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A new amynodontid (Mammalia, Perissodactyla) from the Eocene Clarno Formation, Oregon, and its biochronological significance

SPENCER G. LUCAS
New Mexico Museum of Natural History, 1801 Mountain Road N.W., Albuquerque, NM 87104;
spencer.lucas@state.nm.us

Zaisanamynodon protheroi is a new species of large metamynodontinine amynodontid rhinoceros from the Eocene (late Uintan) Hancock quarry local fauna of the Clarno Formation, Oregon, represented by cranial, dental, and postcranial material. Previously, the Hancock amynodont was referred to *Procadurcodon*, but that genus and its type species are *nomina dubia*, so specimens from the Hancock quarry, and some of the specimens from Russia previously assigned to *Procadurcodon,* are reassigned to the valid genus *Zaisanamynodon*. *Z. protheroi* is distinguished from *Z. borisovi*, the type and only other species of *Zaisanamynodon*, by the following characteristics: relatively long rostrum, anterior margin of orbit above M2, P2 more complex with anterior and posterior crests connected to metaloph, P2-4 have complete lingual cingula, incisors relatively small (especially I3/i3), lower canine relatively massive and straight, less molariform p3 and no labial groove on lower molars. Asian records of *Zaisanamynodon borisovi* are of Ergilian age, and the record of *Z. protheroi* in the Hancock quarry suggests it is late Uintan in age, which is older than Ergilian and equivalent to part of the Sharamurunian. This suggests that the specimen of *Z. protheroi* from Artyom in eastern Russia is of Sharamurunian age.

INTRODUCTION

Amynodontids are an extinct family of rhinoceroses known from the middle Eocene-early Miocene of Asia, the Oligocene of Europe, and the middle Eocene to early Oligocene of North America (Wall 1982, 1989; Lucas and Emry 1996, 2001). In North America, the oldest amynodonts (*Amynodon*) are in Uintan strata, and the youngest are Orellan specimens of *Metamynodon*. In the Hancock mammal quarry (Fig. 1) in north-central Oregon, the Clarno Formation yields an Eocene mammal assemblage that was long assigned either a Duchesnean or Chadronian age (e.g., Emry et al. 1987; Krishtalka et al. 1987; Lucas 1992; Hanson 1996; Robinson et al. 2004). However, radioisotopic ages from the basal welded tuff of the John Day Formation and a reevaluation of the biostratigraphic significance of the Hancock quarry mammals indicate a latest Uintan age (Lucas et al. 2004).

Among the fossil mammal specimens from the Hancock quarry is extensive cranial, dental and postcranial elements of an amynodontid rhinoceros. This material has been referred to the genus *Procadurcodon* by Hanson (1996), which Gromova (1960) originally described from Eocene strata near Artyom in eastern Russia. However, as Wall (1989) noted, Gromova's diagnosis of *Procadurcodon* is inadequate, and the taxonomic status of the genus is thus open to question. Here I describe the amynodont rhinoceros from the Hancock Quarry and resolve the taxonomic status of *Procadurcodon*. I also discuss the biochronological significance of the Hancock amynodontid to the correlation of North American and Asian land-mammal "ages."

Abbreviations—**OMSI**, Oregon Museum of Science and Industry, Portland; **OU**, University of Oregon, Eugene; **PIN**, Paleontological Institute, Moscow, Russia; **UCMP**, University of California Museum of Paleontology, Berkeley.

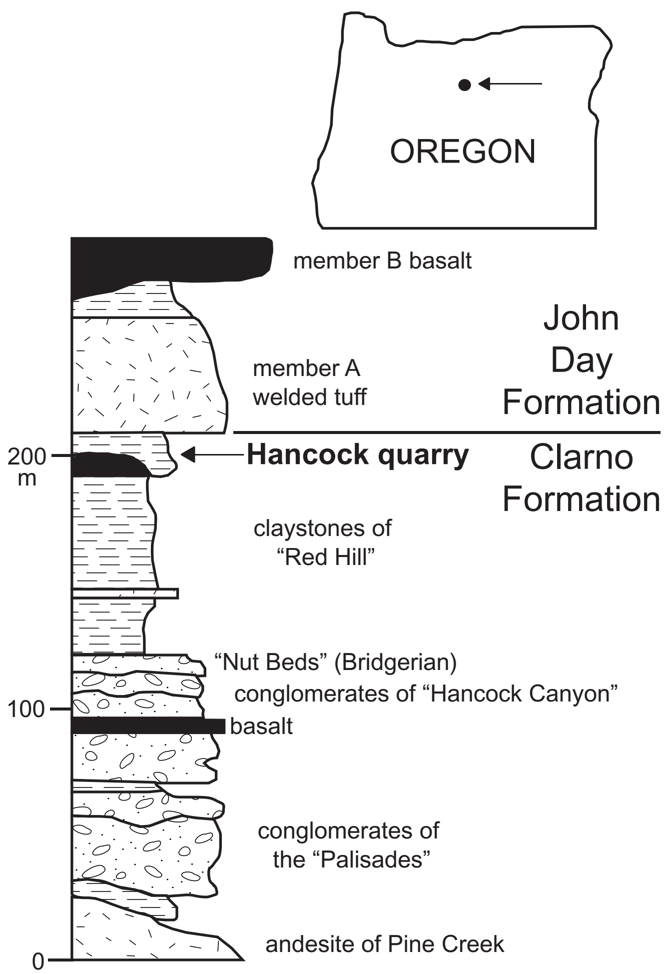

Figure 1. Index map showing location of Hancock quarry and generalized stratigraphic section of the Clarno Formation and base of the overlying John Day Formation (after Lucas et al. 2004).

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus 1758
Order PERISSODACTYLA Owen 1848
Suborder CERATOMORPHA Wood 1937
Superfamily RHINOCEROTOIDEA Cope 1879
Family AMYNODONTIDAE Scott et Osborn 1883
Subfamily AMYNODONTINAE Scott et Osborn 1883
Tribe METAMYNODONTINI Kretzoi 1942
Genus *Zaisanamynodon* Belyaeva 1971

1971 *Zaisanamynodon* Belyaeva, p. 43.
1989 *Zaisanamynodon* Belyaeva: Wall, p. 350.
1996 *Zaisanamynodon* Belyaeva: Lucas et al., p. 52.

Type species—*Z. borisovi* Belyaeva 1971 (Fig. 2).

Included Species—The type species and *Z. protheroi*, new species.

Revised Diagnosis (from Lucas et al. 1996)—*Zaisanamynodon* is a large (length M1-3=200–205 mm) metamynodontinine amynodontid (*sensu* Wall 1989) distinguished from all other members of the tribe by its third loph on P4. *Zaisanamynodon* is much larger than *Paramynodon,* has a more posteriorly positioned orbit and a relatively shorter rostrum with a relatively shorter postcanine diastemata, and lacks the strongly bowed-out zygomatic arches and glenoid shelf of *Paramynodon*. Unlike *Metamynodon, Zaisanamynodon* has relatively long diastemata, low-crowned cheek teeth, a preorbital fossa that is tightly constricted, a large I3, a relatively small infraorbital foramen, three lower incisors, canines that

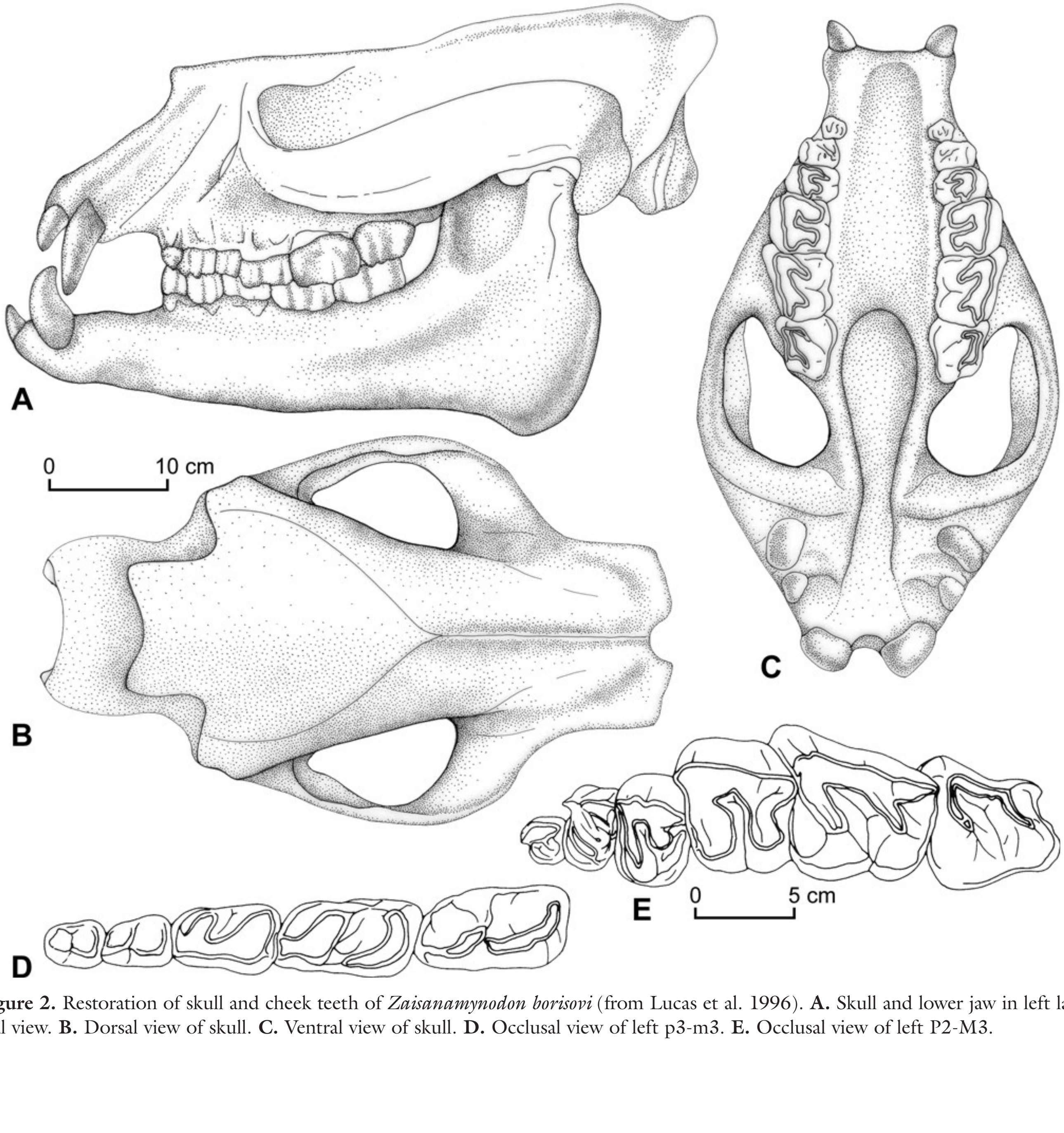

Figure 2. Restoration of skull and cheek teeth of *Zaisanamynodon borisovi* (from Lucas et al. 1996). **A.** Skull and lower jaw in left lateral view. **B.** Dorsal view of skull. **C.** Ventral view of skull. **D.** Occlusal view of left p3-m3. **E.** Occlusal view of left P2-M3.

are not extremely large, curved tusks, an orbit relatively low on the skull, a relatively slender mandibular symphysis, and a less massive zygomatic arch. *Zaisanamynodon* differs from *Megalamynodon* by lacking a glenoid shelf and long diastemata and having a short preorbital portion of the skull and three lower incisors. *Zaisanamynodon* is distinguished from *Cadurcotherium* because the latter has only two upper incisors and one lower incisor, very hypsodont cheek teeth, very narrow lower molars, confluent anterior ribs and parastyles on the upper molars, and a reduced M3 metastyle.

Distribution—Eocene (Sharamurunian or Ergilian) of Kazakhstan, China, eastern Russia and Eocene (late Uintan) of USA (Oregon).

Discussion—I follow Wall (1989) and Lucas et al. (1996) in placing *Zaisanamynodon* in the tribe Metamynodontini, so the diagnosis above distinguishes *Zaisanamynodon* from these other metamynodontinine genera: *Paramynodon* Matthew 1929, redescribed by Colbert (1938); *Metamynodon* Scott and Osborn 1887, redescribed by Scott (1941) and by Wilson and Schiebout (1981); *Megalamynodon* Wood 1945; and *Cadurcotherium* Gervais 1873, redescribed by Roman and Joleaud (1908).

The species of *Zaisanamynodon* named below was previously referred to *Procadurcodon* by Hanson (1996). Gromova (1960) named this genus (type species *P. orientalis*) for a collection of jaw fragments (including the holotype, a right dentary with p3-m2), isolated and loosely associated teeth and postcrania (mostly bones of the manus) collected from a coal mine near Artyom in far eastern Russia (Fig. 3). In 1996, Robert Emry and I conducted an extensive search of the PIN fossil mammal collection in Moscow but could not locate the holotype or referred specimens of *Procadurcodon orientalis*. A subsequent search of the collection also failed to find these specimens (P. Kondrashov written commun. 2004), so my conclusions regarding *Procadurcodon* are based only on Gromova's (1960) published work.

I consider *Procadurcodon* to be a *nomen dubium*, as first alluded to by Wall (1989, p. 351–352), who argued that Gromova's (1960) original diagnosis of *Procadurcodon* inadequately distinguished the genus. Wall (1989, p. 352) claimed that the only potentially diagnostic characters of *Procadurcodon* mentioned by Gromova were "modestly high-crowned upper molars; massive canines; M3 metastyle not strongly bent labially; and trigonid and talonid not strongly separated labially," characteristics observed in several of the metamynodontinine genera. Therefore, he simply referred to the genus as "Amynodontidae *incertae sedis*."

A careful reading of Gromova (1960), examination of

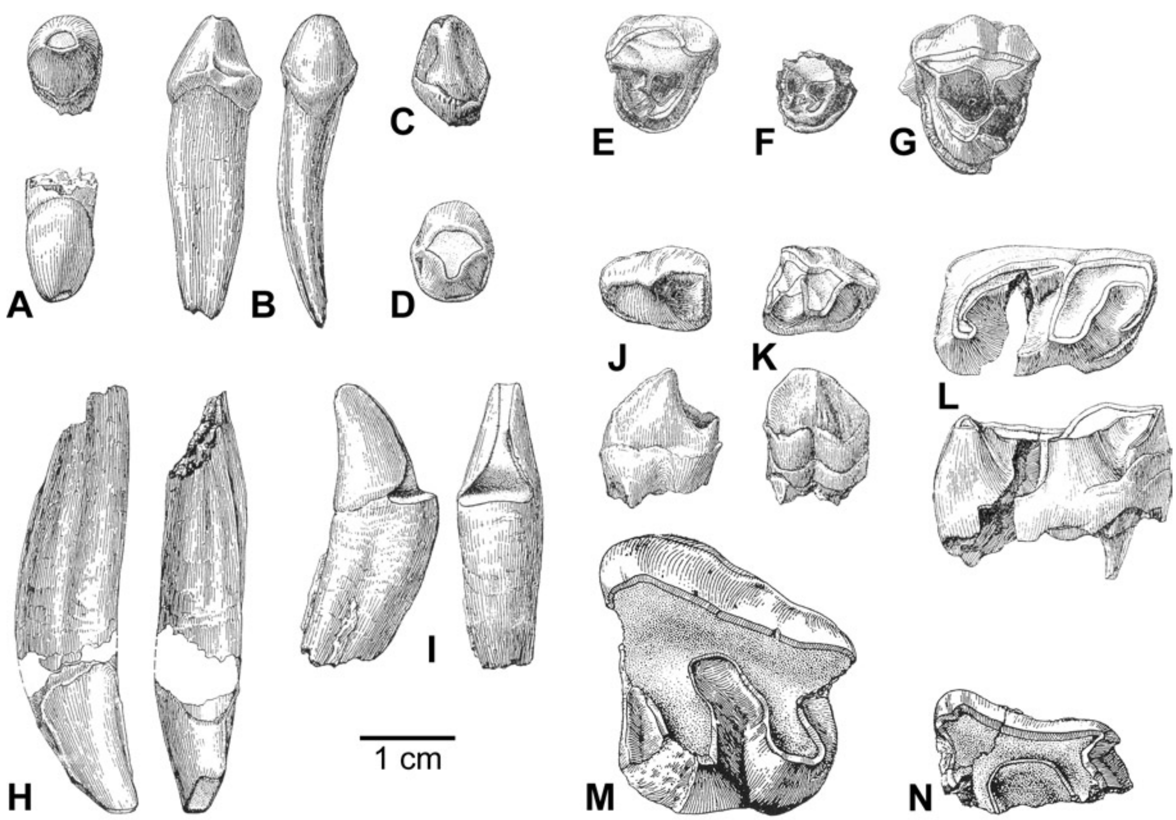

Figure 3. Drawings of selected teeth of "*Procadurcodon orientalis*" (from Gromova 1960). **A.** PIN 858-11, upper incisor. **B**. PIN 858-16, lower incisor. **C.** PIN 858-14, lower incisor crown. **D.** PIN 858-12, lower incisor crown. **E.** PIN 858-39, right P2. **F**. PIN 858-49, incomplete right P2. **G.** PIN 858-41, left P3. **H.** PIN 858-25, upper canine. **I.** PIN 858-28, lower canine. **J**. PIN 858-65, right p3. **K.** PIN 858-63, left p3. **L.** PIN 858-68, left m1. **M.** PIN 858-1, left M2. **N.** PIN 858-53, incomplete left M3.

her illustrations, and comparison with the more complete amynodont specimens from the Hancock quarry allow more definite conclusions regarding the taxonomic status of *Procadurcodon*. Gromova (1960, p. 129) diagnosed *Procadurcodon* as follows:

> Diastema long. I2?/1?C1/1P?/2M?/3. Incisors with low crowns and strongly flattened externally; tusks with interlocking crowns, and relatively massive; lower tusk with deep transverse groove (notch) at base of crown. Teeth relatively low crowned; upper premolars with third transverse crest; upper molars moderately elongate with weak transverse crests; lower molars with flat outer walls and without notch, talonids larger than trigonids. Hand (and foot?) broad and massive; strong angle between lower facets of lunar; articulation facets between the second and third phalanges comparatively mobile; third phalanx moderately reduced, though not as much as second phalanx. Remainder of skeleton unknown.

Most of these characteristics are found in one or more of the metamynodontinine genera, and all are present in *Zaisanamynodon*. Thus, it might be possible to simply regard *Procadurcodon* Gromova 1960 as a senior subjective synonym of *Zaisanamynodon* Belyaeva 1971. However, the holotype of *Procadurcodon* is a right dentary fragment with p3-m2 that could belong to almost any one of the metamynodontinine genera (with the exception of the hypsodont *Cadurcotherium*), given that the p3-m2 morphology is relatively stereotyped in the metamynodontinines. Therefore, I do not regard the holotype dentary fragment of *Procadurcodon orientalis* as diagnostic of a metamynodontinine genus and species, so the taxon is a ***nomen dubium*** (***nomen vanum***). Furthermore, validation of this taxon is hindered by the apparent loss of its holotype and other specimens.

Gromova (1960) assumed that all the amynodont fossils from Artyom represent a single taxon. Size and morphology support this, and their comparison to the more complete Clarno amynodont material suggests that the isolated teeth and bones from Artyom belong to one species. Nevertheless, only a few of the isolated teeth (the upper premolars) described by Gromova (1960) display unequivocal diagnostic characters of a metamynodontinine species. The other isolated teeth and jaw fragments could belong to one of several taxa and thus are undiagnostic of a low-level taxon.

I agree with Hanson (1996) that the diagnostic Artyom amynodont specimens and the Clarno amynodont represent the same taxon. Hanson posited this as generic identity, and he proposed to name the Clarno material a new species of *Procadurcodon*. However, there is nothing in the diagnostic Artyom amynodont material that distinguishes it from the Clarno specimens (see below), so I believe they represent a single species. Because the first name proposed for this species, *Procadurcodon orientalis*, is a ***nomen dubium***, I propose a new species nomen for the Clarno amynodont and refer the diagnostic Artyom material to that species.

The Clarno amynodont displays all the diagnostic features of *Zaisanamynodon*, which is a validly proposed taxon for a giant Asian metamynodontinine with a diagnostic type specimen (Lucas et al. 1996, 2004). Therefore, inclusion of the Clarno amynodont in *Zaisanamynodon* does not require a revision of the generic diagnosis. There are several differences between the Clarno amynodont and *Z. borisovi*, the type and previously only known species of *Zaisanamynodon*, that warrant its description as a new species (see below).

Zaisanamynodon borisovi Belyaeva 1971
Fig. 2, Tables 1–2

1971 *Zaisanamynodon borisovi* Belyaeva, p. 43, figs. 2–11.

1989 *Zaisanamynodon borisovi* Belyaeva: Wall, p. 350.

1996 *Zaisanamynodon borisovi* Belyaeva: Lucas et al., p. 52, text-figs. 2–3, pls. 1–2.

Revised diagnosis—A species of *Zaisanamynodon* distinguished from *Z. protheroi* by the following characteristics: relatively short rostrum (about 12% of skull length), anterior margin of orbit above M1, P2 less complex without anterior and posterior crests connected to metaloph, P2-4 lack complete lingual cingula, incisors relatively large (especially I3/i3), lower canine relatively slender and curved, p3 more molariform, and a slight labial groove (cleft) between trigonid and talonid on lower molars.

Comments—Lucas et al. (1996) provided a comprehensive review of *Zaisanamynodon borisovi* that obviates the need for additional description or illustration of this species. However, at the time of their review, Lucas et al. (1996) recognized only one species of *Zaisanamynodon,* the type species *Z. borisovi* (Fig. 2). Therefore, they only diagnosed the genus *Zaisanamynodon* (see revised diagnosis above). The characters that distinguish *Z. protheroi* n. sp. from *Z. borisovi* are discussed below under *Z. protheroi.*

Hanson (1996, and written commun., 2004) suggested that *Metamynodon mckinneyi* from the Duchesnean Porvenir local fauna of Texas may belong to *Zaisanamynodon*. *M. mckinneyi* is known only from lower jaws and teeth (Wilson and Schiebout 1981, p. 48–52, figs. 17–20, table 15) but differs substantially from *Zaisanamynodon* in the following features: significantly smaller size (e.g., the m1 length of *M. mckinneyi* is 36–38 mm, whereas that of *Zaisanamynodon* is 46–53 mm), much more procumbent incisors, a more massive and strongly recurved lower canine, a broader and more massive symphysis, less molariform p3-4 and strong labial grooves on the lower cheek teeth. It is apparent that most of the distinctive characters of *M. mckinneyi* distinguish *Metamynodon* from *Zaisanamynodon*. Therefore, I maintain Wilson and Schiebout's (1981) original assignment of this species to *Metamynodon*.

Zaisanamynodon protheroi new species
Figs. 3E–G, 4–8, Tables 1–2

1996 *Procadurcodon* n. sp.: Hanson, p. 230, fig. 13.

2004 *"Procadurcodon"* sp.: Lucas et al., p. 92.

Table 1. Measurements (in mm) of upper cheek teeth of *Zaisanamynodon protheroi* compared to measurements of upper cheek teeth of "*Procadurcodon orientalis*" (from Gromova, 1960) and mean values for *Z. borisovi* (from Lucas et al. 1996).

specimen	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
Z. protheroi:												
OMSI 608											68.8	73.2
OU 20505											63.8	70.6
OU 27686											67.3	77.2
OU 27729	21.7	26.8	27.2	39.1	29.2	53.9						
OU 38337											60.5	69.9
UCMP 125898+	21.4	24.8	28.1	42.5	33.2	57.6	55.5	69.9	86.4	80.8	61.9	70.4
UCMP 125899	21.4*	27.2*	26.6	42.8*	31.8	53.6	51.3*	67.8	80.8	78.7	63.6	73.8
UCMP 125912			28.9	36.6								
UCMP 125913			24.6	39.5								
UCMP 125915											63.4	75.7
UCMP 125916									83.4	77.3		
mean	21.5	26.2	27.1	40.1	31.4	55.0	53.4	68.9	83.5	78.9	64.2	73.0
SD	0.1	1.0	1.5	2.3	1.6	1.8	2.1	1.1	2.3	1.9	2.7	2.6
CV	0.7	3.8	5.5	5.7	5.1	3.3	3.9	1.6	2.7	2.4	4.2	3.7
"*P. orientalis*:"												
PIN 858-1							59	66	79	76		
PIN 858-2											68	72
PIN 858-39	23	25										
PIN 858-40			27	34								
PIN 858-41			27	36								
PIN 858-42	21	23										
PIN 858-54							59					
Z. borisovi:												
mean values	27.5	25.5	30	38	34	54	65	65	77	74	63	74

+ holotype

Holotype—UCMP 125898, skull with left I1, C, P2-M3, right I1-2 roots, I3, C, P2-M3 and incomplete lower jaw with left i1-3, c, p3-m3 (Figs. 4A–C, 5A, 6A–B, 7B).

Horizon and Locality of Holotype—Clarno Formation, Oregon (UCMP locality I-V75203, the Hancock quarry).

Diagnosis—A species of *Zaisanamynodon* distinguished from *Z. borisovi* by the following characteristics: rostrum relatively long (about 24% of skull length), anterior margin of orbit above M2, P2 relatively complex with anterior and posterior crests connected to metaloph, P2-4 have complete lingual cingula, incisors relatively small (especially I3/i3), lower canine relatively massive and straight, p3 less molariform and no labial groove (cleft) between trigonids and talonids on lower molars.

Etymology—Named after Donald Prothero, to honor his many contributions to our knowledge of rhinoceros evolution.

Referred specimens—From the Clarno Formation, Oregon (all from UCMP locality I-V75203, the Hancock quarry): OMSI 608, left M3 (Fig. 5F); OMSI 611, upper canine; uncatalogued left m3; OU 20492, incomplete right m1; OU 20505, left M3; OU 20945, upper canine; OU 21380, fragment of lower molar; OU 21402, upper canine; OU 21408, left m3 talonid fragment; OU 21410, tooth fragment; OU 21413, tooth fragment; OU 21414, lingual portion right M3; OU 21415, tooth fragment; OU 21425, upper canine; OU 27686, right M3 (Fig. 5D); OU 27716, left p4; OU 27722, mandible with left p4-m3 and right p3-

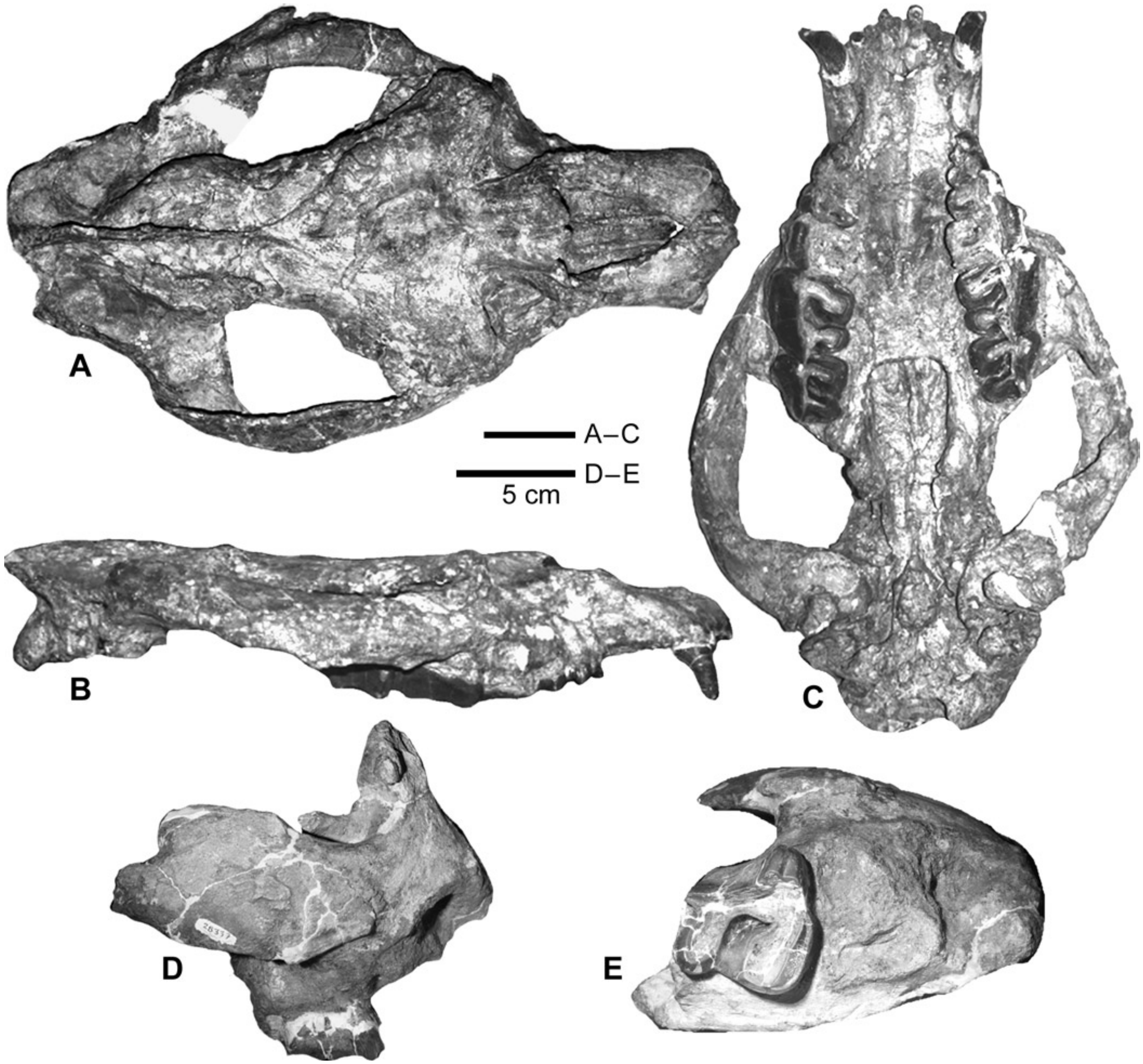

Figure 4. *Zaisanamynodon protheroi* from the Clarno Formation, Oregon. **A–C.** UCMP 125898, skull (holotype) in dorsal (**A**), right lateral (**B**) and ventral (**C**) views. **D–E.** OU 28337, part of right facial region with M3 in lateral (**D**) and occlusal (**E**) views.

m3, most teeth very worn and damaged; OU 27723, right m3 (Fig. 7E); OU 27724, left p4 (Fig. 7D); OU 27725, right p3; OU 27729, right maxillary fragment with P2-4 (Fig. 5B; Hanson 1996, fig. 13); OU 28337, fragment of facial region of skull with right M3 (Fig. 4D–E); OU 35219, left dentary fragment with p4, part m1, complete m2-3; UCMP 125899, dorso-ventrally crushed skull with right C, P2-M3 and left P2-M3; UCMP 125900, posterior portion of skull; UCMP 125901, left premaxillary with I1-3 roots and C; UCMP 125902, juvenile left and right squamosals, right dentary fragment with roots of d i1-3 and crowns of dp3-4; UCMP 125903, fragment of zygomatic arch; UCMP 125905, C fragment; UCMP 125906, upper canine fragment; UCMP 125907, deciduous canine; UCMP 125908, incomplete left C; UCMP 125909, canine root; UCMP 125910, right upper canine (Fig. 6C); UCMP 125911, fragment of left p2; UCMP 125912, right P3 (Fig. 5D); UCMP 125913, left P3; UCMP 125914, P4 fragment; UCMP 125915, left M3; UCMP 125916, left M2 (Fig. 5E); UCMP 125917, upper molar fragment; UCMP 125918, incisor; UCMP 125919, incisor root; UCMP 125920, lower jaw with left c root, incomplete p4, m1-3 and right p3; UCMP 125921, fragment

Table 2. Measurements (in mm) of lower cheek teeth of *Zaisanamynodon protheroi* compared to measurements of lower cheek teeth of "*Procadurcodon orientalis*" (from Gromova 1960) and mean values for *Z. borisovi* (from Lucas et al. 1996).

specimen	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
Z. protheroi:										
OU 27716			34.1	24.2						
OU 27722	25.9	19.1	33.0	23.5	49.0	31.4		38.2	72.8	35.5
OU 27723									69.1	36.3
OU 27724	25.5	18.1								
OU 27725	24.4	17.5								
UCMP 125898+	26.4	18.2	29.5	21.4	52.6	31.8	65.5	36.9	67.7	35.5
UCMP 125911				21.4						
UCMP 125920	25.6	17.8		21.8		28.4	70.4	38.2		36.1
UCMP 125922									73.9	37.4
UCMP 125923									65.9	34.6
UCMP 125924	22.5	15.5	32.5	20.8	50.6	30.5	64.1	35.6	69.6	33.5
UCMP 125925			29.8	22.5	49.9	32.4	66.5	36.6	63.4	33.5
UCMP 125926	24.3	18.5	34.1	24.1	51.5	32.5	60.9	36.4	69.1	37.2
UCMP 125927			30.5	21.9	48.6	32.2	62.8	37.6	67.8	36.5
UCMP 125939							67.5	38.2		
UCMP 125949				21.4						
mean	24.9	17.8	31.9	22.3	50.4	31.3	65.3	37.2	68.8	35.6
SD	1.2	1.1	1.8	1.2	1.4	1.3	3.1	2.4	4.4	3.7
CV	4.8	6.5	5.6	5.4	2.8	4.2	4.7	6.5	6.4	10.4
"*P. orientalis*:"										
PIN 858-4+	25	19	34	23.5	50	32				
PIN 858-6	23	18								
PIN 858-7	23.5	19								
PIN 858-63	23	20								
PIN 858-65	25	18								
PIN 858-68							63	38		
PIN 858-70									70	33
Z. borisovi:										
mean values	24	20	33.7	23	48	30	66	38.7	63.7	33.7

+ holotype

of right P4; UCMP 125922, right dentary fragment with m3 (Fig. 7F); UCMP 125923, left dentary fragment with m3; UCMP 125924, right dentary fragment with p3-m3 (Fig. 7A); UCMP 125925, right dentary fragment and symphysis with left c and right p4-m3 (Fig. 6D, 7C); UCMP 125926, lower jaw with very worn left and right p3-m3 and right i2; UCMP 125927, right dentary fragment with very worn p4-m3; UCMP 125928, condyle of right dentary; UCMP 125929, left i2; UCMP 125930, left i3; UCMP 125931, left i3; UCMP 125932, right i2; UCMP 125933, left C; UCMP 125934, right c; UCMP 125935, canine fragment; UCMP 125938, fragment of right p4; UCMP 125939, right m2; UCMP 125940, left scaphoid (Fig. 8C–D); UCMP 125941, right unciform; UCMP 125942 fragment of trap-

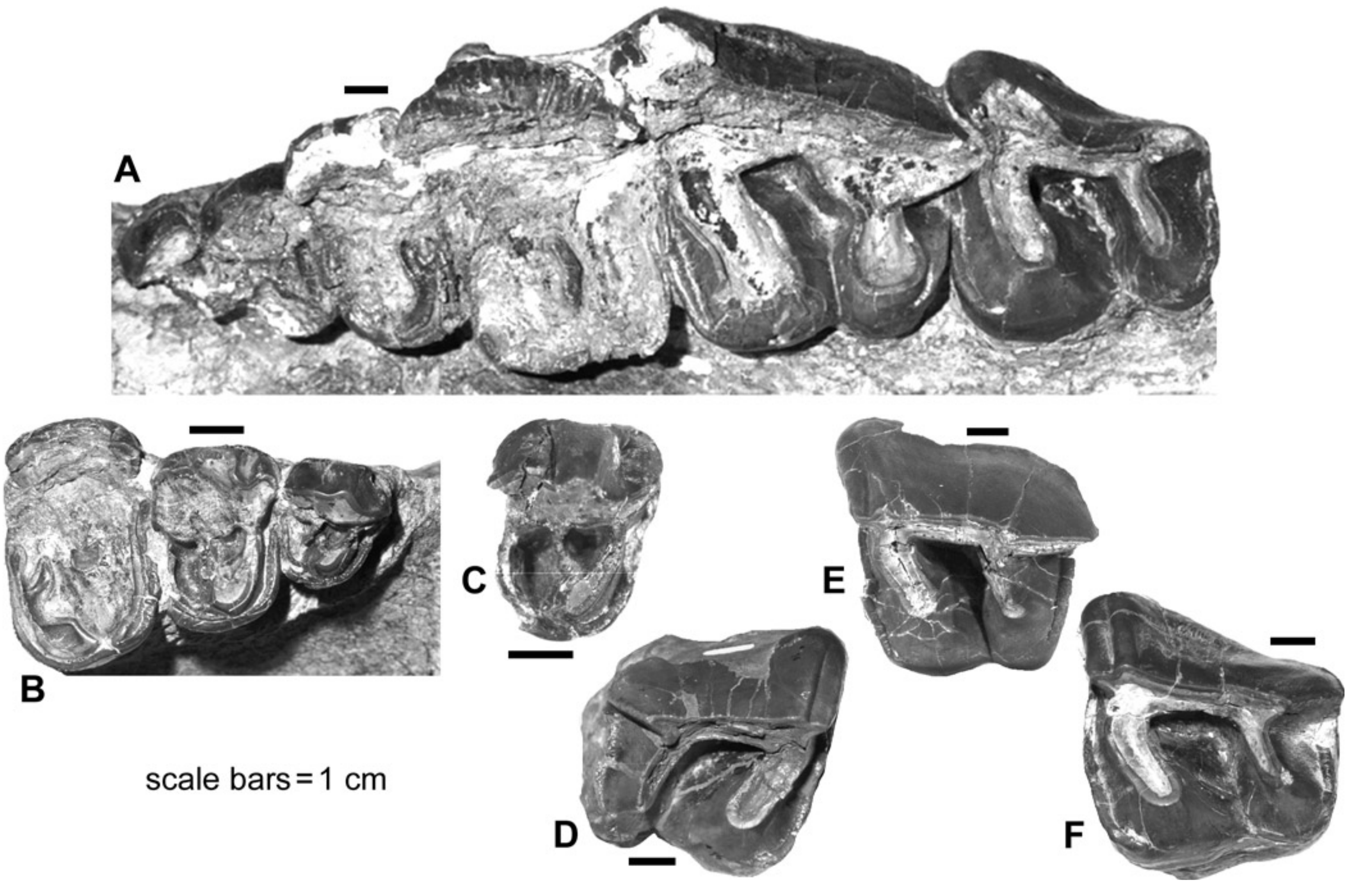

Figure 5. Occlusal views of upper cheek teeth of *Zaisanamynodon protheroi* from the Clarno Formation, Oregon. **A.** UCMP 125898 (holotype), left P2-M3. **B.** OU 27729, right P2-4. **C.** UCMP 125912, right P3. **D.** OU 27686, right M3. **E.** UCMP 125916, left M2. **F.** OMSI 608, left M3.

ezoid; UCMP 125943, distal fragment of left metacarpal 4; UCMP 125944, left metacarpal 3; UCMP 125945, right metacarpal 3; UCMP 125946, right metacarpal 2; UCMP 125947, distal metatarsal 3; UCMP 125948, left astragalus (Fig. 8K–L); UCMP 125949, incomplete right P4; UCMP 125950, left premaxillary fragment with I3; UCMP 125966, right humerus; UCMP 125967, left humerus (Fig. 8A–B); UCMP 125968, right femur (Fig. 8G–H); UCMP 125969, right tibia (Fig. 8I–J); UCMP 126091, proximal carpal of phalanx 3; UCMP 126092, proximal carpal of phalanx 3 (Fig. 8E–F).

From the coal formation at Artyom, eastern Russia: PIN 858-39, right P2 (Fig. 3E; Gromova 1960, fig. 3A); PIN 858-40, left P3 (Fig. 3G; Gromova 1960, fig. 3V); PIN 858-41, left P3 (Gromova 1960, fig. 3G); PIN 858-49, incomplete right P2 (Fig. 3F; Gromova 1960, fig. 3B).

Description—The skull of *Zaisanamynodon protheroi* is moderately brachycephalic, has a large and massive zygomatic arch, a reduced preorbital portion of the skull, a frontal-maxilla contact, and an orbit positioned high on the skull. These are characteristic metamynodontinine features (Wall 1989), but the Clarno skull also shares a unique feature with *Zaisanamynodon borisovi*: the preorbital fossa is so deep that it constricts the rostrum so that it is narrower than the braincase across the orbit. Selected measurements of the holotype skull of *Z. protheroi* (UCMP 125898) are: basicranial length = 646 mm, width across orbits = 307 mm, width across zygomatic arches = 445 mm, width across postglenoid processes = 328 mm.

The posterior limit of the nasal incision of *Zaisanamynodon protheroi* is above the P4. The premaxilla strongly slopes anteroventrally to root a large, slightly procumbent upper canine. The maxillaries are narrowed by the deep preorbital fossa, and the external nares face anteriorly as a broad, box-like opening. A large infraorbital foramen in the preorbital fossa opens to face anteriorly.

The anterior margin of the orbit is above the anterior portion of the M2. A blunt supraorbital ridge slightly overhangs the orbit. The skull roof is broadest above the orbits and sharply constricted posteriorly at the anterior end of the braincase. Thus, the braincase is much narrower than the frontals, and it bears a low, blade-like sagittal crest dorsally.

The zygomatic arch is massive, but not strongly flexed dorsally nor broadly flared-out laterally. Its squamosal root is a plate of bone at a near right angle to the sagittal plane of the skull. The lambdoidal crest is low and sharp, sloping

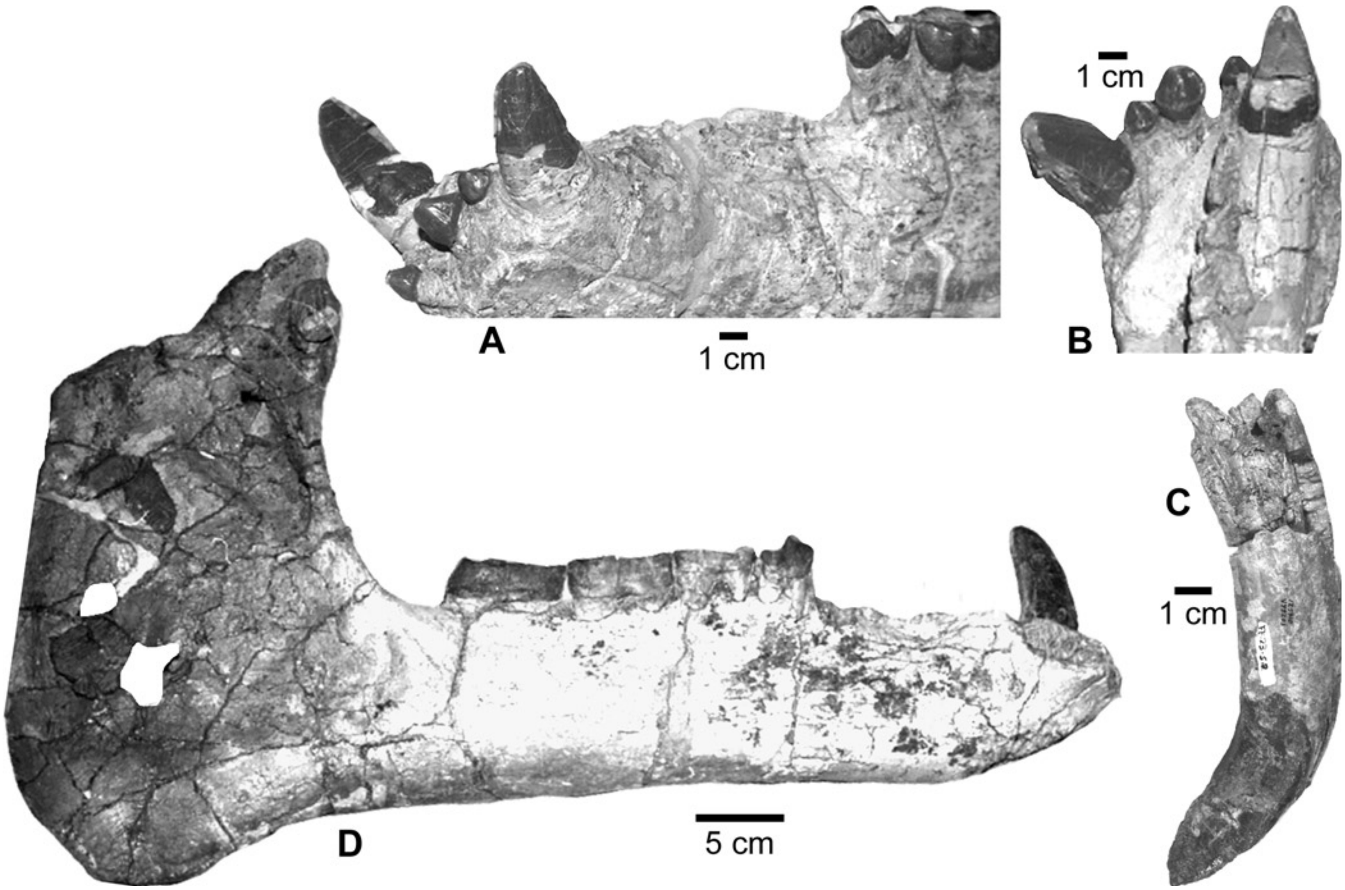

Figure 6. *Zaisanamynodon protheroi* from the Clarno Formation, Oregon. **A–B.** UCMP 125898 (holotype), anterior lower dentition in left lateral (**A**) and occlusal (**B**) views. **C.** UCMP 125910, right upper canine in lateral view. **D.** UCMP 125925, lower jaw with left c and right p4-m3 in lateral view.

slightly postero-dorsally. The occiput is slightly oblique and deeply recessed above the large, rounded occipital condyles. The foramen magnum is circular and opens posteriorly.

In ventral view, the palate is broad and not arched (vaulted). The large canines have thick maxillary roots that are followed, after distinct diastemata, by parallel upper cheek tooth rows composed of the P2-M3.

The anterior edge of the internal nares is between the anterior portions of the M3s, and the internal narial opening is a broad fossa. The pterygoid flanges are low and rim this fossa posterior to the postorbital constriction. The basisphenoid is a narrow, cylindrical bone with a flat, digitate suture posteriorly to the basioccipital. The basioccipital is cylindrical anteriorly and flares posteriorly to the roots of the massive occipital condyles. The hypoglossal foramen opens just anterolateral to the occipital condyle. The glenoid fossa is shallowly concave and oriented slightly oblique to the sagittal plane. The postglenoid process is long, thick, and antero-ventrally curved, and has a blunt tip. The external auditory meatus is a deep, short recess that separates the postglenoid process from the mastoid-paroccipital process. The glenoid fossa is well above the cheek tooth plane.

The lower jaw of *Zaisanamynodon protheroi* has a slightly flared anterior dental row that bears three closely spaced incisors. The i1 is procumbent, but the i2 and i3 are less procumbent. The dentary bulges out at the massive roots of the canines and is slightly constricted at the symphysis immediately behind the canines. The thick symphysis is slightly concave dorsally and extends to under the p3. The horizontal rami are thick and relatively shallow. The ascending ramus is tall, and the coronoid process is higher than the condyle. The ascending ramus has a deep temporal fossa laterally, and a thick curved mandibular angle posteriorly. The dentaries diverge slightly posterior to the symphysis, but the lower cheek-tooth rows are essentially parallel.

Zaisanamynodon protheroi has three small upper incisors in which I1 and I3 are approximately the same size and both are smaller than I2. The upper incisor crowns are globose, slightly convex outward, and slightly concave medially, and have a rounded occlusal edge. There are no diastemata between the upper incisors, which form a broad shallow arc between the canines. There is a short diastema between I3 and the C.

The upper canine is trihedral in cross section, pointed, slightly recurved, and much larger than any of the incisors. The anterior edge of the upper canine wore against the pos-

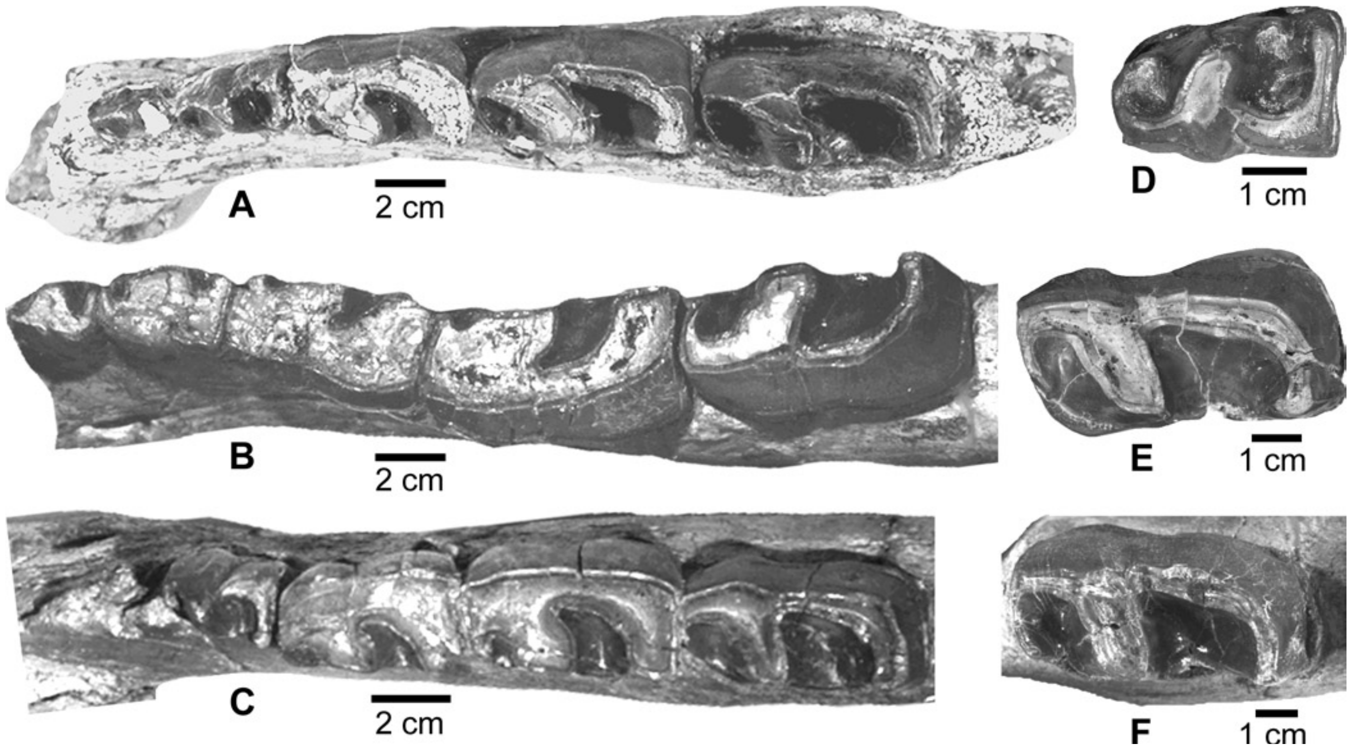

Figure 7. Occlusal views of lower cheek teeth of *Zaisanamynodon protheroi* from the Clarno Formation, Oregon. **A.** UCMP 125924, right p3-m3. **B.** UCMP 125898 (holotype), left p3-m3. **C.** UCMP 125925, right p4-m3. **D.** OMSI 27724, left p4. **E.** OMSI 27723, right m3. **F.** UCMP 125922, right m3.

terior edge of the lower canine in chisel-like fashion.

The P1 is not present on *Zaisanamynodon protheroi.* The P2-4 increase in size posteriorly and are similar to each other in having tall ectolophs dominated by the large paracones, which form a thick rib on the ectoloph. The P2 lacks a metacone and has a short metaloph and complete lingual cingulum. Small crests extend anteriorly and posteriorly from the middle of the metaloph. A small metacone forms a rib on the P3 ectoloph. The protoloph connects the protocone to the ectoloph at the parastyle. A short, transverse metaloph extends lingually from the ectoloph at the metacone and connects to the protocone. Like P2, the P3 has a complete lingual cingulum. A third loph is posterior to the metaloph that connects the lingual cingulum to the ectoloph. The P4 is similar to the P3 but much wider.

The M1 is about as wide as long and has a long, tall, nearly flat ectoloph and slightly oblique protolophs and metalophs. The antecrochet is poorly developed, and there is a pocket behind the metaloph. The parastyle is a distinct rib on the anterior end of the ectoloph.

The M2 is generally similar to the M1 but much larger and also longer relative to its width. This is because the M2 parastyle is very large, the ectoloph is very long, and there is a much more distinct cleft between the parastyle and anterior rib on M2. There is also a weak anterochet.

The M3 is a trapezoidal tooth smaller than M2 and about the same size as the M1. The anterior rib is smaller than the paracone, and the ectoloph is slightly concave labially, terminating posteriorly at a prominent metacone. The protolophs and metalophs are oblique and slightly concave posteriorly. As on M1-2, there is a shelf posterior to the metaloph.

The three lower incisors are generally similar to the upper incisors—they are small conical to rounded teeth, of which i2 is the largest, and i1 and i3 are approximately of equal size. Each have lingual cingulids, slightly concave lingual faces, slightly convex labial faces, and rounded to triangular occlusal edges. There are no diastemata between the incisors, and only a very short diastema between i3 and the lower canine.

The lower canine is a massive, trihedral, pointed tooth that flares out and is only slightly recurved. It is much larger than any of the incisors, and a long diastema separates the lower canine from the p3.

The p2 of *Zaisanamynodon protheroi* is not known. The p3 has a larger talonid than trigonid. The tall and large protoconid dominates the trigonid and is posterior to a small paracristid. The metalophid is connected to a smaller hypolophid by a prominent cristid obligua. The trigonid has a strong lingual cingulid and a weak, rugose labial cingulid.

The p4 is molariform, with a talonid wider than the trigonid. It has a well-developed paracristid and hypolophid, a weak labial cingulid, and lingual cingulids on the trigonid and the talonid ectoflexids. A strong, labially positioned cristid obliqua connects the hypolophid to the metalophid.

The m1 has the typical amynodontid lower molar crown

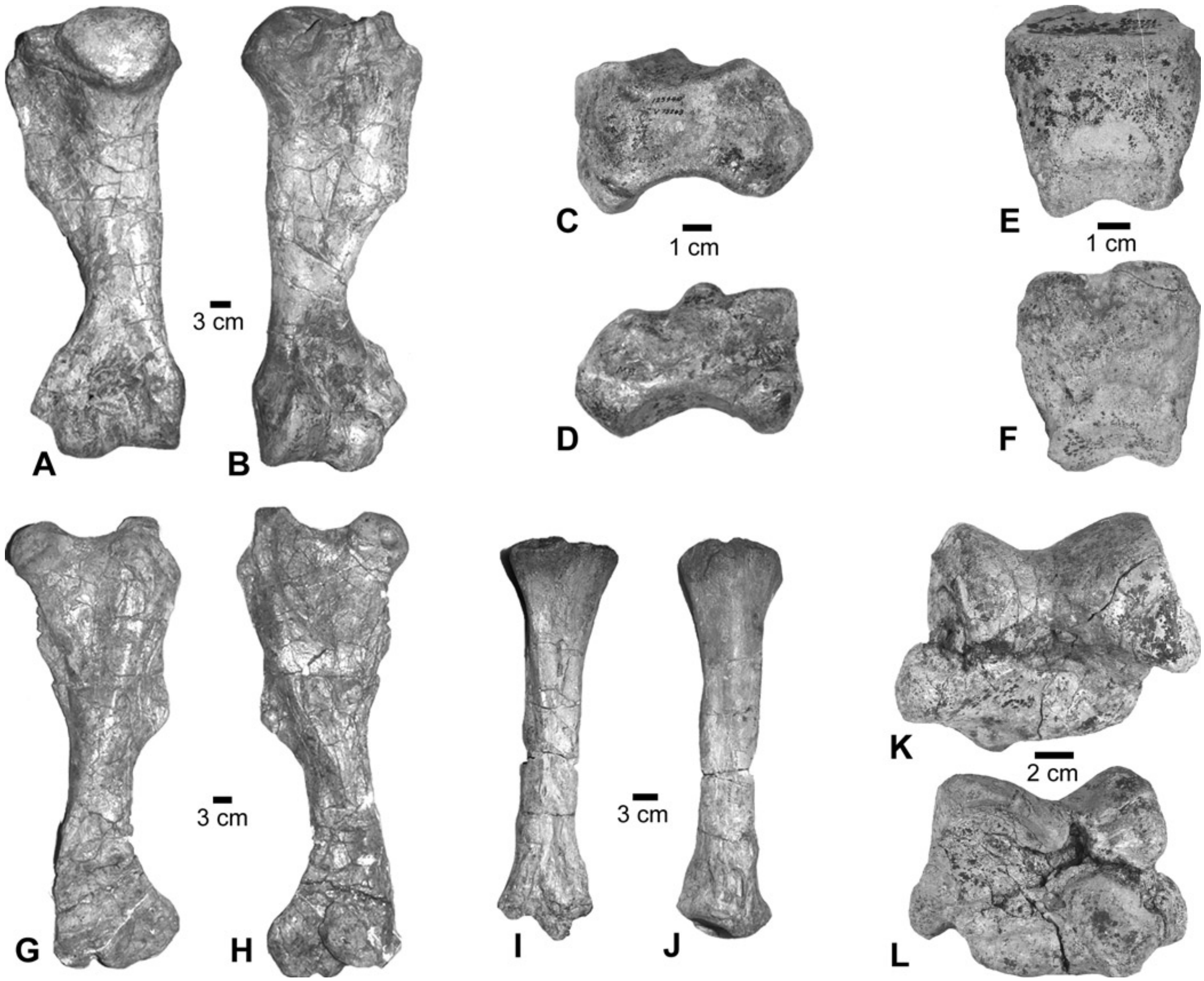

Figure 8. Selected postcrania of *Zaisanamynodon protheroi* from the Clarno Formation, Oregon. **A–B.** UCMP 125967, right humerus, anterior (**A**) and posterior (**B**) views. **C–D.** UCMP 125940, left scaphoid lateral (**C**) and medial (**D**) views. **E–F.** UCMP 126092, right proximal phalanx of manus, anterior (**E**) and posterior (**F**) views. **G–H.** UCMP 125968, left femur, anterior (**G**) and posterior (**H**) views. **I–J.** UCMP 125969, right tibia, posterior (**I**) and anterior (**J**) views. **K–L.** UCMP 125948, left astragalus, dorsal (**K**) and ventral (**L**) views.

pattern of slightly oblique metalophids, and hypolophids bordered and connected labially by a continuous crest that begins anteriorly as the paracristid and posteriorly is composed of the hypolophid. The prominent paracristid forms an anterior lobe on the molar, and there is a nearly continuous lingual cingulid.

The m2 and the m3 are similar to the m1, but they have stronger lingual cingulids. On m1-3, no groove (cleft) separates the cristid obliqua from the metalophid.

The only deciduous teeth known of *Zaisanamynodon protheroi* are the dp3-4 (UCMP 125902). The dp3 has a large trigonid and a small talonid, and differs little from the p3 except in having a relatively larger paracristid. The dp4 is molariform and similar to the p4, except that the dp4 has a relatively smaller trigonid. Measurements of these deciduous teeth are: dp3 length = 34.4 mm, width = 20.3 mm, dp4 length = 40.3 mm, width = 26.4 mm.

Various postcrania of *Zaisanamynodon protheroi* from the Hancock quarry are present in the UCMP collection and all are appendicular elements. They include a humerus (Fig. 8A–B), part of an ulna, some carpals (e.g., Fig. 8C–D), metacarpals and phalanges of the manus (e.g., Fig. 8E–F), a femur (Fig. 8G–H), a tibia (Fig. 8I–J), and a metatarsal. The humerus is a robust bone with a long and thick deltoid ridge very similar to the humeri of *Zaisanamynodon borisovi* (Belyaeva 1971, fig. 9) and *Metamynodon* (Scott 1941, pl. 94, fig. 3). Measurements of the humerus of *Z. protheroi* (of two specimens, UCMP 125966 and 125968) are: total length = 525/620 mm, proximal width = 228/240 mm, and distal width = 190/228 mm.

The carpals, metacarpals, and phalanges of the manus of *Zaisanamynodon protheroi* are similar to those of *Z. borisovi* (Belyaeva 1971, figs. 10–11) and *Metamynodon* (Scott 1941, pl. 95, fig. 4). For example, the scaphoid is a stout, curved bone with a broad and nearly flat scaphoid-radius facet dorsally and a deeply concave trapezoid facet ventrally. The metacarpals of *Z. protheroi* are long but stout (length ranges from 212 to 238 mm). The proximal phalanges are short and robust. Measurements of UCMP 126092 are: length = 74 mm, proximal width = 64 mm, distal width = 49 mm.

The femur of *Zaisanamynodon protheroi* is long and robust, with a very prominent greater trochanter and lesser trochanter, a relatively small head and small third trochanter (the latter is a synapomorphy of Metamynodontini: Wall 1989). It is similar to the femur of *Metamynodon* (Scott 1941, pl. 94, fig. 6). Measurements of the femur of *Z. protheroi* (UCMP 125968) are: length = 758 mm, proximal width = 261 mm, distal width = 219 mm.

The tibia of *Zaisanamynodon protheroi* has a thick cnemial crest anteriorly, a prominent malleolus distally, and a low intercondylar spine proximally. It is similar to but more slender than the tibia of *Metamynodon* (Scott 1941, pl. 94, fig. 7). Measurements of the tibia (UCMP 125969) are: length = 470 mm, proximal width = 138 mm, distal width = 115 mm.

The astragalus of *Zaisanamynodon protheroi* is like that of *Metamynodon* (Scott 1941, pl. 95, fig. 5). It has a broad, asymmetrical tibial trochlea, a short and slightly concave navicular facet ventro-medially, and a larger, flatter cuboid facet ventro-laterally. The trochlear width of UCMP 125948 = 87 mm.

The postcrania of *Zaisanamynodon protheroi* suggest it had a relatively massive postcranial skeleton like that of other metamynodontinines. This skeleton is similar to that of *Metamynodon* in most features, although the distal hind limb of *Z. protheroi* appears to have been relatively longer and more slender than that of *Metamynodon*.

Discussion—Features that distinguish *Zaisanamynodon protheroi* from *Z. borisovi* (see diagnoses above) reveal a difference in the functional complex of the anterior dentition and associated modifications of the facial region. *Z. protheroi* has relatively small incisors, more massive and straighter canines, slightly more complex upper premolars, less molariform p3, a relatively longer rostrum, and a somewhat larger facial fossa than does *Z. borisovi*. These differences are apparent in several skulls and many upper dentitions, and their consistency in the Clarno material supports the conclusion that *Z. protheroi* merits species-level taxonomic distinction from *Z. borisovi*. Nonetheless, dental measurements (Tables 1–2) indicate that the sizes of these two species are nearly identical.

I view *Zaisanamynodon protheroi* as a species somewhat more primitive than *Z. borisovi*. Thus, *Z. protheroi* has a relatively long rostrum and deeper facial fossa than the more derived (shortened) facial region of *Z. borisovi*. *Z. protheroi* also has less specialized incisors that are all relatively small and nearly of equal size, as opposed to *Z. borisovi*. The more complex upper premolar structure of *Z. protheroi* is more primitive than the more simply lophodont upper premolars of *Z. borisovi*, as is the less molariform p3 of *Z. protheroi*. Whereas *Z. protheroi* appears to be geologically older than *Z. borisovi* (Fig. 9), the two species may form a chronomorphocline.

BIOCHRONOLOGY

Correlations of Asian and North American land-mammal "ages" are relatively imprecise because of a low number of shared taxa and a general absence of magnetostratigraphy and radioisotopic ages from the Asian strata that yield mammal fossils (e.g., Holroyd and Ciochon 1994). The occurrence of *Zaisanamynodon protheroi* at the Hancock quarry in Oregon and at Artyom in Russia augments the list of shared Asian-North American Eocene mammal taxa. This addition is of some value to correlation of the North American and Asian middle to late Eocene land-mammal "ages" (Fig. 9).

Occurrences of *Z. borisovi* in Nei Monggol, China are of Ergilian age. These are records from the Ulan Gochu, Baron Sog, and Houldjin formations (Russell and Zhai 1987; Lucas et al. 1996). Lucas et al. (1996) also assigned an age of Ergilian to the type locality of *Zaisanamynodon* in the Zaysan basin of northeastern Kazakhstan.

The only records of *Z. protheroi* are those from the Hancock quarry in North America and Artyom in Russia. The Artyom mammal locality is in a coal mine north of Vladivostok in eastern Russia in strata termed the "Uglov svita" (literally, "coal formation") (Russell and Zhai 1987). Fossil mammals from this locality are undescribed carnivores (Tro-

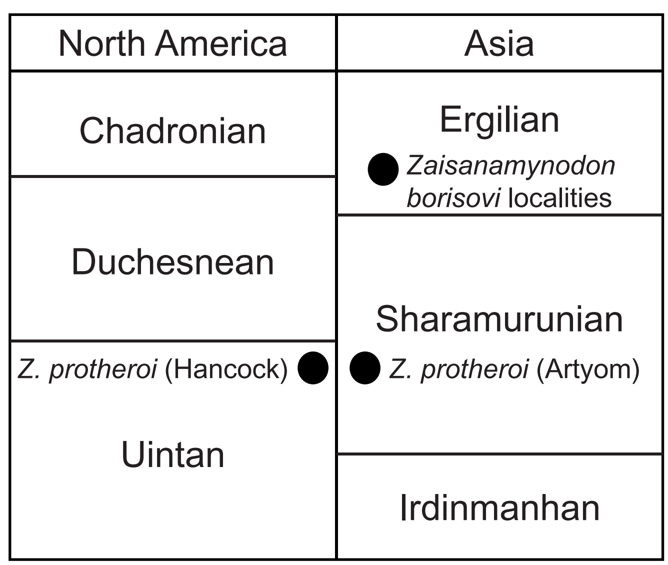

Figure 9. Correlation of North American and Asian middle-late Eocene land-mammal "ages" (after Holroyd and Ciochon 1994) showing temporal distribution of *Zaisanamynodon* localities.

fimov 1953), the brontothere *Rhinotitan orientalis* (Yanovskaya 1957), the rhinocerotoid *Teletaceras borissiaki* (Belyaeva 1959; Hanson 1989), and the amynodontid "*Procadurcodon orientalis*" (Gromova 1960), some specimens of which are here assigned to *Z. protheroi.* Russell and Zhai (1987, p. 233) regarded the Artyom locality as Sharamurunian in age, "based largely on the stage of evolution" of its few mammal taxa. Lucas et al. (2004) believed the locality might just as easily be assigned an Ergilian age.

Rhinotitan orientalis Yanovskaya 1957 is a *nomen dubium* because its type material is indistinguishable from *Parabrontops gobiensis*, *Embolotherium andrewsi*, or *Metatitan*. This means that its age can be Irdinmanhan, Sharamurunian, or Ergilian (Lucas et al. 2004).

Teletaceras has no other Asian occurrences, but the Artyom specimen (holotype of *Eotrigonias borissiaki*) has also been assigned to *Forstercooperia* and *Juxia*, hyracodontid taxa of Sharamurunian-Ergilian age (Belyaeva 1959; Belyaeva et al. 1974; Lucas et al. 1981; Lucas and Sobus 1989). Therefore, grade level of evolution suggests either a Sharamurunian or Ergilian age for *Teletaceras borissiaki.*

A Sharamurunian or Ergilian age for the Artyom locality seems certain, but deciding between the two ages has been difficult. Most workers (e.g., Li and Ting 1983; Dashzeveg 1993; Ducroq 1993; Holroyd and Ciochon 1994; Tong et al. 1995) correlate the Sharamurunian to parts of the North American Uintan-Duchesnean and the Ergilian to parts of the North American Duchesnean-Chadronian (Fig. 9). A late Uintan age for the Hancock quarry local fauna makes a Sharamurunian age for the Artyom locality seem most probable. The occurrence of *Z. protheroi* in Oregon and Russia is consistent with correlation of the late Uintan with part of the Sharamurunian (Fig. 9).

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