner valley of m_3 closed by a marginal inner crest, posterior inner valley more widely open."

As indicated by the measurements in table 1, there is a continuous size range, from the largest specimen, A.M.N.H. No. 20638, the type of *A. olseni*, to the smallest, the juvenile A.M.N.H. No. 20371. The largest specimen that Matthew and Granger referred to *A. chihi*, and A.M.N.H. No. 20369, which they did not identify specifically, bridge the gap between the others. The most divergent measurements are those of P_4–M_3 and premolar and incisor measurements on the juvenile A.M.N.H. No. 20371, where the incisor is small because it is a juvenile. The other measurements are low because P_4 is only partially erupted, dP_4 having been removed from above it for the present study. A 10 per cent size difference is not significant, particularly with such a small sample. The cheek teeth of the smaller specimens are smaller, but no more so than would be expected. All specimens that are not badly worn show a mesostylid extending backward from the metaconid along the buccal margin, on all the cheek teeth. Whether this actually reaches the entoconid seems to be a matter of minor individual variation, at least partly resulting from differences in wear (although the greatest closure of the valley occurs on the juvenile, A.M.N.H. No. 20371). The openness of the valley between the entoconid and the posterolophid is variable and does not seem important.

There are differences in the pattern of some teeth, especially the structure of the posterior half of P_4, as discussed below, but many of the differences seem to be due to wear, and the others are not very important.

Therefore, there seems to be no reason for considering *A. chihi* as anything but a synonym of *A. olseni*.

Vinogradov and Gambarian (1952, pp. 15–17) recognized three species of *Ardynomys* in their material from Mongolia and Kazakstan. They referred two specimens (P.I.N. No. 473–106, a left lower jaw with all the teeth and P.I.N. No. 473–49, an edentulous alveolar portion of a left lower jaw) to *A. olseni*. Their illustrations (1952, figs. 2, 4), the measurement they gave (length of tooth row, 14.5 mm.), and the measurements made from their figures (table 1) confirm the correctness of this allocation.

The angle is not preserved on any specimen in the American Museum of Natural History, but seems to have been somewhat more complete on the specimen illustrated by Vinogradov and Gambarian (1952, fig. 2).

Although the illustrations given by Matthew and Granger (1925, figs. 8, 9) are excellent, additional features are detectable, especially in the tooth pattern, and a redescription of the material is desirable.

The lower jaw (figs. 1A, 2A) is massive in the chin region, and the angular process extends well ventrad, but the bone is rather slender beneath the tooth row. The prominent chin process bears a few nutritive foramina. This region is broken off in the specimens Matthew and Granger referred to *A. chihi.* The mental foramen is small, and faces upward, dorsal to the incisor and just in front of P_4. In the type, there are two small foramina, the larger of which shows in figure 1A, along the diastema in front of P_4. Other specimens show one or neither of these, and may show an accessory mental foramen behind the main one. There is a prominent "tongue groove" running the entire length of the symphysis, not well developed in the juvenile. The symphysis, as shown by Matthew and Granger, is highly rugose, and very large. The pit for the genioglossus is prominent. The scar of insertion of the masseter superficialis is a triangular area beneath M_2 (fig. 1A), below which the angular process curves abruptly downward and backward. The angle is broken in all specimens, but perhaps shows the beginnings of the complexities found in *Tsaganomys* and *Cylomylus.* The ascending ramus is displaced laterally from the tooth row, and passes the alveolar border by the front of M_3. Removal of matrix showed that the coronoid process (figs. 1A, 2A) was higher and more slender than shown in either of Matthew and Granger's figures, and that there was no notch between it and the condyle. The restoration of the coronoid process by Vinogradov and Gambarian (1952, fig. 2) is surely wrong. The condyle is well above the level of the tooth row, and has a prominent mesial overhang. There is a heavy strut, extending from the rear of M_3 to the condyle. Just above this, about halfway from M_3 to the rear of the condyle, and above the level of the tooth row, is the large mandibular foramen (fig. 2A). The fossa for the internal pterygoid is very large, deep, and rounded anteriorly.

In general, the lower cheek teeth are brachydont, with the height of crown significantly less than the length of the tooth, except at the hypoconid, which has developed unicuspal hypsodonty. The height of an unworn hypoconid is equal to, or greater than, the length of the tooth. Interdental wear thins the enamel, but the enamel is usually not interrupted until wear reaches the base of the crown. The most brachydont part of the enamel cap is at the anterior end of the teeth (fig. 1A).

The pattern of the premolar is clearly preserved on all specimens

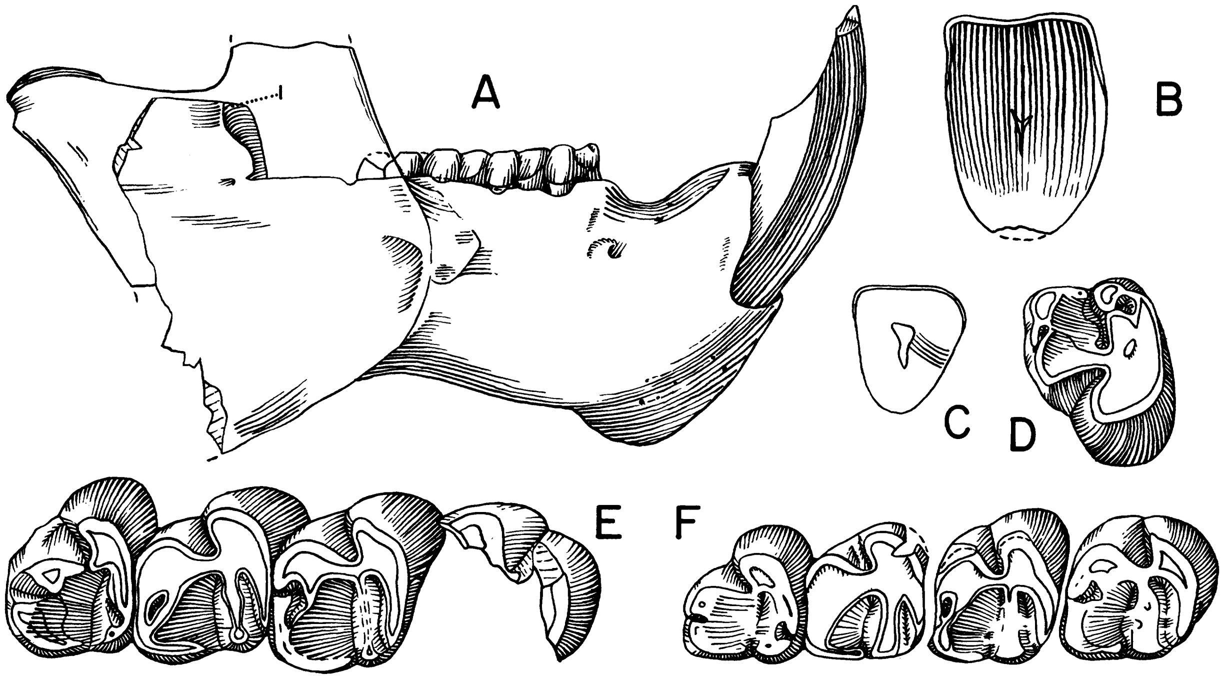

FIG. 1. Teeth and jaw of *Ardynomys olseni*. A. Type, A.M.N.H. No. 20368, lateral view of lower jaw, ascending ramus and condyle restored by enlargement from A.M.N.H. No. 20370 (type of *A. chihi*). I = Alveolus of incisor. B. Wear surface, RI_1, A.M.N.H. No. 20368, type. C. Cross section, below front of diastema, juvenile RI_1, A.M. N.H. No. 20371. D. LP_4, A.M.N.H. No. 20372. E. RP_4–M_3, A.M.N.H. No. 20368, type. F. RP_4–M_3, A.M.N.H. No. 20370, type of *A. chihi*. Jaw $\times 2$; teeth approximately $\times 5$.

(figs. 1D–F; 2E, F). The narrow anterior half consists of a high metaconid with a much lower protoconid on its buccal flank. An anterior cingulum from the metaconid cuts off a small trigonid basin. In most specimens, the protoconid and metaconid are connected at the rear of the trigonid basin, but in A.M.N.H. Nos. 20368 (fig. 1E) and 20371 (fig. 2F) the basin opens into the talonid basin. A posterior arm from the metaconid extends along the lingual margin of the tooth, nearly reaching the entoconid, from which it is separated by a narrow gorge. A prominent ridge runs backward from the metaconid into the talonid basin (A.M.N.H. No. 20371); with wear, the ridge is worn down to the level of the rest of the anterior part of the talonid basin, but the lighter color of the enamel shows that it is much thinner in this area (A.M.N.H. Nos. 20368, 20369); ultimately, it persists only as a bulge into the bottom of the talonid valley (A.M.N.H. Nos. 20371, 20372). A basal cuspule is present on the buccal side of the protoconid of A.M.N.H. No. 20371; suggestions of it are found on several other specimens. The hypoconid is the largest cusp of the tooth, and is continued through a posterolophid along the posterior margin of the tooth. A distinct hypoconulid is visible only in the unerupted tooth of A.M.N.H. No. 20371. The exact relationships of the entoconid and posterolophid are variable. The entoconid forms part of the rear border of the tooth, and the posterolophid is correspondingly short except in A.M.N.H. No. 20372 (fig. 1D), in which the entoconid is displaced forward, and the valley between the entoconid and posterolophid is on the lingual side of the tooth. The hypolophid is even more variable. In the unerupted tooth (fig. 2F), the hypolophid arises from the mesolophid linguad of the hypoconid, and curves backward to the entoconid, with a cusplike enlargement at its middle. A.M.N.H. No. 20372 seems to have been the same. The condition in A.M.N.H. No. 20369 (fig. 2E) is the same, except that the hypolophid is much less elevated, being well below the wear surface. The hypolophid runs from the entoconid to about the position of the hypoconulid in A.M.N.H. No. 20370. Finally, in A.M.N.H. No. 20368, there is a slight bulge on the lingual surface of the hypoconid, marking the buccal end of the hypolophid, and a short ridge from the entoconid, lying very close to the posterolophid, but the main part of the hypolophid is absent.

The molar pattern apparently is rather uniform, most of the variants resulting from wear. The hypoconid is the largest cusp on all teeth. The posterolophid shows a distinct hypoconulid only in unworn or slightly worn teeth. The valley between the posterolophid and the entoconid is open until after extensive wear. The hypolophid arises from the ecto-

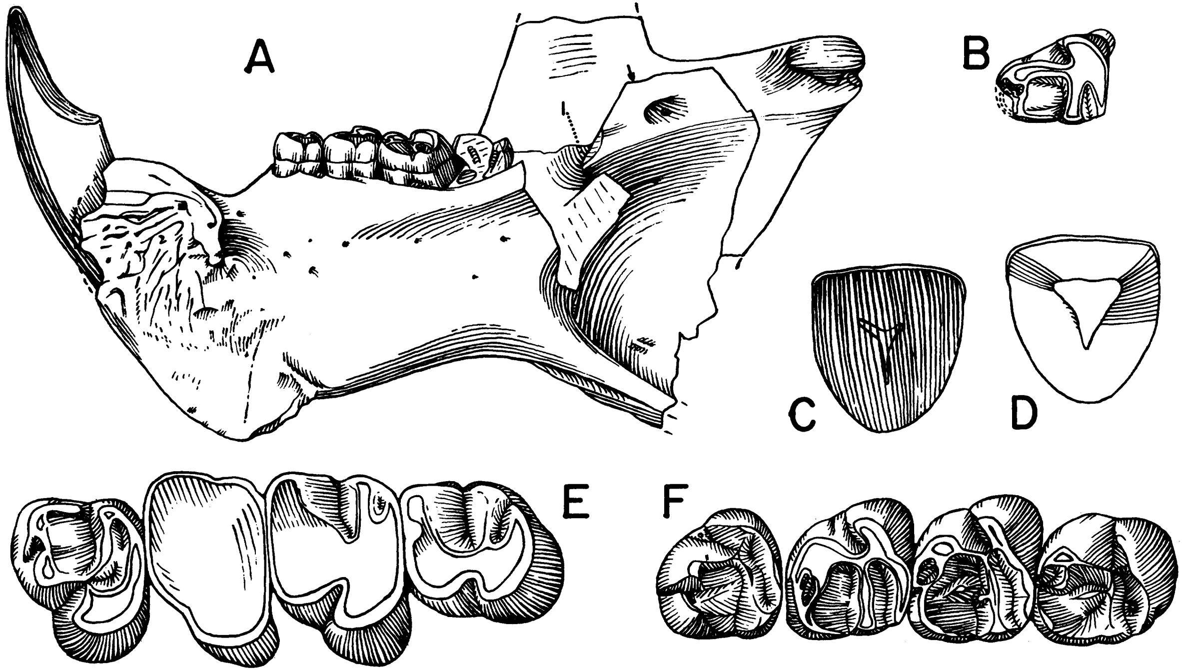

FIG. 2. Teeth and jaw of *Ardynomys olseni.* A. Type, A.M.N.H. No. 20368, median view of lower jaw, ascending ramus and condyle restored by enlargement from A.M.N.H. No. 20370 (type of *A. chihi*). I=Alveolus of incisor. Arrow points to internal part of mandibular foramen. B. RdP_4, A.M.N.H. No. 20371. C, D. LI^1, A.M.N.H. No. 20361. C. Wear surface, D. Posterior end. E. LP_4–M_3, A.M.N.H. No. 20369. F. RP_4–M_3, A.M.N.H. No. 20371. Crowns rotated to be co-planar, and P_4 drawn without being obscured by overhang of M_1. Jaw ×2; teeth approximately ×5.

lophid just in front of the hypoconid, but wear makes it appear to come directly from the hypoconid. A slight cusplike enlargement may be present in the middle of the hypolophid. The most characteristic features of the molars are the connections between the metaconid and protoconid. The former is a large crescentic cusp, one arm continued backward along the lingual side of the tooth, to or nearly to the entoconid, and the other arm curving buccally, to about the middle of the anterior margin of the tooth (fig. 2F). Here it is met by two crests from the protoconid, an anterior cingulum and a metalophid arm. Sometimes (fig. 2F, M_{1-2}) there is a third crest in this area. With wear, the metalophid connects, diagonally, to some point on the posterior side of the metaconid, but never to the lingual end of the metaconid. Highly variable accessory crestlets are present on the posterior slope of the metaconid and from the hypolophid in A.M.N.H. No. 20371 (fig. 2F). These are suggested on A.M.N.H. No. 20370 (fig. 1F). The other specimens are too worn to permit a decision to be made as to whether such minor irregularities were present.

The deciduous tooth (dP_4, fig. 2B) was removed from over the premolar of A.M.N.H. No. 20371. It is somewhat damaged and considerably worn. The metaconid was forward of the protoconid, but has been broken off. It was continued backward along the lingual margin of the tooth by a crest. Apparently a swelling runs backward from the middle of the metalophid into the talonid basin, but has been worn nearly flat. The entoconid is on the median side of the crown, and the posterolophid forms the entire rear of the tooth.

As shown by Matthew and Granger (1925) the lower incisor is heavy, with a flat anterior face along which is a faint groove (fig. 1B). The groove is very faint in the juvenile (fig. 1C), but deepens with age. The enamel extends one-third to one-half of the way around the lateral side, and for about one-fifth of the way onto the median face. The pulp cavity may reach the wear surface, in which case it is Y-shaped. Farther back, it is T-shaped.

An isolated upper incisor, A.M.N.H. No. 20361, is of the correct size and shape to belong to this form. The anterior face is flat, with a very faint longitudinal stria along the center. The pulp cavity is Y-shaped at the wear surface (fig. 2C), and is a pinched triangle at the opposite end (fig. 2D).

cf. *Ardynomys* sp.

Figure 3A

PUBLISHED FIGURES: Vinogradov and Gambarian, 1952, figures 3 and 5.

Vinogradov and Gambarian (1952, p. 16) referred a right lower jaw (P.I.N. No. 473–111) and some fragmentary specimens (P.I.N. No. 473–28) from the Ardyn Obo (Argeel-Obo according to those authors) to *Ardynomys chihi*. They stated that the dimensions of *A. chihi* were not one-tenth smaller than *A. olseni*, as indicated by Matthew and Granger (1925) but rather one-fourth to one-third smaller, and gave the length of the lower jaw from the rear of the condyle to the alveolus of the lower incisor as 29.5 mm. and the alveolar length of the lower tooth row as 9.0 mm.

In addition to the small size of their specimens, there seem to be differences in the tooth pattern (fig. 3A). These include the strong hypolophid on P_4, distinctly separated from the posterolophid; the isolation of the protoconid of M_3 from the metaconid; and the apparently minute valley between the posterior cingulum and the hypolophid of M_3 (Vinogradov and Gambarian, 1952, fig. 5).

Since Matthew and Granger (1925) *were* correct about the size differences between *A. olseni* and *A. chihi* (see table 1), Vinogradov and Gambarian (1952) were mistaken in referring their material to the latter species. The size measurements (other than length of tooth row) in table 1 were scaled from the illustration given by Vinogradov and Gambarian. The differences in size and tooth pattern seem clearly to warrant separation of this material as a new species, but it should only be described by someone who has access to the material, to determine just what the diagnostic characters are.

Ardynomys kazachstanicus Vinogradov and Gambarian, 1952

Figure 3B

PUBLISHED FIGURE: Vinogradov and Gambarian, 1952, figure 6.

TYPE: A.N.K. No. 451/47–1, right lower jaw.

The material (the type, isolated upper teeth and other fragments, only the type being figured or mentioned in the original description) comes from middle Oligocene beds in Kazakstan, slightly younger than the Ardyn Obo.

This species was defined by Vinogradov and Gambarian (1952, pp. 16–17) as follows: length of lower tooth row, 11.5 mm.; lower jaw less massive than in *A. olseni;* eversion of angle greater than in *A. olseni.* Their further discussion consisted merely of pointing out general similarities between this species and *Ardynomys,* although (p. 17) they raised the question as to whether further research might show that this species belonged in a different genus.

It is impossible to determine the importance of the greater eversion of the angle, or the less massive jaw, since Vinogradov and Gambarian did not figure the jaw of this species. A less massive jaw would be expected in a smaller animal and the amount of eversion of the angle of *A. olseni* is uncertain. The tooth pattern of the molars (fig. 3B) shows no differences from that of *A. olseni;* the pattern of the premolar shown in figure 3B may or may not be close to the real pattern of the tooth, as the illustration given by Vinogradov and Gambarian (1952, fig. 6) is by no means clear for this tooth. However, a comparison of the tooth

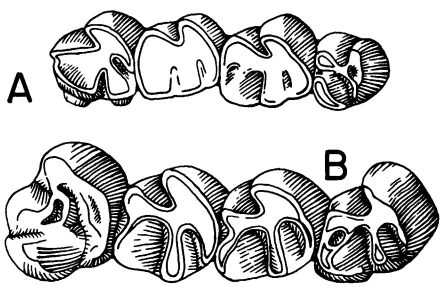

FIG. 3. Teeth of *Ardynomys,* redrawn from Vinogradov and Gambarian, 1952, figures 5 and 6 respectively. Probably about ×5. A great deal of personal interpretation has gone into these redrawings. A. RP_4–M_3, P.I.N. No. 473-111, cf. *Ardynomys* sp. (*A. chihi* of Vinogradov and Gambarian, *nec* Matthew and Granger). B. RP_4–M_3, A.N.K. No. 451/47-1, type of *Ardynomys kazachstanicus.*

measurements given in table 1 indicates that the type of *A. kazachstanicus* is considerably smaller than any specimen of *A. olseni.* This, together with the fact that there is a difference in age and geographic location, permits the tentative retention of this species.

Ardynomys occidentalis Burke, 1936

Figure 4

PUBLISHED FIGURES: Burke, 1936, figures 1-5.

TYPE: Carn. Mus. No. 1056, lower jaw with right P_4-M_2 and incisor.

HYPODIGM: Type; Carn. Mus. No. 1055, partial skull; Carn. Mus. No. 1083, right maxilla; Carn. Mus. No. 1105, jaw with LM_{1-2} and incisor; Carn. Mus. No. 9991, partial skull with I^1, P^3–M^3 left; Carn. Mus. No. 9992, posterior end of skull and fragments; Carn. Mus. No. 12010, anterior half of skull and jaw with LP_4–M_3 and incisor; Carn. Mus. No. 16740, fragment of left maxilla with P^4; Carn. Mus. No. 16994, jaw with LP_4–M_3 and incisor; Carn. Mus. No. 16995, skull with worn left teeth; Carn. Mus. No. 21701, partial skull with RP^3–M^2; F.M.N.H. No. PM 50, skull fragment with LM^{1-3} and incisors; U.M. No. 0740, snout fragment with incisors and cheek teeth; U.M. No. 0741, jaw with badly worn left teeth; U.M. No. 0747, jaw with LP_4–M_3; U.M. No. 0748, left jaw with badly weathered teeth; U.M. No. 0799, left and right jaw fragments with badly worn teeth; U.M. No. 0800, right jaw fragment with worn M_2; U.M. No. 0923, jaw with slightly worn LP_4, M_{2-3} and incisor; U.M. No. 0929, badly weathered snout; U.T.B.E.G. No. 40504–256, skull fragment with no cheek teeth; and U.T.B.E.G. No. 40504–263, partial lower dentition.

DISTRIBUTION: Early Oligocene; Carnegie Museum and University of Montana specimens from McCarty's Mountain, Montana; others from Chambers Tuff and Capote Mountain Tuff, Vieja Group of Trans-Pecos Texas.

As Burke surmised (1936, p. 138), the nasals are flattened, and extend backward on the dorsum as far as do the premaxillaries and maxillaries.

There was no interpremaxillary foramen. As Burke pointed out, the premaxillary-maxillary suture crosses the palate just behind the incisive foramina (fig. 4A), in strong contrast to the situation in *Pseudocylindrodon,* in which the suture reaches the side of the foramen (Burke, 1938, pl. 26, fig. 1). The incisive foramina are continued forward by paired grooves that reach the rear of the incisors. As Burke indicated (1936, pp. 138–139), there is a central ridge in the palate, with a depression of variable depth on either side of it. The posterior palatine foramina lie in these grooves opposite the first molars.

The palatine forms the posterior wall of the posterior palatine foramina and crosses the palate in an irregular line opposite the posterior half of M^1 (fig. 4A). The palatine then runs backward, close to the alveoli of M^{2-3}. The posterior margin of the palate is considerably thickened.

The principal additions that can be made to Burke's description of the skull involve details within the orbit. The lacrimal is quite large (fig. 4B), and the large lacrimal foramen lies at its dorsal border, leading down into the snout. Burke mentioned crushing of the skull walls within the orbit. This occurs on nearly all known skulls or skull fragments of this species, primarily along or just below the lacrimal-maxillary suture. However, before crushing, the lacrimal and maxillary bulged laterally into the orbit, leaving the infraorbital passage as a distinct and rather narrow canal, ventral to the bulge. Preparation of Carn. Mus. No. 1055 permitted this situation to be clearly demonstrated. Investigation of the skull fragments from Texas shows that this bulge is formed by the growing base of the upper incisors, which have migrated posteriorly and laterally, expanding into the orbit. This is also clearly shown by U.M. No. 1105. There is a peculiar denticulate portion of the lacrimal-frontal suture, which seems to be characteristic of this species. On one side of

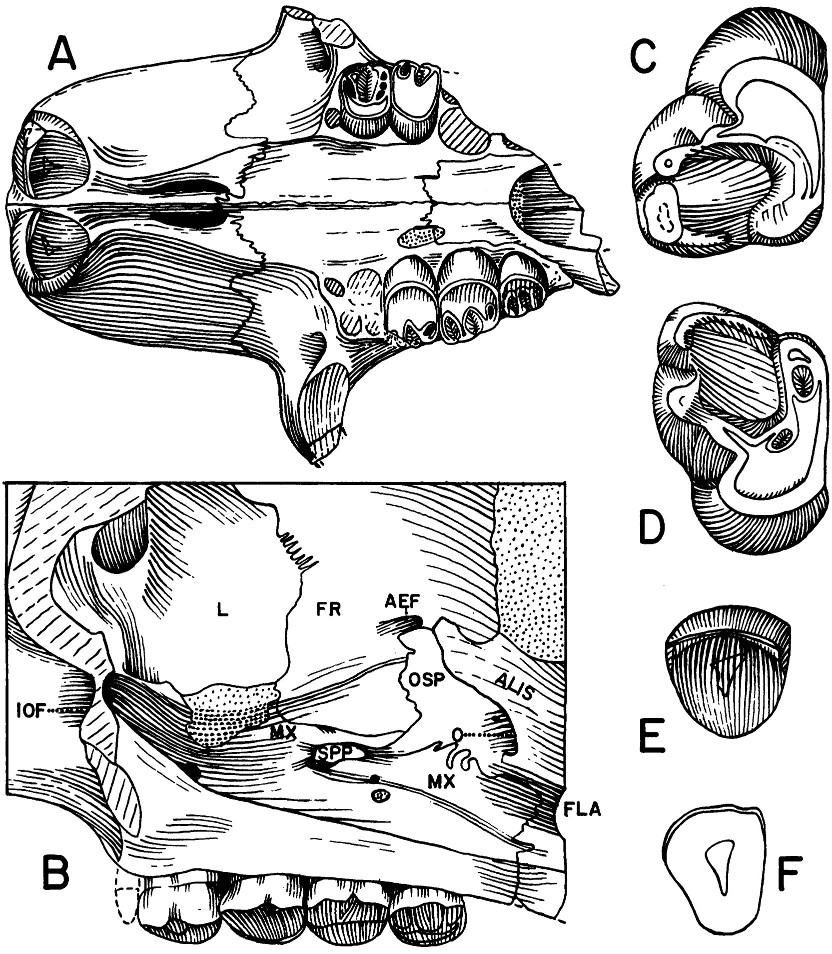

FIG. 4. *Ardynomys occidentalis.* A, B. Anterior part of skull, Carn. Mus. No. 12010. A. Ventral view ×3. B. Lateral view of ventral two-thirds of orbit, partly restored from opposite side. ×5. C. RP_4, Carn. Mus. No. 1056, type. ×10. D. LP_4, Carn Mus. No. 12010. ×10. E. RI^1, Carn. Mus. No. 12010, wear surface. ×5. F. RI_1, Carn. Mus. No. 1056, type, section below P_4. ×5.

Abbreviations: AEF, anterior ethmoid foramen; ALIS, alisphenoid; FLA, foramen lacerum anterius; FR, frontal; IOF, infraorbital foramen; L, lacrimal; MX, maxillary; NL, nasolacrimal foramen; O, optic foramen; OSP, orbitosphenoid; SPP, sphenopalatine foramen.

Carn. Mus. No. 12010, there is what appears to be a foramen at the lacrimo-maxillary suture (fig. 4B). Breakage obscures the other side. This opening may be due to crushing, but a small foramen is clearly present at this point in the uncrushed U.M. No. 0746.

The infraorbital foramen is a vertical oval. On the infraorbital canal, below the lacrimal, there are either one or two rather large nutritive foramina in the maxillary, presumably the foramina for the superior alveolar artery. The maxillary-frontal suture extends backward as a long slender process above the sphenopalatine foramen, a large opening above M^2 (fig. 4B). The maxillary extends backward, ventral to the orbitosphenoid, to a point behind M^3, and below the optic foramen.

The orbitosphenoid is a very irregular bone, sending a narrow process forward to the sphenopalatine foramen, and another dorsally, as far as what seems to be the anterior ethmoid foramen (fig. 4B). The large optic foramen (in whose median wall is a small foramen, presumably nutritive) lies between the alisphenoid and the orbitosphenoid. Only the groove leading to the foramen lacerum anterius is preserved in Carn. Mus. No. 12010, and this area is crushed in Carn. Mus. No. 1055. A little more of the area is present in Carn. Mus. No. 16995.

Double mental foramina occur in Carn. Mus. Nos. 1105 and 16994. The other specimens have single foramina.

Very little can be added at the present time to the description of the cheek teeth as given by Burke (1936, pp. 140–144). As he pointed out, the condition of the hypolophid of P_4 is at first puzzling. However, it is clear that in Carn. Mus. No. 12010 (fig. 4D) there is a hypolophid that curves backward, close to but distinct from the posterolophid. Careful study of the type (fig. 4C) indicates that in this tooth there is an even closer appression of the hypolophid to the posterolophid, as Burke clearly stated (1936, p. 143). A similar situation occurs in U.M. Nos. 0747 and 0923, and is one of the strongest points of resemblance between *A. occidentalis* and *A. olseni.* The hypolophid of unworn M_3 may be a complete crest (U.M. No. 0923) or may be interrupted (U.M. No. 0747).

As Burke indicated, the incisors, both upper and lower, have slightly rounded anterior faces, in contrast to the flat anterior face of the genotype (fig. 4E–F). The Y-shaped pulp cavity extends to the wear surface. The enamel reaches about as far around onto the sides as in *A. olseni.* There is a faint groove near the median side of the lower incisor of the type, not present on the incisor of any of the remaining specimens. In U.M. No. 0747, the posterior end of the incisor extends nearly vertically into the ascending ramus, about as it does in *A. olseni* (fig. 1A).

RELATIONSHIPS

Ardynomys occidentalis is closer to the central stock of the cylindrodonts than is *A. olseni* in its smaller size, and in the rounder anterior faces of the incisors. It probably has less eversion of the angle. The strong hypoconid hypsodonty is characteristic of many of the members of the family. The similarities between the two species involve the general structure of the jaw, the vertical posterior end of the lower incisor, the buccal displacement of the point at which the metalophid joins the metaconid, and the backward migration of the hypolophid of P_4. Since cylindrodonts are known from the middle and late Eocene of North America and are unknown from the Eocene of Asia, it is quite probable that their origin occurred in North America, and that something very similar to *A. occidentalis* migrated to Asia, giving rise to the Asiatic members of the family.

There are no known North American descendants of *A. occidentalis.* As indicated by Wilson (1949, p. 95) and Ferrusquia (MS., p. 44), *Ardynomys, Pseudocylindrodon,* and *Cylindrodon,* of the early Oligocene, are all distinct, though perhaps the first two are more closely related than either is to the more hypsodont *Cylindrodon.* In this respect, *A. occidentalis* is appreciably closer to *Pseudocylindrodon* than is *A. olseni,* which may indicate that the Ardyn Obo beds are somewhat later than those at McCarty's Mountain.

From the description of *Pseudotsaganomys* given by Gromov and Guriev (1962, p. 137), *Ardynomys olseni* seems to foreshadow the middle Oligocene genus in the reduction of the anterior cingulum, the diagonal metalophid, and the lesser hypsodonty.

It is impossible to tell whether the complicated angular process of *Tsaganomys* was present in *Ardynomys,* but the eversion of that part of the angle that is preserved in *A. olseni* may foreshadow such a structure. The specimens of *Cyclomylus* and *Tsaganomys* in the American Museum of Natural History, although incompletely prepared, especially in the orbital region, show an incisive bulge, extending across the orbit and ending lateral to the cheek teeth. The paratype of *C. lohensis,* A.M.N.H. No. 19099, shows such a bulge clearly, the lower or posterior end reaching almost to the alveolar border by M^1. Another specimen of *C. lohensis* (A.M.N.H. No. 83644), a fragment with RP^4–M^1, is broken so that it shows the incisor, lying in the bulge, reaching the alveolar level buccad of M^1 and crowding the buccal roots of M^1. There is no possible channel for the infraorbital nerve and blood vessels ventral to the incisor, so they must have passed laterad of it. The same condition is present in *Tsaga-*

nomys altaicus (as A.M.N.H. No. 19033), in which the incisive bulge is larger, extending laterad of M^1 and M^2. Again, there is no channel for the infraorbital nerves and blood vessels. This incisor structure is so clearly homologous to that of *Ardynomys occidentalis,* and so clearly derived from it, that it seems reasonable to postulate that such a condition was also present in *A. olseni,* and that the series *A. occidentalis–A. olseni–Cyclomylus* and *Tsaganomys* is a real phylogenetic sequence.

Because of the suggestions that *Tsaganomys* and *Cyclomylus* should be referred to the Bathyergidae, skulls of living bathyergids were checked in the American Museum of Natural History. The incisive bulge could usually be detected crossing the orbit, but it was nowhere as prominent as in *Ardynomys, Cyclomylus* and *Tsaganomys.* In *Cryptomys* (A.M.N.H. [M.] No. 118315), the incisive alveolus reaches the alveolar border behind M^3. In *Heliophobius* (A.M.N.H. [M.] No. 162551) the posterior end of the incisor lies in the palatine just in front of the pterygoid fossa, but the incisor protrudes only slightly into the orbit. *Georychus capensis* (A.M.N.H. [M.] No. 168327) seems identical to *Heliophobius.* However, in a series of skulls of *Bathyergus,* the condition is rather different. There is no suggestion that the incisor extends into the orbit in A.M.N.H. (M.) No. 89039 (*B. suillus*), No. 161617 (*B. suillus janetta*), or No. 168283 and No. 168284 (*Bathyergus* sp.). In A.M.N.H. (M.) No. 89037, *B. janetta,* the posterior end of the incisor can be detected just inside the front end of the orbit, within the lacrimal and high above P^4.

Bathyergus is presumably the most primitive of the living Bathyergidae. If this is the case, it is more primitive in the size of the incisor not only than *Cyclomylus* and *Tsaganomys,* but also than *Ardynomys occidentalis.* The other genera of Bathyergidae are more advanced than *Cyclomylus* and *Tsaganomys,* but it seems more reasonable to derive their incisor pattern from that of *Bathyergus* than from that of *Cyclomylus* and *Tsaganomys.*

For the present, the most conservative taxonomic arrangement is to consider that *Cyclomylus* and *Tsaganomys* are cylindrodonts, derived from *Ardynomys,* and to leave open the possibility of a cylindrodont-bathyergid relationship. Among other reasons for this is that Lavocat's current studies (In press) of the Miocene rodents of Kenya may determine whether there is any phiomyid-bathyergid link. Only one of these two relationships is possible.

In view of the noted propensity for parallelism in rodents, it is entirely possible that both the changes in the incisors and the changes in the angular process of *Tsaganomys, Cyclomylus,* and the Bathyergidae are the result of the modification of the incisors for digging tools, and that they have evolved independently.

REFERENCES

Black, C. C.
1965. Fossil mammals from Montana. Pt. 2. Rodents from the early Oligocene Pipestone Springs local fauna. Ann. Carnegie Mus., vol. 38, pp. 1-48, figs. 1-6.

Burke, J. J.
1936. Ardynomys and Desmatolagus in the North American Oligocene. Ann. Carnegie Mus., vol. 25, pp. 135-154, figs. 1-7.
1938. A new cylindrodont rodent from the Oligocene of Montana. *Ibid.,* vol. 27, pp. 255-274, figs. 1-4. pls. 26-27.

Ferrusquia-Villafranca, I.
[MS.] Rancho Gaitan local fauna, early Chadronian, northeastern Chihuahua, Mexico. Unpublished M.A. thesis, The University of Texas, Austin.

Gromov, I. M.
1962. (Otryd Rodentia. Grezune [Order Rodentia, Rodents]). *In* Gromova, V. I. (ed.) (Osnovy Paleontologii [Fundamentals of Paleontology]) vol. 13 (Mlekopitayushchie [Mammals]). Acad. Nauk S.S.S.R., Ministry Geol. Min. Conserv. Moscow, pp. 117-129, 134-170, figs. 72-75, 89-173.

Lavocat, R.
[In Press.] Les Rongeurs du Miocène d'Afrique Orientale. Academic Press.

Matthew, W. D., and W. Granger
1925. New creodonts and rodents from the Ardyn Obo formation of Mongolia. Amer. Mus. Novitates, no. 193, pp. 1-7, figs. 1-9.

Schaub, S.
1958. Simplicidentata. *In* Piveteau, Jean (ed.), Traité de Paléontologie. Paris, Masson et Cie., vol. 6, pt. 2, pp. 659-818, figs. 1-283.

Stehlin, H. G., and S. Schaub
1951. Die Trigonodontie der simplicidentaten Nager. Schweizerischen Paläont. Abhandl., vol. 67, pp. 1-385, figs. 1-620.

Vinogradov, B. C., and P. P. Gambarian
1952. (Oligotsenovie Tsilindrodonti Mongolii i Kazakhstana [Oligocene cylindrodonts of Mongolia and Kazakhstan].) (Cylindrodontidae, Glires, Mammalia). Trudy Paleont. Inst. Acad. Nauk S.S.S.R., Moscow, vol. 41, pp. 13-42, figs. 1-25.

Wilson, R. W.
1949. Early Tertiary rodents of North America. Carnegie Inst. Washington, Publ. 584, pp. 67-164, figs. 1-13.

Wood, A. E.
1937. Rodentia. *In* Scott, W. B., G. L. Jepsen, and A. E. Wood, The mammalian fauna of the White River Oligocene. Trans. Amer. Phil. Soc., new ser., vol. 28, pp. 155-270, pls. 23-33, figs. 8-70.