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Zaisanamynodon, a Late Eocene amynodontid (Mammalia, Perissodactyla) from Kazakhstan and China

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Abstract: Previously undescribed specimens of the amynodontid rhinoceros *Zaisanamynodon borisovi* Belyaeva, 1971 from the Late Eocene (Ergilian) of Nei Monggol, China augment knowledge of the morphology of this taxon and indicate an Ergilian age for its type locality in the Zaysan basin of northeastern Kazakhstan. Distinctive features of *Zaisanamynodon* among metamynodontinine amynodontids include a dental formula of 3-1-3-3/3-1-3-3, large I3, P4 with third (posterior) cross loph, short preorbital portion of the skull, large preorbital fossa, great constriction of the maxillaries across the preorbital fossae and lack of a glenoid shelf. *Gigantamynodon* Gromova, 1954 is a *nomen dubium*, and Chinese species referred to this genus -- *"G." promissus* and *"G." giganteus* -- are of uncertain generic assignment. *Zaisanamynodon* is of Late Eocene (Ergilian) age in Kazakhstan and northern China and may be an index taxon of the Ergilian.

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INTRODUCTION

Amynodontids are an extinct family of rhinoceroses known from the Middle Eocene-Early Miocene of Asia, the Oligocene of Europe and the Middle-Late Eocene of North America (Wall, 1982, 1989). One of the least known of the amynodontids is *Zaisanamynodon borisovi*, named by Belyaeva (1971) for a partial skeleton from the Zaysan basin of northeastern Kazakhstan (Text-fig. 1). Despite an extensive record of Asian amynodontids, especially in China and Mongolia, this remains the sole published report of *Zaisanamynodon*. Here, we document additional specimens of *Zaisanamynodon* from Nei Monggol (Inner Mongolia), China. These specimens add to morphological knowledge of the genus and further establish its taxonomic distinctiveness. They also aid in more precise correlation of the type locality and horizon of *Zaisanamynodon* in northeastern Kazakhstan. In this paper, AMNH refers to the Department of Vertebrate Palaeontology, American Museum of Natural History, New York; and ANPIN refers to the Palaeontological Institute of the Russian Academy of Sciences, Moscow.

Text-fig. 1. *Zaisanamynodon borisovi* localities in Asia.
1. - Zaysan basin, northeastern Kazakhstan. 2. - Nei Monggol, northern China.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order PERISSODACTYLA Owen, 1848

Suborder CERATOMORPHA Wood, 1937

Superfamily RHINOCEROTOIDEA Cope, 1879

Family AMYNODONTIDAE Scott & Osborn, 1883

Subfamily Amynodontinae Scott & Osborn, 1883

Tribe Metamynodontini Kretzoi, 1942

Genus *Zaisanamynodon* Belyaeva, 1971

1971 *Zaisanamynodon* Belyaeva, p. 43.
1989 *Zaisanamynodon* Belyaeva: Wall, p. 350.

Type and only known species: *Z. borisovi* Belyaeva, 1971.

Revised diagnosis: *Zaisanamynodon* is a large (LM1-3 = 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, a relatively shorter rostrum and 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 are not extremely large and curved tusks, an orbit relatively low on the skull, a relatively slender mandibular symphysis and a less massive zygomatic arch. *Zaisanamynodon* differs from *Megalamynodon* in 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: Late Eocene (Ergilian) of Kazakhstan and China.

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

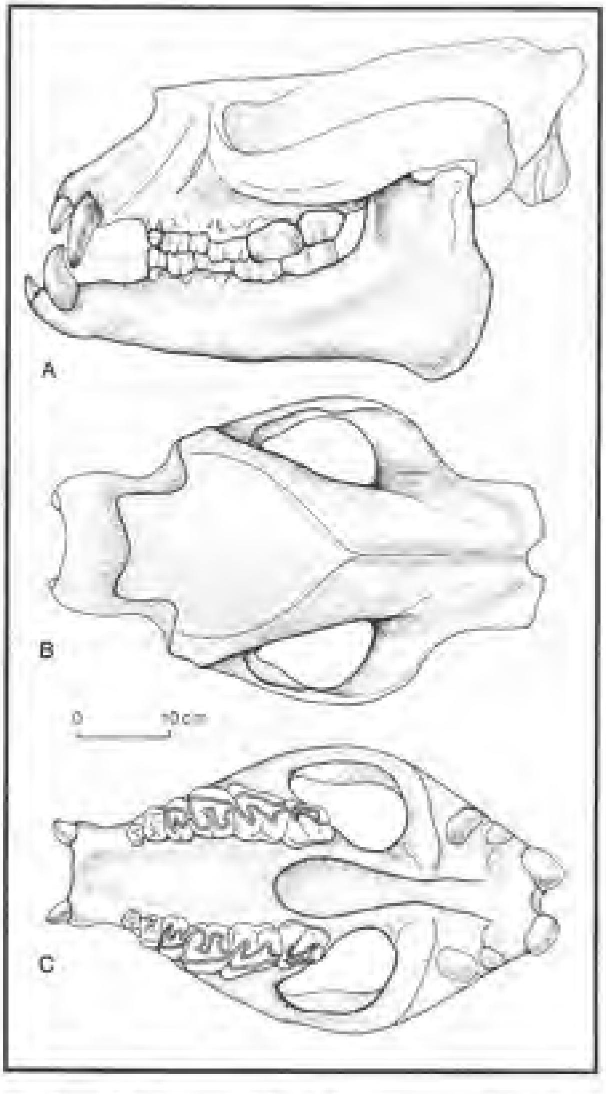
Zaisanamynodon borisovi Belyaeva, 1971

Text-figs 2-3, Pls 1-2, Table 1

1971 *Zaisanamynodon borisovi* Belyaeva, p. 43, figs. 2-11.
1989 *Zaisanamynodon borisovi* Belyaeva: Wall, p. 350.

Holotype: ANPIN 2761/1-22, incomplete skull, lower jaw and part of postcranial skeleton including most of the cervical vertebrae and forelimb (Belyaeva, 1971, figs 2-11).

Horizon and locality of holotype: Belyaeva (1971: 43) described the type locality of *Z. borisovi* as the lower subsvita of the Aksyir svita at Kiin Kerish Mountain. With the help of V. Chkhikvadze we relocated this site, which is on the southern limb of the Kiin Kerish anticline (Borisov, 1963; Russell & Zhai, 1987: fig. 180) north-west of Kiin Kerish Mountain at Universal Transverse Mercator 45312592E, 5333951N.



Text-figure 2. Restoration of the skull of *Zaisanamynodon borisovi*. A, Left lateral view of skull and lower jaw. B, Dorsal view of skull. C, Ventral view of skull

Referred specimens: From the Ulan Gochu Formation at Ulan Shireh Obo, Nei Monggol, China: AMNH 26034, skull with left C, P2-M2, M3 in crypt, right C, incomplete P2-M2, M3 in crypt (Plate 1).

From the Baron Sog Formation 4 miles (6.4 km) north of Baron Sog Lamasery, Nei Monggol, China: AMNH 21602, lower jaw with left i3, c, p2-m3 and right i3, c and p3-m3 (Plate 2, figs 2-4).

From the Ulan Gochu Formation at Urtyn Obo, East Mesa, Nei Monggol, China: AMNH 26049, lower jaw with right and left i2, left p3 and right p3-m3 (Plate 2, fig 1); 26052, left dentary fragment with m2-3.

From the Baron Sog Formation at Urtyn Obo, Nei Monggol, China: AMNH 26170, symphysis of lower jaw with left and right i2 and c.

From the Houldjin Formation at Camp Margetts, Nei Monggol, China: AMNH field number 840, right m2.

Description: Belyaeva (1971: 43-53, figs 2-12) provided a detailed description, illustrations and measurements of the holotype of *Z. borisovi*. We focus our description on the Chinese specimens, which provide information not available from the holotype on the structure of the skull, lower jaw and dentition of *Z. borisovi*.

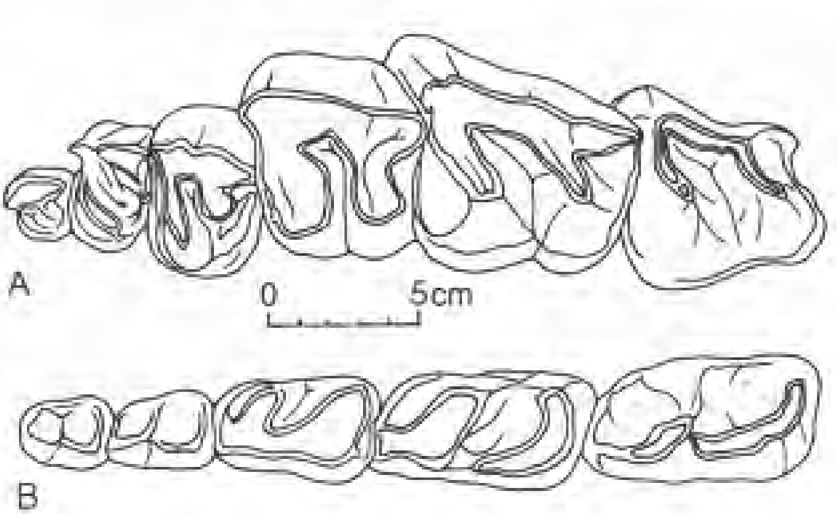
The skull of *Z. borisovi* is typically metamynodontinine in being moderately brachycephalic and having a large and massive zygomatic arch, a reduced preorbital portion of the skull , a frontal-maxilla contact and an orbit positioned relatively high on the skull. However, unlike other metamynodontinines, the preorbital fossa of *Z. borisovi* is so deep it constricts the rostrum so it is narrower than the braincase across the orbits. The posterior limit of the nasal incision of *Z. borisovi* is above the anterior end of the P4. The premaxilla strongly slopes antero-ventrally to root a large, slightly procumbent C. The deep preorbital fossa narrows the maxillaries. The external nares face anteriorly as a broad, box-like opening, and there is a large infraorbital foramen in the preorbital fossa that opens to face anteriorly.

The anterior margin of the orbit is above the anterior portion of the M1, and a blunt supraorbital ridge slightly overhangs the orbit. The skull roof is broadest across the frontals above the orbits and constricts sharply posteriorly at the anterior end of the braincase. The braincase is much narrower than the frontals and bears a low, blade-like sagittal crest dorsally. Comparison with the holotype of *Z. borisovi* indicates that the skull of AMNH 26034 has been slightly compressed dorso-ventrally. This has lowered the frontals and braincase and compressed the orbit dorso-ventrally, factors eliminated in our restoration (Text-fig. 2).

The zygomatic arch is massive, not strongly flexed dorsally nor broadly flared- out laterally. Its squamosal root is a tall plate of bone at a near right-angle to the sagittal plane of the skull. The lambdoidal crest is low, sharp and slopes slightly postero-dorsally. The occiput is slightly oblique and deeply recessed above the very large occipital condyles. The foramen magnum is a circular opening that faces directly posteriorly.

Viewed ventrally, the palate is broad and not arched. The large canines have thick maxillary roots and are followed, after a short diastema, by parallel upper cheek-tooth rows composed of the P1(2)-M3. The anterior edge of the internal nares is between the posterior portions of the M2s, and the internal narial opening is a broad fossa. The pterygoid flanges are low and rim this fossa posteriorly 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 orientated slightly oblique to the sagittal plane. The postglenoid process is long, thick, blunt-tipped and curved antero-ventrally. A deep short recess - the external auditory meatus - separates it from the mastoid-paroccipital process. The glenoid fossa is slightly above the plane of the cheek teeth in AMNH 26032, probably due to dorso-ventral compression of the skull; the type specimen of *Z. borisovi* (Belyaeva, 1971: fig. 2) indicates it was well above the plane of the cheek teeth (Text-fig. 2).

The lower jaw has a slightly flared anterior dental row bearing closely spaced alveoli for three incisors. The i1 alveoli face anteriorly, are dorso-ventrally ovoid and are between and ventral to the i2 alveoli. The i2 alveoli are the largest incisor alveoli and are round in cross section. The i3 alveoli are smaller than the i1 and i2 alveoli, round and are ventro-lateral to the i2 alveoli. The dentary bulges out at the massive roots of the canines and is slightly constricted at the symphysis. The thick symphysis is slightly concave dorsally and extends to under the posterior portion of the p3. The horizontal rami are shallow, but very thick medio-laterally. The ascending ramus is tall, and the coronoid process is much higher than the condyle. The ascending



Text-figure 3. Occlusal views of upper (A) and lower (B) cheek teeth of *Zaisanamynodon borisovi* ramus has a deep temporal fossa laterally and a thick, semicircular mandibular angle posteriorly. The dentaries diverge slightly posterior to the symphysis, but the lower cheek-tooth rows are essentially parallel.

The I1-2 are unknown, and the I3 is known only from the holotype. The I3 is large, with a crown that is slightly convex outward, slightly concave medially and with a rounded to triangular occlusal edge. The C is trihedral in cross section, pointed and much larger than the I3. The anterior edge of the C wore against the c in chisel-like fashion.

The P1 is a rounded tooth whose cusp morphology has been essentially obliterated by wear. It is present only in the left dental arcade of AMNH 26034, and probably is the vestigial DP1. The P2-4 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 any trace of a metacone and has a short metaloph and complete lingual cingulum. The P3 has a small metacone that forms a small rib on the ectoloph. The protoloph connects the protocone to the ectoloph at the parastyle. A short, transverse metaloph extends linguad from the ectoloph at the metacone but does not meet the protocone. The P3 has a complete lingual cingulum. The P4 is similar, but the metaloph is longer and is followed posteriorly by a third loph that extends linguad at the metastyle toward the postero-lingual cingulum.

The M1 is approximately as wide as long, with a very long, tall, nearly flat ectoloph and slightly oblique proto- and metalophs. There is a distinct antecrochet and a shelf-like pocket behind the metaloph. The parastyle forms a small but distinct anterior rib on the anterior end of the ectoloph.

The M2 is generally similar to the M1 but much larger and longer relative to its width. The M2 parastyle is much larger, the ectoloph is much longer and there is a more distinct cleft between parastyle and the anterior rib. There is no antecrochet. The M3 is in the crypt on AMNH 26034, but fully erupted on the holotype, ANPIN 2671/1 (Text-fig. 3). It is a trapezoidal tooth much smaller than the M2 and about the same size as the M1. The anterior rib is smaller than the paracone, and the ectoloph is concave labially, terminating posteriorly in a prominent metacone. The proto- and metalophs are oblique and slightly concave posteriorly. Like the M1-2, there is a shelf posterior to the metaloph. The upper cheek teeth are not as high crowned as in *Metamynodon* and *Cadurcotherium*.

The i2 is the only lower incisor known. Its crown is trihedral with a blunt occlusal edge. The anterior face is convex, and the two posterior faces are of equal size. The base of the crown has a discontinuous cingulid.

The c is also a trihedral, pointed tooth that flares out slightly and is recurved. The postcanine diastema is about 60 mm long on AMNH 21602.

The p2 is very worn but probably generally similar to the p3. It has a lingual cingulid and a larger paracristid than the p3. Viewed occlusally, the p2 is a long acute triangle pointed anteriorly.

The p3 has a larger talonid than trigonid. The large, tall protoconid dominates the trigonid and is preceded by a small paracristid. A prominent cristid obliqua connects the metalophid to a smaller hypolophid. There is a strong lingual cingulid on the trigonid and a weak, rugose labial cingulid.

The p4 is a molariform tooth with a talonid that is wider than the trigonid, though the p4 is much smaller than the m1. The p4 has a well-developed paracristid and hypolophid, a weak labial cingulid and lingual cingulids on the trigonid and talonid ectoflexids. The strong cristid obliqua connects the hypolophid to the metalophid.

The m1 shows the typical amynodontid pattern but with a prominent paracristid forming an anterior lobe. This tooth has a nearly continuous lingual cingulid and no cleft between the cristid obliqua and the metalophid.

The m2 and m3 are similar teeth to the m1, but they have better developed lingual cingulids. The cristid obliqua does not meet the metalophid on the m3, being separated from it by a distinct cleft.

Discussion: Wall (1980) made reference to some of the specimens from Nei Monggol we refer here to *Z. borisovi* when he mentioned the occurrence of *Zaisanamynodon?* in the Ulan Gochu and Houldjin Formations (also see Russell & Zhai, 1987: pp. 247, 250). The Chinese specimens so closely resemble the holotype in morphology and dental measurements (Table 1) that we feel no hesitation in assigning them to *Z. borisovi*. This increases the distribution of *Z. borisovi* from a single locality - the type locality in the Zaysan basin of northeastern Kazakhstan - across eastern Asia to northern China.

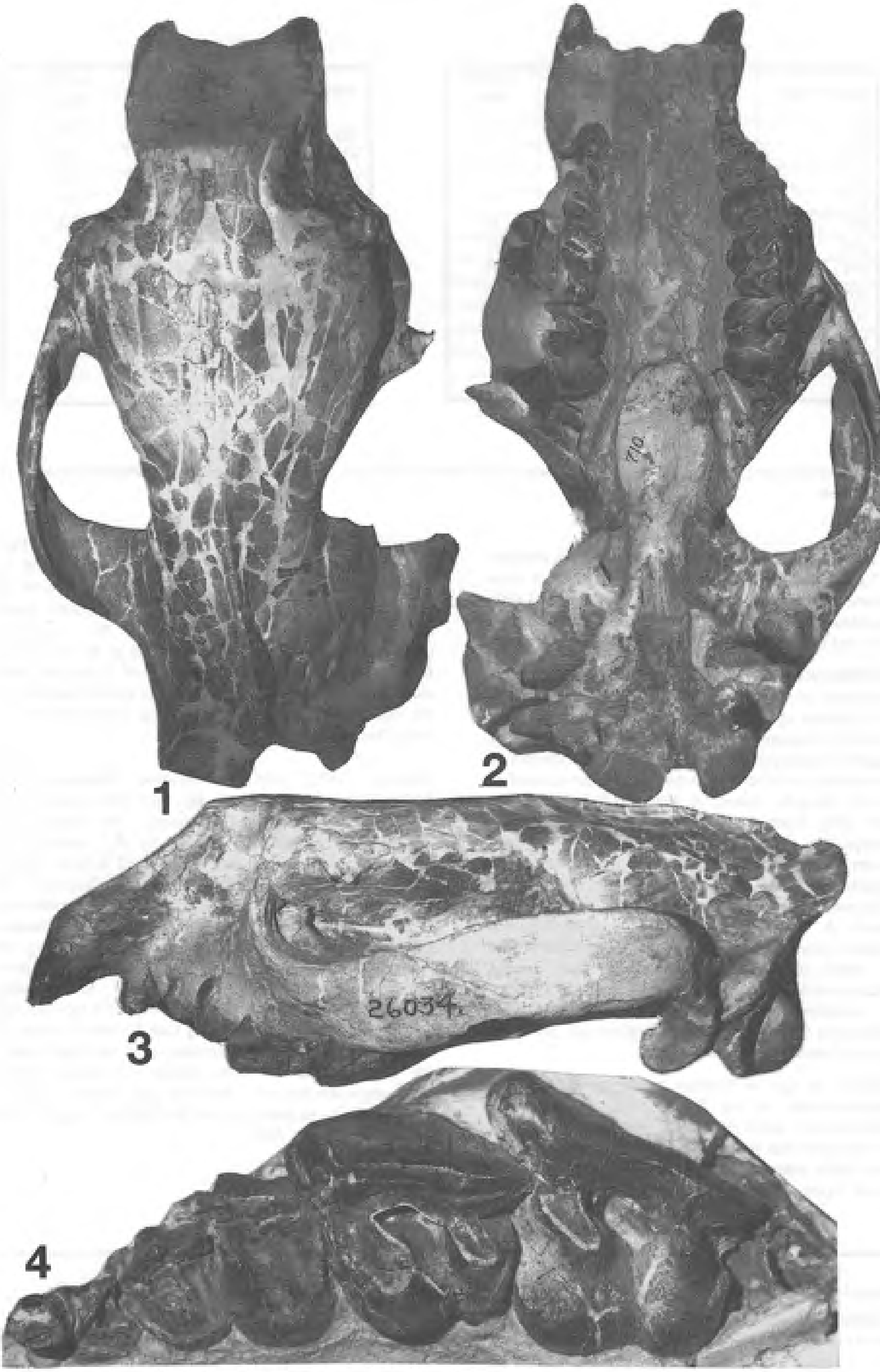
ZAYSANAMYNODON AND *GIGANTAMYNODON*

Gromova (1954: 161) coined the name *Gigantamynodon cessator*, new genus and species, for a left dentary fragment with m3 from the Ergilin-Dzo svita at Khoer-Dzan, Mongolia. We agree with Wall (1989) that *G. cessator* is a *nomen dubium* because its holotype is not sufficient to diagnose a taxon; it could pertain to any of several large amynodontid genera, including *Zaisanamynodon*. The Chinese species of "*Gigantamynodon*" named by Xu (1961, 1966) thus are of uncertain generic assignment.

"*Gigantamynodon*" *promissus* Xu, 1966, from the Sharamurun Formation of Nei Monggol, is much smaller than *Zaisanamynodon borisovi* and has the large, curved tusks characteristic of other genera, such as *Metamynodon*. It does not belong to *Zaisanamynodon*, but we are currently uncertain to which genus "*G.*" *promissus* should be referred. "*G.*" *giganteus* Xu, 1961, from the Ergilian Caijichong Formation of Yunnan, is about the same size and morphology as *Z. borisovi*. However, its holotype is a left dentary fragment with m1-3 and could represent any of

Plate 1. Skull of *Zaisanamynodon borisovi* from China, AMNH 26034.

1. Dorsal view, x 0.25. 2. Ventral view, x 0.25. 3. Left lateral view, x 0.25. 4. Occlusal view of left P1-M3, x 0.7.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measurement	ANPIN 2761/1	AMNH 21602	AMNH 26049
p2	---	19	---
p2w	---	10	---
p3l	27	21	24
p3w	23	18	19
p4l	36	31	34
p4w	27	21	21
m1l	52	46	46
m1w	33*	28	29
m2l	71*	68	59
m2w	42	41	33
m3l	69	62	60
m3w	38	32	31

measurement	ANPIN 2761/1	AMNH 26034
P2L	26	9*
P2W	29	22*
P3L	30	30*
P3W	39	37*
P4L	33	35
P4W	54	54
M1L	61	69
M1W	66	64
M2L	79	75
M2W	77	71
M	65	61*
M3W	74	--

Table 1. Measurements (in mm) of cheek teeth of specimens of *Zaisanamynodon borisovi*. Asterisks (*) indicate approximate measurements of damaged teeth.

the large amynodontid genera. We therefore consider *"G." giganteus* to also be a *nomen dubium*. Clearly more complete (especially cranial) material of large Asiatic amynodontids referred to *"Gigantamynodon"* needs to be discovered to appraise fully their taxonomic status.

BIOCHRONOLOGY

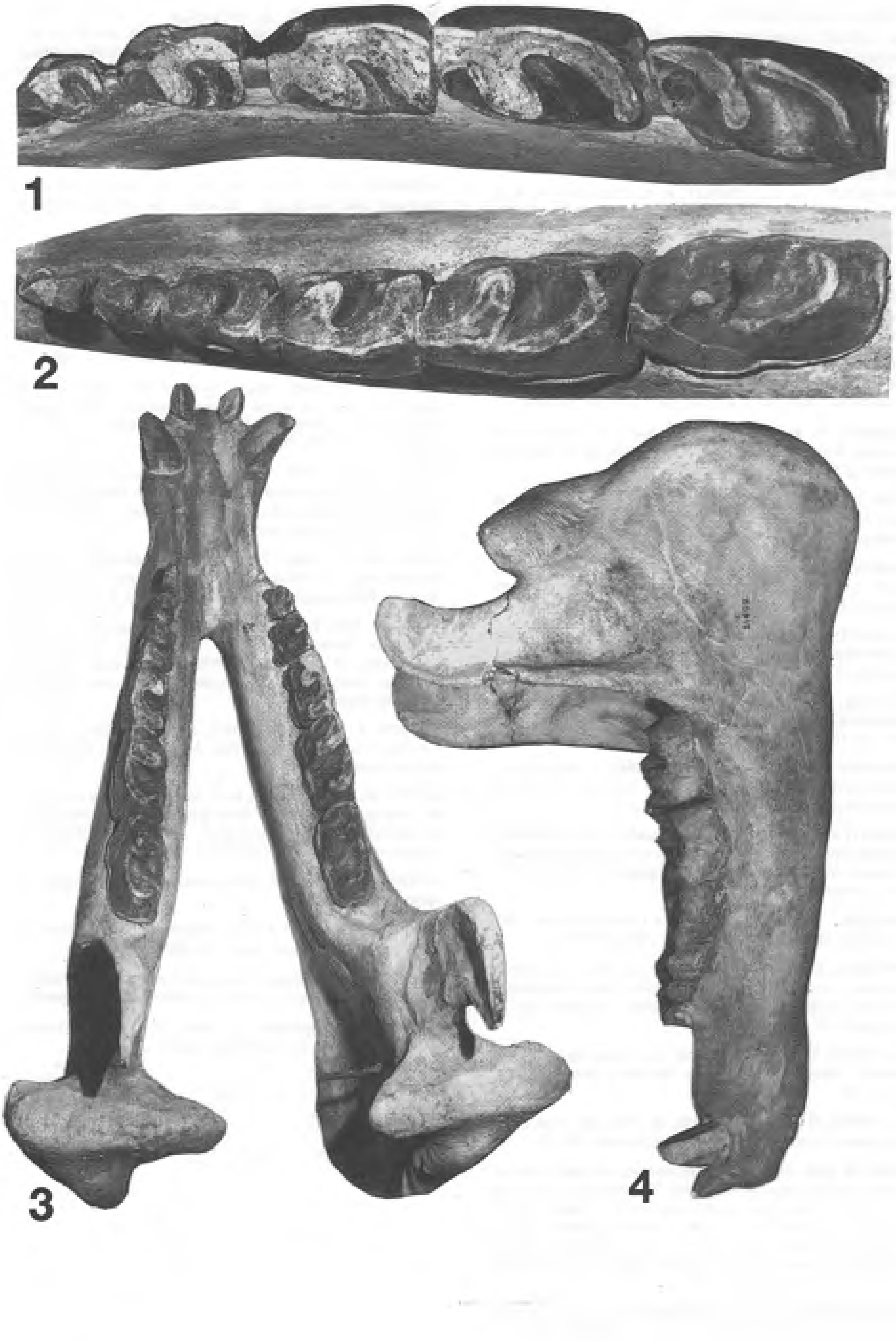
Occurrences of *Zaisanamynodon* in Nei Monggol, China are of Ergilian age. The Ulan Gochu Formation produces an extensive mammalian fauna of lagomorphs, rodents, an anagalid, a mesonychid and brontotheriid and amynodontid perissodactyls correlative with the Ergilin-Dzo mammalian fauna of Mongolia (Russell & Zhai, 1987: 249-250). The Baron Sog Formation, overlying the Ulan Gochu, produces the bronthotheriid *Embolotherium ultimum* Granger & Gregory, 1943 and the chalicothere *Schizotherium avitum* Matthew & Granger, 1923 as well as *Zaisanamynodon borisovi*, and is also of Ergilian age (Russell & Zhai, 1987: 248-249). The Houldjin Formation produces a composite mammalian fauna of taxa that range in age from Middle to Late Eocene (Irdinmanhan-Ergilian). It seems most reasonable to regard the *Zaisanamynodon* occurrence from the Houldjin Formation at Camp Margetts as of Ergilian age, given that its other Chinese records are Ergilian.

Assigning an age of Ergilian to the type locality of *Zaisanamynodon* in the Zaysan basin of northeastern Kazakhstan thus seems reasonable. Russell & Zhai (1987: 231) concluded that mammalian evidence of the age of the lower Aksyir subsvita in the Zaysan basin is "indecisive" because reported (but largely unsubstantiated) mammalian taxa are a mixture of Middle and Late Eocene forms. Part of this mixture results from including taxa found north of Lake Zaysan, such as *Z. borisovi*, with taxa found south of the lake, even though thickness and facies changes make exact correlation uncertain across the lake. We, therefore, apply an Ergilian age to the horizon north of the lake at the Kiin Kerish anticline where the holotype of *Z. borisovi* was collected. We are less certain that this age also applies to the strata termed lower Aksyir subsvita south and east of Lake Zaysan.

Belyaeva (1971) originally assigned *Zaisanamynodon borisovi* a "late(?) Eocene" age, and Akhmetiev *et al.* (1986) advanced the same correlation. We support this conclusion by assigning the type locality of *Z. borisovi* an Ergilian age. However, note that Russell & Zhai (1987) originally assigned the Ergilian to the Early Oligocene, an assignment followed by Wang (1992) and Dashzeveg (1993). Designation of a global stratotype for the Eocene-Oligocene boundary in marine strata (Premoli-Silva & Jenkins, 1993) and correlation of this boundary to non-marine strata in the western United States using magnetostratigraphy and Ar/Ar geochronometry indicates the Chadronian land-mammal "age" is Late Eocene (Prothero & Swisher, 1992). The Asian correlative of the Chadronian, the Ergilian, thus is Late Eocene (Ducrocq, 1993). *Zaisanamynodon borisovi* thus is of Late Eocene (Ergilian) age and may be an index taxon of the Ergilian across a wide geographical area of Asia.

Plate 2. Lower dentition and lower jaw of *Zaisanamynodon borisovi* from China.

1. AMNH 26049, occlusal view of right p3-m3, x 0.7. **2.** AMNH 21602, occlusal view of left p2-m3, x 0.7. **3.** AMNH 21602, occlusal view of lower jaw, x 0.25. **4.** AMNH 21602, left lateral view of lower jaw, x 0.25.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