

BIOCHRONOLOGICAL SIGNIFICANCE OF AMYNODONTIDAE (MAMMALIA, PERISSODACTYLA) FROM THE PALEOGENE OF KAZAKHSTAN

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ABSTRACT—Five taxa of amynodontid rhinoceroses have been named from Kazakhstan. We consider only two of these valid, and recognize three amynodontid taxa from Paleogene deposits in Kazakhstan: *Cadurcodon ardynensis* (= *Cadurcodon zaisanensis*; = *Amyndon tuskabakensis*) from the upper Eocene (Ergilian)–lower Oligocene (Shandgolian) of the Zaysan basin, *Zaisanamynodon borisovi*, from the Ergilian of the Zaysan basin and *Cadurcodon kazakademius*, from Shandgolian strata in the vicinity of the Chelkar-Teniz lake basin. *Gigantamynodon akespensis*, from the upper Oligocene north of the Aral Sea is a rhinocerotid, not an amynodontid. Close similarity of the amynodontids of Kazakhstan to those of Mongolia and China supports direct correlation of Ergilian and Shandgolian strata across Asia.

INTRODUCTION

AMYNODONTIDS WERE middle Eocene–early Miocene rhinocerotoids known from Asia, North America and Europe. Typically considered to have been amphibious, they actually represent a range of body plans from subcursorial and terrestrial to graviportal and amphibious (Wall, 1982, 1989).

In eastern Asia (China and Mongolia), amynodontids first appeared during the middle Eocene (Irdinmanhan land-mammal “age” [lma] of Russell and Zhai, 1987) and persisted until the end of the Oligocene (Tabenbulukian lma). The latest known amynodontids are two specimens of the derived, hypsodont genus *Cadurcotherium* from the lower Miocene Bugti Formation of Pakistan (Pilgrim, 1912; Raza and Meyer, 1984). The westernmost Asian occurrences of amynodontids are in Kazakhstan (Figure 1), where five amynodontid taxa have been named. Here, we review their taxonomic status and discuss their biochronological significance. AMNH refers to the Department of Vertebrate Paleontology, American Museum of Natural History, New York; KAN to the Institute of Zoology, Academy of Sciences of the Republic of Kazakhstan, Almaty; and PIN to the Paleontological Institute of the Russian Academy of Sciences, Moscow.

AMYNODONT TAXONOMY

Amynodontids are not common in the Paleogene strata of Kazakhstan, and virtually all published specimens are the holotypes of species. Here, we review the taxonomic status of these specimens.

Cadurcodon kazakademius Biryukov, 1961.—Biryukov (1961) named *Cadurcodon kazakademius* for KAN 663-160/54-T, a lower jaw with right P_3 – M_3 and left M_3 ; the tusks and left P_3 – M_2 have been restored in plaster (Figure 2.3–2.5). This fossil is from the Myneske-Suyek locality in central Kazakhstan east of the salt lake Chelkar-Teniz (approximately lat. 48°40'N, long. 66°E) (Figure 1). Biryukov (1961) identified the stratigraphic unit here as Kutambulak svita, but Lavrov (1959; Lavrov and Bazhanov, 1948) referred to it as the indricothere svita (Russell and Zhai, 1987; Kordikova, 1994). A svita is a Soviet stratigraphic term that refers to a lithostratigraphic unit with supposed isochronous boundaries.

The holotype of *C. kazakademius* has a lower dental formula of 1–1–2–3, cheek teeth that are not very high crowned, little or no labial groove between the lower cheek tooth trigonids and

talonids and a long lower jaw that suggests a dolicocephalic skull. In these features it closely resembles *Cadurcodon ardynensis* (Figure 2.1, 2.2; Osborn, 1924, figure 1; Gromova, 1954, figures 2–5), but *C. kazakademius* is 20–30 percent larger in virtually all dental measurements (Table 1). We thus consider *C. kazakademius* a valid, large species of *Cadurcodon*.

Cadurcodon zaisanensis Belyaeva, 1962.—Belyaeva (1962) named *Cadurcodon zaisanensis* for PIN 1979, a left dentary fragment with P_4 – M_3 (Belyaeva, 1962, figure 1). This specimen is from the Buran svita (Borisov, 1963) at Kalmakpay Mountain southeast of Lake Zaysan at UTM 5257260N, 380050E, zone 45 (Figure 1). It clearly belongs to *Cadurcodon*: note especially the lack of labial folds between the trigonids and talonids and the apparent presence of only two premolars. Indeed, the holotype of *C. zaisanensis* is indistinguishable from specimens of *C. ardynensis* except for the length of the M_3 , which is about 20 percent longer than the largest specimens of *C. ardynensis* reported by Gromova (1954, table 10) and 30 percent longer than the largest AMNH specimens (Table 1). We are hesitant to recognize a distinct species of *Cadurcodon* solely on the basis of one unusually long M_3 , so we regard *C. zaisanensis* as a junior subjective synonym of *C. ardynensis*.

Cadurcodon ardynensis.—In the Kiin Kerish anticline on the north shore of Lake Zaysan at the locality known as “pantsernyy sloy” (“turtle plain”) in the Kusto svita (UTM 5334660E, 311667N, zone 45), we collected canines and a left P_4 (KAN 35-18-50: Figure 3.6–3.7) of *Cadurcodon ardynensis*. With a length of 32 mm and width of 16 mm, this specimen is well within the range of measurements of the species, though its slightly oblique metalophid is unusual for *C. ardynensis*.

Amyndon tuskabakensis Biryukov, 1963.—Biryukov (1963, p. 34) named *Amyndon tuskabakensis* for a right M^3 (he called it a left M^2), KAN Z-K-57-260/1419 (Figure 3.1). He also referred a left M^3 (Figure 3.3) and three canines, one of which is illustrated here (Figure 3.4, 3.5), to the taxon. These specimens are from the Kusto svita in the Kiin Kerish anticline near the locality where we collected *Cadurcodon ardynensis* (see above), but no more exact record of Biryukov’s locality is available.

Belyaeva (1971) referred *Amyndon tuskabakensis* to Gromova’s (1954) genus *Hypsamynodon* as *H. tuskabakensis*. Wall (1982), however, suggested that *Hypsamynodon* is a junior subjective synonym of *Cadurcotherium*. Thus, Russell and Zhai (1987) referred to Biryukov’s (1963) taxon as *Cadurcotherium tuskabakensis*.



FIGURE 1—Aminodontid localities in Kazakhstan discussed in the text. 1, Kalmakpay. 2, Kiin Kerish. 3, Kur-Say. 4, Myneske-Suyek. 5, Akespe.

The holotype M^3 of *A. tuskabakensis* is not particularly high crowned, its parastyle and anterior rib are not confluent and it has a large (not reduced) metastyle, quite different from *Cadurcotherium* (= *Hypsamynodon*) (see Roman and Joleaud, 1908, plate 1, figures 1, 7, 9A; Gromova, 1954, figure 10a). Size of the tooth (M^3 length—51 mm, M^3 width—43 mm) is within the range for *C. ardynensis* reported by Gromova (1954, table 9). Indeed, the holotype of *A. tuskabakensis* closely resembles AMNH 19154, the holotype of *Cadurcodon ardynensis* (Figure 3.2), in its very long ectoloph, antecrochet, the anteriorly inclined cross lophs and size (AMNH 19154, length—49 mm, width—44 mm). Therefore, we consider *Aminodon tuskabakensis* to be a junior subjective synonym of *Cadurcodon ardynensis*. The other M^3 referred by Biryukov, KAN Z-K-57 260/1419, belongs to a rhinocerotid, not an aminodontid (compare Brunet, 1979, plates 13, 14). Two of the canines, including the one illustrated here (Figure 3.4, 3.5), belong to a brontotheriid, not an aminodontid (compare Osborn, 1929, plates 67, 68, 101–103). The other canine, KAN Z-K-57 233/1418, illustrated by Biryukov (1963, figure 3a) but not seen by us, is of an aminodontid, and cannot be distinguished from the canine of *C. ardynensis*.

Cadurcodon cf. *C. kazakademius*—Belyaeva (1970, figure 1) reported a single, well worn right M_2 , PIN 478–393, from the Chiliky svita at Kur-Say gulley near the Chelkar-Teniz salt lake (Figure 1). She identified the specimen as “*Cadurcodon* (?)”. Its size (length M_2 = 61 mm, width = 33 mm) and lack of a labial groove between the trigonid and the talonid indicate close resemblance to *Cadurcodon kazakademius* (Table 1). Furthermore, the Kur-Say molar is much larger than *Cadurcodon ardynensis*. We therefore identify the Kur-Say tooth as *Cadurcodon* cf. *C. kazakademius*.

Zaisanamynodon borisovi Belyaeva, 1971.—Belyaeva (1971) named *Zaisanamynodon borisovi* for PIN 2761/1–22, a skull, lower jaw and partial skeleton (Belyaeva, 1971, figures 2–11)

from the lower Aksyir svita in the Kiin Kerish anticline north of Lake Zaysan at UTM 45312592E, 5333951N. Lucas et al. (in press) redescribe the holotype as well as referred specimens of *Z. borisovi* from Ergilian strata in Inner Mongolia, China.

This allows us to rediagnose *Zaisanamynodon* as a distinct genus of metamynodontine (*sensu* Wall, 1989) aminodontid as follows: *Zaisanamynodon* is a large (LM^{1-3} = 205 mm) metamynodontine aminodontid (*sensu* Wall, 1989) distinguished from all other members of the tribe by its third loph on P^4 . *Zaisanamynodon* is much larger than *Paramynodon*, has a more posteriorly positioned orbit, a relatively shorter rostrum, 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 I^3 , a relatively small infraorbital foramen, three lower incisors, canines that 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 *Megalaminodon* in lacking a glenoid shelf and having a short preorbital portion of the skull and three lower incisors. *Zaisanamynodon* is distinguished from *Cadurcotherium* in that the latter has only two upper incisors and one lower incisor, very hypsodont cheek teeth, very narrow lower molars, anterior ribs and parastyles confluent on the upper molars and a reduced M^3 metastyle. *Z. borisovi* is known in Kazakhstan only from its holotype.

Gromova (1954, p. 161) coined the name *Gigantamynodon cessator*, new genus and species, for a left dentary fragment with M_3 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 aminodontid 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 Caijiachong Formation of Yunnan, is about the same size and morphology as *Z. borisovi*. However, its holotype is a left dentary fragment with M_{1-3} and could represent any of several large aminodontid genera. Therefore, we consider “*G.*” *giganteus* to also be a *nomen dubium*.

Gigantamynodon akespensis Bayshashov, 1993.—Bayshashov (1993) based the new species *Gigantamynodon akespensis* on KAN PK 11/6, a left dentary fragment with a damaged M_3 (Figure 3.8, 3.9). The specimen is from the lower part of the Aral Formation near Akespe (Agyspe) on the northern shore of the Aral Sea at UTM 41315113E, 5186634N (Figure 1). This locality is 3.4 m above the base of the Aral Formation and at approximately the same stratigraphic level as the *Paraceratherium* quarry of Oriov (1939), which is to the southeast at UTM 41316737E, 5185226N. Mammals associated with the holotype of *Gigantamynodon akespensis* are tragulids and *Aprotodon* sp. The mammalian fauna of the Aral Formation is either latest Oligocene (Russell and Zhai, 1987) or earliest Miocene (Akhmetiev and Sychevskaya, 1994).

Bayshashov (1993) identified KAN PK 11/6 as an aminodontid close in morphology to the holotype of *Gigantamynodon cessator* (Gromova, 1954, p. 162, figure 22). The holotype M_3 (length = 46 mm, width = 31 mm) of *G. akespensis* is a bilophodont tooth without labial or lingual cingulids. Depth of the horizontal ramus below the M_3 is approximately 74 mm. The

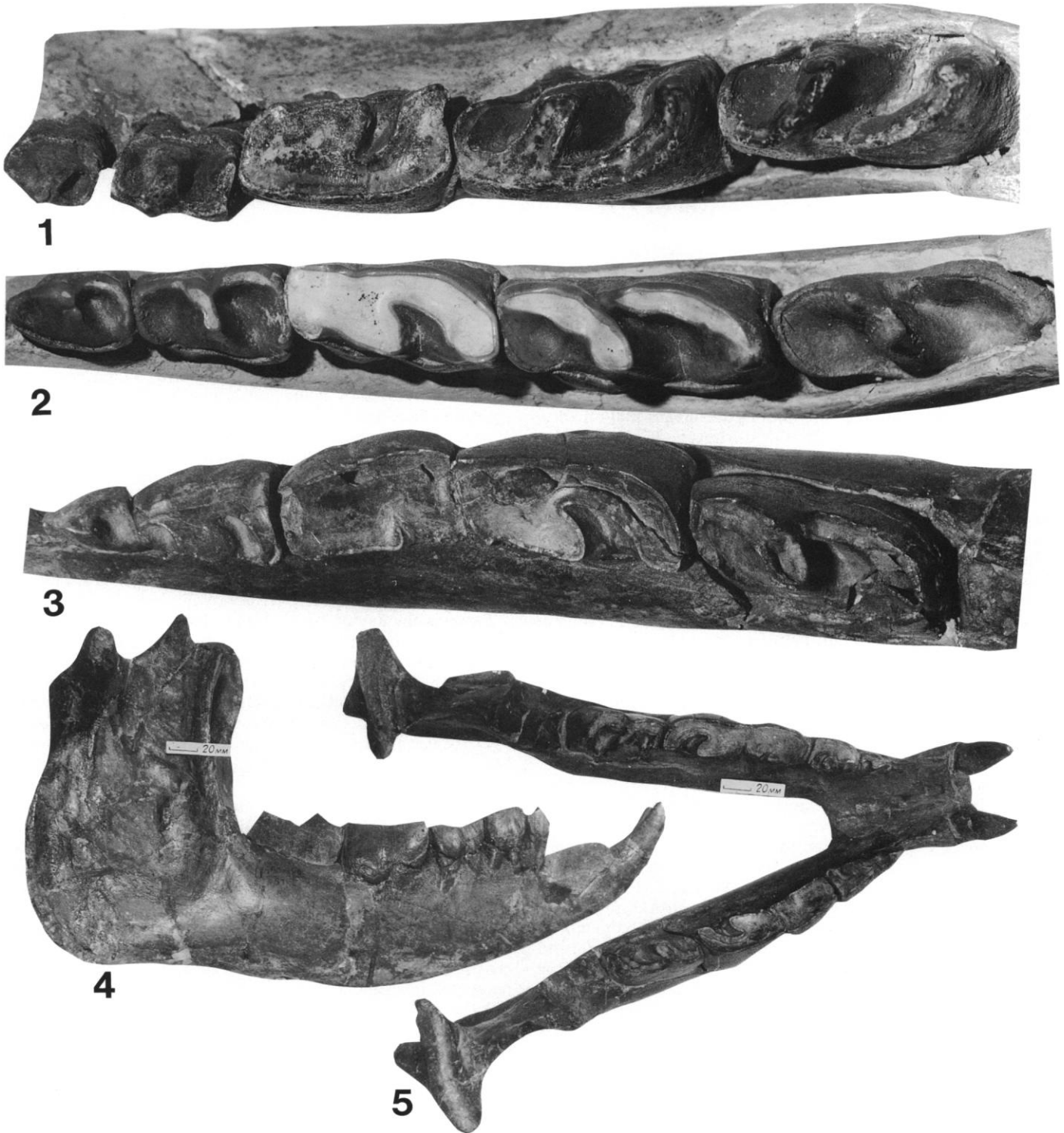


FIGURE 2—*Cadurcodon ardynensis* from Inner Mongolia, China and *Cadurcodon kazakademius* from Kazakhstan. 1, AMNH 204421, paratype of *C. ardynensis*, occlusal view of left P_3 – M_3 , $\times 1$. 2, AMNH 26054, *C. ardynensis*, occlusal view of right P_3 – M_3 , $\times 1$. 3–5, KAN 663–160/54–T, holotype of *Cadurcodon kazakademius*. 3, occlusal view of right P_3 – M_3 , $\times 0.75$. 4, right lateral view of lower jaw, $\times 0.25$. 5, occlusal view of lower jaw, $\times 0.25$.

M_3 has a short ectoflexid, and its metalophid is transverse and wears transversely, indicating that the specimen is not an amyndodontid, rather it is a rhinocerotid such as *Aceratherium* or *Protaceratherium* (Belyaeva, 1960, p. 108).

BIOCHRONOLOGY

Reevaluation of the taxonomy of amyndodontids from Kazakhstan is of biochronological significance because it helps to

TABLE 1—Measurements (in mm) of lower dentitions of *Cadurcodon*.

	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
<i>Cadurcodon ardynense</i> :										
AMNH 20441(a)			21	18	37	20	42	22	45	21
AMNH 26135	15	12	22	16	33	18	42	19	43	20
AMNH 26054	19	15	28	19	33	22	45	22	47	21
AMNH 26055	21	15	26	17	39	20	49	20		
PIN1979(b)			28	18	38	24	48	29	65	
<i>Cadurcodon kazakademius</i> :										
KAN 663-160/54-T(c)	27	18	38	28	47	30	63	33	68	34

(a) holotype

(b) holotype of *Cadurcodon zaisanensis*; measurements from Belyaeva (1962)

(c) holotype

clarify the age relationships of amynodontid-bearing strata in Kazakhstan (Figure 4). These are Paleogene deposits in the Zaysan basin and Turgay depression. Removal of "*Gigantamynodon*" *akespensis* from the Amynodontidae means that no amynodontids are known from the Oligo-Miocene of the Aral Sea region of western Kazakhstan.

Two amynodontid taxa, *Zaisanamynodon borisovi* and *Cadurcodon ardynensis* are known from the Zaysan basin of northeastern Kazakhstan. *Zaisanamynodon* occurrences in the Ulan Gochu, Baron Sog and Houldjin Formations of Nei Monggol, China are of Ergilian age. The Ulan Gochu Formation contains an extensive mammalian fauna of lagomorphs, rodents, an anagalid, a mesonychid and brontotheriid and amynodontid perissodactyls correlative with the Ergilin-Dzo mammal fauna of Mongolia (Russell and Zhai, 1987, p. 249–250). The overlying Baron Sog Formation contains the brontotheriid *Embolotherium ultimum* and the chalicothere *Schizotherium avitum* as well as *Zaisanamynodon borisovi* and is also of Ergilian age (Russell and Zhai, 1987, p. 248–249). The Houldjin Formation contains 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 and Zhai (1987, p. 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 if this age also applies to the strata termed lower Aksyir subsvita south of Lake Zaysan.

Belyaeva (1971) originally assigned *Zaisanamynodon borisovi* a "late(?) Eocene" age, as did Akhmetiev et al. (1986). We support this conclusion by assigning the type locality of *Z. bor-*

isovi an Ergilian age. However, note that Russell and 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 and Jenkins, 1993) and correlation of this boundary to nonmarine strata in the western United States using magnetostratigraphy and Ar/Ar geochronometry indicates the Chadronian land-mammal "age" is late Eocene (Prothero and 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 geographic area of Asia.

Strata in the Zaysan basin that produce fossils of *Cadurcodon ardynensis*—the Kusto svita and overlying Buran svita—are younger than the type locality of *Zaisanamynodon borisovi*. Fossil mammals indicate the Kusto svita is of Ergilian age and that the Ergilian-Shandgolian boundary lies within the Buran Svita (Russell and Zhai, 1987; Emry et al., 1995). *Cadurcodon ardynensis* has an Ergilian-Shandgolian distribution in China and Mongolia consistent with its Ergilian-Shandgolian distribution in the Zaysan basin (Figure 4).

The mammalian fauna from the indricothere svita near Lake Chelkar-Teniz associated with the holotype of *Cadurcodon kazakademius* consists of tsaganomyid (*Cyclomytus turgaicus*), cylirodontid (*Ardynomys kazachstanicus*) and castorid (*Agnotocastor aubekerovi*) rodents; a hyaenodontid creodont (*Hyaenodon dubius*); a chalicothere (*Schizotherium turgaicum*); a he-laletid (*Colodon orientalis*); an indricothere (*Paracatherium transouralicum*); another hyracodontid (*Ardynia kazachstanicus*); a rhinocerotid (*Eggysodon turgaicus*); an entelodont (*Entelodon major*); and an indeterminate tragulid (Russell and Zhai, 1987, p. 338). The fauna is Shandgolian (early Oligocene) in age (Russell and Zhai, 1987). A very similar but much more diverse mammalian fauna from the nearby Chilikty svita is associated with the single molar we identify as *Cadurcodon* cf. *C. kazakademius*. Records of *Cadurcodon kazakademius* in the Chelkar-Teniz region thus appear to be of Shandgolian age. Amynodontids from Kazakhstan thus support correlation of the Ergilian and Shandgolian lmas from eastern China and Mongolia across Asia.

FIGURE 3—Perissodactyls from Kazakhstan and Inner Mongolia, China. 1, KAN Z-K-57 260/1419, holotype of *Amynodon tuskabakensis*, occlusal view of right M³, ×1. 2, AMNH 19154, holotype of *Cadurcodon ardynensis*, occlusal view of right M²⁻³, ×1. 3, KAN Z-K-57 260/1419, rhinocerotid, occlusal view of left M³, ×1. 4–5, KAN Z-K-57 238/264, brontotheriid, internal (4) and external (5) views of canine, ×0.7. 6–7, KAN 35–18–50, *Cadurcodon ardynensis*, occlusal (6) and lingual (7) views of left P₄, ×1.5. 8–9, KAN PK 11/6, holotype of *Gigantamynodon akespensis*, lingual (8) and occlusal (9) views of left dentary fragment with M₃, ×0.75 (8) and ×0.9 (9).



1



2



3



4



5



8



6



7



9

TAXA	AGE					
		Irdinmanhan	Sharamuruniian	Ergilian	Shandgolian	Tabenbulukian
<i>Amynodon</i>						
<i>Cadurcodon</i>						
<i>Cadurcotherium</i>						
<i>Caenolophus</i>						
" <i>Gigantamynodon</i> "						
<i>Lushiamynodon</i>						
<i>Paramynodon</i>						
<i>Procadurcodon</i>						
<i>Rostriamynodon</i>						
<i>Sharamynodon</i>						
<i>Sianodon</i>						
<i>Teilhardia</i>						
<i>Zaisanamynodon</i>						

FIGURE 4—Temporal ranges of amynodontid taxa in Asia (from data in Russell and Zhai, 1987).

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