PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
114(2):517–525. 2001.

Sharamynodon (Mammalia: Perissodactyla) from the Eocene of the Ily basin, Kazakstan and the antiquity of Asian amynodonts

Spencer G. Lucas and Robert J. Emry

(SGL) New Mexico Museum of Natural History, 1801 Mountain Road N. W., Albuquerque, New Mexico 87104, U.S.A.;
(RJE) Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0121, U.S.A.

Abstract.—The brontothere bone bed at Kyzyl Murun near Aktau Mountain in the Ily basin of eastern Kazakstan is a 0.5-m-thick layer of green bentonitic mudstone in the Kyzylbulak Formation that yields numerous skeletons of the middle Eocene (Irdinmanhan) brontothere *Protitan.* An incomplete skull, lower jaw and some fragmentary postcrania from this bed belong to an amynodontid rhinoceros. This specimen can be assigned to *Sharamynodon mongoliensis* (Osborn) because it displays numerous diagnostic features of that taxon, including three closely spaced incisors, a short nasal incision that extends back to the postcanine diastema, a deep and tall preorbital fossa, and a relatively short preorbital portion of the skull. This is the first record of *Sharamynodon* from Kazakstan and the oldest Kazak amynodontid. Previous reports of this taxon indicate it had a broad geographic (China, Mongolia, Japan) and temporal (Irdinmanhan-Ergilian, i.e., middle-latest Eocene) distribution in Asia. There is no evidence that any Asian amynodont record is older than Irdinmanhan. Thus, we consider the record of "*Andarakodon*" from Andarak, Kyrgyzstan to be Irdinmanhan, not older. Indeed, "*Andarakodon*" is a junior subjective synonym of *Sharamynodon.*

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 (Japan, Korea, China and Mongolia), amynodontids first appeared during the middle Eocene (Irdinmanhan land-mammal "age" [lma] of Russell & Zhai 1987) and persisted until the end of the Oligocene (Tabenbulukian lma). The latest known Asian amynodontids are two specimens of the derived, hypsodont genus *Cadurcotherium* from the lower Miocene Bugti Formation of Pakistan (Pilgrim 1912, Raza & Meyer 1984). The westernmost Asian occurrences of amynodontids are in Kazakstan (Fig. 1), where five amynodontid taxa have been named (Lucas & Emry 1996, Lucas et al. 1996). Here, we add to this record the occurrence of *Sharamynodon mongoliensis* in Irdinmanhan-age strata of the Ily basin (Fig. 1). We also re-evaluate the taxonomy and age of the supposedly oldest Asian amnyodont records from Kyrgyzstan to reaffirm that Amynodontidae first appear in Asia during the Irdinmanhan.

Abbreviations used.—When used in dental notations, upper case letters denote upper (skull) teeth and lower case letters denote lower (dentary) teeth. Institutional abbreviations are: AMNH – Department of Vertebrate Paleontology, American Museum of Natural History, New York; KAN – Institute of Zoology, Academy of Sciences of the Republic of Kazakstan, Almaty.

Fig. 1. Map of Kazakstan showing location of the *Sharamynodon* locality at Aktau Mountain.

Systematic Paleontology

Family Amynodontidae Scott & Osborn, 1883

Genus *Sharamynodon* Kretzoi, 1942

Sharamynodon mongoliensis (Osborn, 1936)

Figs. 2–3

Referred specimen.—KAN-N2/872, incomplete skull, lower jaw frargments and teeth isolated from these elements. Most of the right side of the skull is preserved, but the specimen is laterally crushed. The right P2-M3 are present, and M3 is not fully erupted. The left P3 is present, as are the right upper canine and right I1. The lower right canine, right i1-2, right p2-3 and symphysis are preserved, as are fragments of the postcrania, most notably the scapular glenoid.

Locality and horizon.—Brontothere bonebed at Kyzyl Murun, near Aktau Mountain, Ily basin, eastern Kazakstan (Fig. 1). The bonebed, at UTM 44361142E, 4872826N, is a 0.5-m-thick green bentonitic mudstone of the Kyzulbulak Formation (= unit 26 of Lucas et al. 1997, fig. 3).

Description.—The skull (Fig. 2) has an approximate maximum length of 430 mm and is very similar to AMNH 20278, the holotype skull of *Sharamynodon mongoliensis* (Osborn, 1936, fig. 3). Among its diagnostic characteristics are a relatively short preorbital region of the skull, a short nasal incision that extends to above the postcanine diastema, a weak ascending process of the premaxilla, a deep and tall preorbital fossa, a small postorbital process, presence of three closely spaced incisors, relatively small canines and a long postcanine diastemata.

The upper canine (Fig. 3A) is characteristically amynodontid in being laterally compressed and having a triangular crown in lateral view because of the prominent wear facet on its anterior face for the corresponding lower canine. Crown length = 18.4 mm.

The I1 (Fig. 3B–C) has a tall, blade-like crown with a pointed tip. The crown is convex anterior, less convex posterior and has a low, lingual cingulum that extends up the crown surface. Crown width = 12.8 mm.

The P2 (Fig. 3L) has a triangular crown dominated by a tall, thick ectoloph that peaks at the paracone. Lingually, a ridge begins at the protocone and extends anterolabially. Lingual to this ridge is a low cingulum that connects to the anterior and posterior edges of the ectoloph, thus enclosing the trigon basin. A small loph projects lingually from the ectoloph posterior to the paracone. P2 length = 19.1 mm, w = 19.8 mm.

The P3 (Fig. 3K) is much more molariform than the P2. It has a nearly square occlusal outline. A tall ectoloph dominates the crown, and it has four distinct ribs that project labially—a small parastyle anteriorly, a very large paracone, a smaller metacone and a very small metastyle posteriorly. The protoloph is a thick crest confluent with the ectoloph. A low cingulum extends from the parastyle lingually then posteriorly and labially to close the trigon basin. It is broken by two cristae—one on the anterior edge of the protoloph near the parastyle, the other directly lingual to the protoloph. As on the P2, a small cristid projects lingually into the trigon basin from the ectoloph at the metacone. P3 length = 23.1 mm, width = 27.3 mm. The P4 (Fig. 3J) is very similar to but larger and relatively wider (more transverse) than the P3. P4 length = 26.5 mm, width = 36.4 mm.

The M1 (Fig. 3M) is incomplete—much of its anterior half is missing. It is a square tooth with a large ectoloph and two prominent lophs (protoloph and metaloph) essentially perpendicular to the ectoloph. A cingulum circles the anterior, lingual and posterior edges of the crown but is discontinuous just lingual to the metaloph and paraloph. M1 width is about 43.6 mm.

The M2-3 have been plastically deformed, mostly in the labial-lingual direction. Distortion of the M2 (Fig. 3P–Q) has pushed the two lophs together antero-posteriorly. The ectoloph is very large, long and slightly concave labially. Anteriorly, there is a prominent parastyle followed immediately by an equal-sized paracone rib. There is no trace of a metacone, and there is a nearly complete lingual cingulum. M2 length = 56.2 mm, width = 49.4 mm (but note that distortion has altered the tooth shape significantly).

The M3 (Fig. 3N–O) is extremely deformed so that the ectoloph has been "squeezed" over the protoloph and metaloph. This tooth has a long, concave-labial ectoloph with a large paracone closely appressed to a slightly smaller parastyle. A prominent metacone terminates the ectoloph posteriorly. Like M2, the M3 has tall, transverse metaloph and protoloph and a nearly complete lingual cingulum. M3 length = 60.5 mm, width = 43.1 mm (but note that distortion has altered the tooth shape significantly).

The i1 (Fig. 3D–E) has a nearly round crown that peaks at a central cuspid. A ridge divides the lingual face of the crown

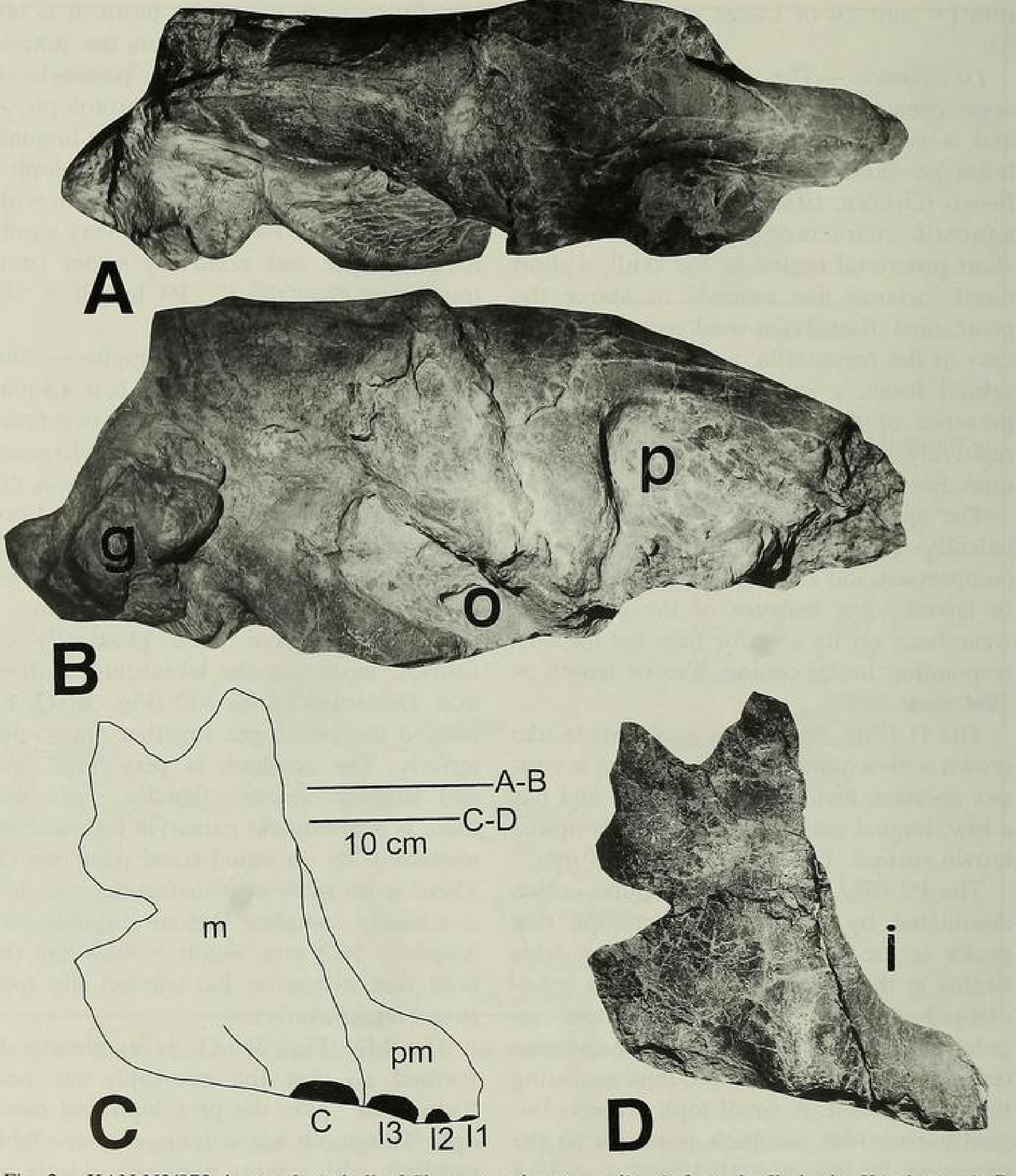

Fig. 2. KAN-N2/872, incomplete skull of *Sharamynodon mongoliensis* from the Ily basin, Kazakstan. A–B, Incomplete skull, dorsal (A) and right lateral (B) views. C–D, lateral views of premaxilla-maxilla. Abbreviations are: g - glenoid process, i - nasal incision, m - maxilla, o - orbit, p - preorbital fossa, pm - premaxilla.

into two "pockets," and the labial face is convex with a basal cingulid. Width of i1 = 12.8 mm.

The i2 (Fig. 3F–G) is similar to the i1 but larger. It also differs from i1 in not having such a distinct ridge on the lingual face of the crown. Width of i2 = 14.7 mm.

The p2 is a nearly rectangular tooth with a tall protoconid and prominent lingual cingulid. A cristid oblique connects the protoconid to the posterior end of the tooth. The p2 length = 14.7 mm, width = 10.2 mm.

The p3 (Fig. 3H–I) is very similar to the

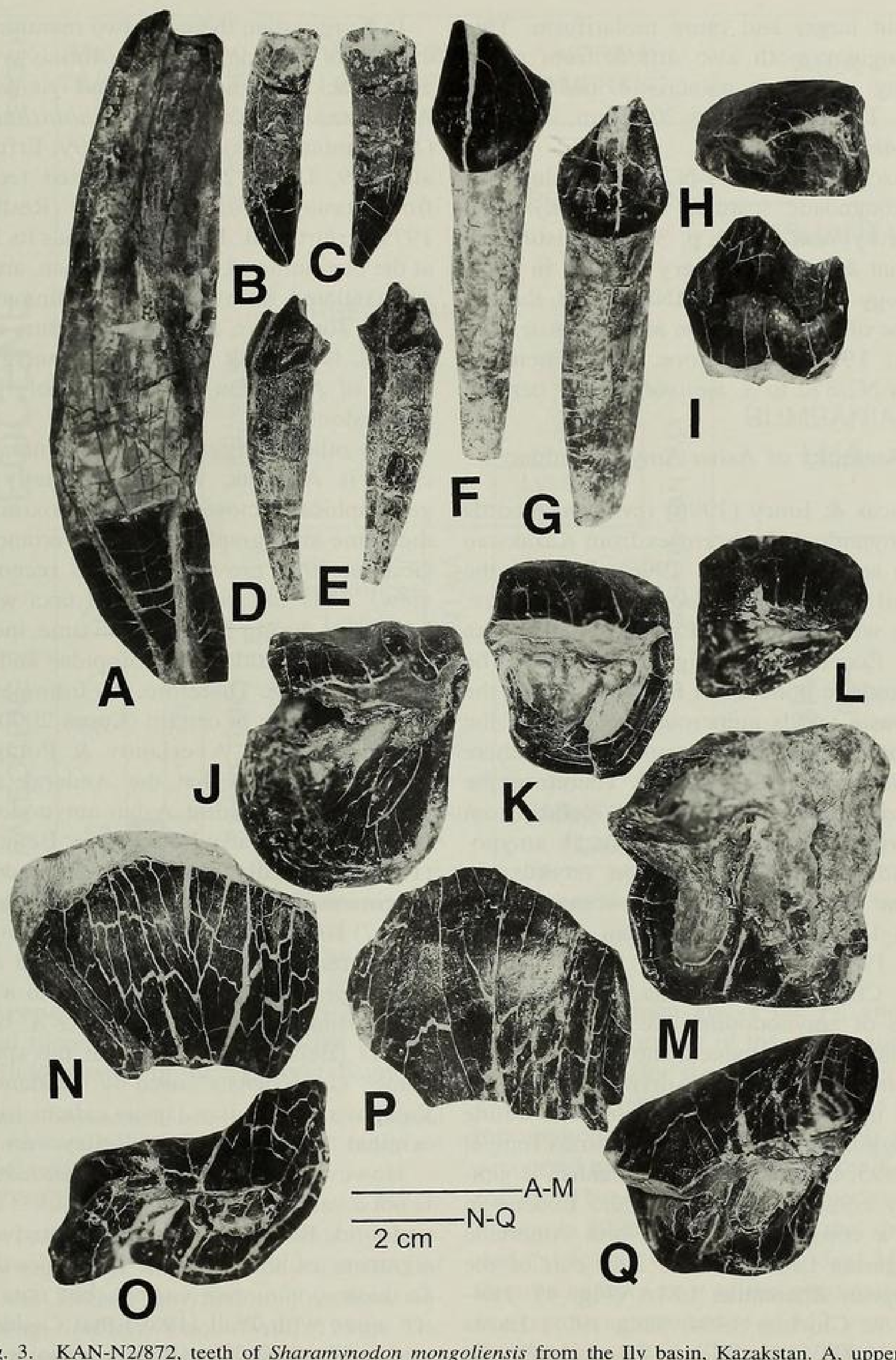

Fig. 3. KAN-N2/872, teeth of *Sharamynodon mongoliensis* from the Ily basin, Kazakstan. A, upper right canine, medial view. B–C, right I1, in medial (B) and lateral (C) views. D–E, right i1, in medial (D) and lateral (E) views. F–G, right i2, in lingual (F) and labial (G) views. H–I right p3, in occlusal (H) and lingual (I) views. J, right P4, occlusal view. K, right P3, occlusal view. L, right P2, occlusal view. M, right M1, occlusal view. N–O, right M3, in buccal (N) and occlusal (O) views. P–Q, right M2, in boccal (P) and occlusal (Q) views.

p2 but larger and more molariform. This rectangular tooth also differs from p2 in having a distinct paracristid and hypolophid. The p3 length = 20.6 mm, width = 13.7 mm.

Discussion.—KAN-N2/872 displays all the diagnostic features of *Sharamynodon* listed by Wall (1989, p. 346) as distinctive of that taxon. It is very similar in morphology and size to AMNH 20278, the holotype of *Sharamynodon mongoliensis* (Osborn, 1936). Therefore, assignment of KAN-N2/872 to *S. mongoliensis* is certain.

Antiquity of Asian Amynodontidae

Lucas & Emry (1996) reviewed records of amynodont rhinoceroses from Kazakstan (also see Lucas et al. 1996). Prior to the record of *Sharamynodon* documented here, these were records in Ergilian-Shandgolian (late Eocene-early Oligocene) strata. The brontothere bonebed at Kyzyl-Murun in the Ily basin yields numerous skeletons of the characteristically Irdinmanhan brontothere *Protitan* (Emry et al. 1997). Therefore, the *Sharamynodon mongoliensis* record from Kyzyl Murun is the oldest Kazak amynodontid. Other *Sharamynodon* records—in China, Mongolia and Japan—range in age from Irdinmanhan to Ergilian (Russell & Zhai 1987).

In China and Mongolia, the oldest records of amynodontids are in strata of Irdinmanhan age; indeed, the FAD (first appearance datum) of Amynodontidae has been used as one of the criteria to define the beginning of Irdinmanhan time (Tong et al. 1995; Lucas 2000). Irdinmanhan is generally considered to be middle Eocene in age, a correlative of the North American Bridgerian LMA and the later part of the European Rhenanian LMA (Fig. 4) (Holroyd & Ciochon 1994, Ting 1998, Lucas 1998, 2000). Localities in China, Mongolia and Kazakstan of the immediately older time interval, the Arshantan LMA, conspicuously lack amynodontids (Tong et al. 1995; Lucas 2000).

In Kyrgyzstan, there are two mammal localities of Eocene age. The Toruaygyr locality lacks amynodontids and yields the Arshantan index fossil *Gobiatherium* (Agadjanian & Kondrashov 1999, Erfurt et al. 1999, Lucas 2000). Supposed records from Toruaygyr of *Teleolophus* (Reshetov 1979, Erfurt et al. 1999), which has its FAD at the beginning of the Irdinmanhan, are unsubstantiated, so assigning an Irdinmanhan age to Toruaygyr, as done by Erfurt et al. (1999), is difficult to accept. Toruaygyr is older, of Arshantan age, and notably lacks amynodontids.

The other Kyrgyz Eocene mammal locality is Andarak, which is actually two geographically close sites at approximately the same stratigraphic level (Averianov & Godinot 1998 provide the most recent review). This site yields several taxa whose FAD's are during Irdinmanhan time, including Amynodontidae, Eomoropidae and Anthracotheriidae. Therefore, the Irdinmanhan age of Andarak is certain (Lucas 2000).

Nevertheless, Averianov & Potapova (1996) concluded that the Andarak amynodontid is the oldest Asian amynodontid, assigning it an early Eocene age. Beliayeva (1971) originally described amynodontid specimens from Andarak as *Lushiamynodon* (?) *kirghisensis.* Averianov & Potapova (1996) redescribed this material, and additional specimens, assigning them to a new genus, *Andarakodon,* type species *A. kirghisensis* (Beliayeva). (Note that the species name "*kirghisiensis*" used by Averianov & Potapova (1996) is a lapsus calami for the original "*kirghisensis*" of Beliayeva.)

However, we conclude that *Andarakodon* is not a valid genus, nor is it the oldest amynodontid. Beliayeva's original tentative assignment of the Andarak amynodontid to *Lushiamynodon* was correct, but note that we agree with Wall (1989) that *Lushiamynodon* Chow & Xu, 1965 is a junior subjective synonym of *Sharamynodon* Kretzoi, 1942. Therefore, we identify the Andarak amynodontid as *Sharamynodon kirghisensis* (Beliayeva, 1971).

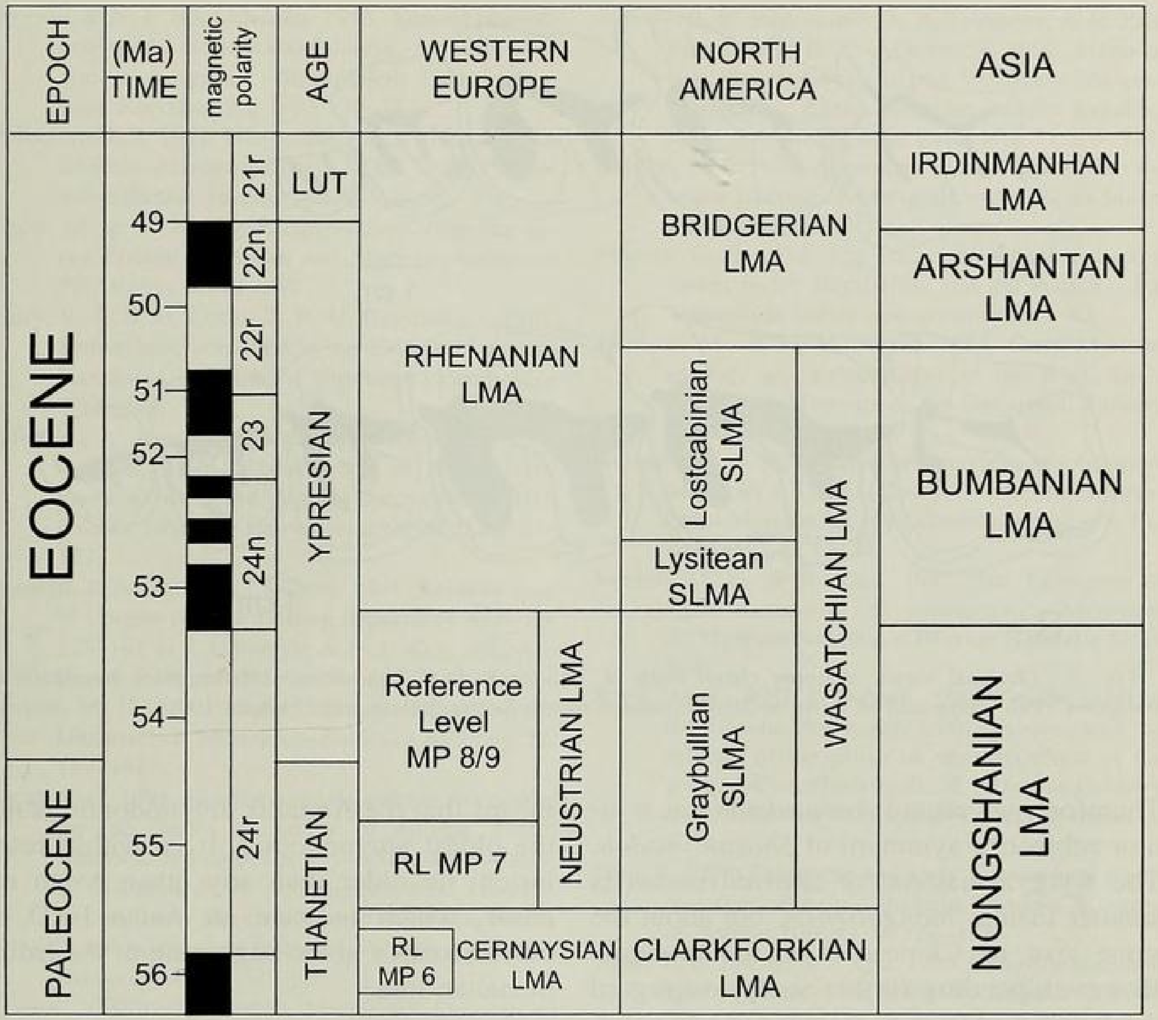

Fig. 4. Correlation of European, North American and Asian lmas across the Paleocene/Eocene boundary (modified from Lucas 1998).

Averianov & Potapova (1996, p. 1062) listed three supposedly distinctive features of *Andarakodon* in their generic diagnosis:

> Small amynodontid with relatively low-crowned cheek teeth; upper molar with nearly complete and well marked lingual cingulum.
> Infraorbital foramen placed over P4.

However, small size and relatively low-crowned cheek teeth are characteristic of several Eocene amynodontid genera, including *Sharamynodon* (Wall 1989). The upper molars of *Sharamynodon* have well developed, nearly complete lingual cingula (Fig. 3; Osborn 1936, fig. 4; Chow & Xu 1965, pl. 1, fig. 1; Xu 1966, pl. 4, fig. 1). And, the claim that *Andarakodon* has an infraorbital foramen above the P4 and also that the anterior root of the zygomatic arch is above M1 (for these reasons Averianov & Potapova 1996 assigned the genus to the metamynodontini sensu Wall 1989) is not supported by the photographs of the Kyrgyz fossils. These illustrations (Averianov & Potapova 1996, fig. 1) indicate that the preorbital fossa extends back to over M1 and that the anterior root of the zygomatic arch is over the anterior edge of M2, exactly as in *Sharamynodon* (Osborn 1936, fig. 3). The upper premolar and molar morphology of "*Andarakodon*" (Beliayeva 1971, fig. 1; Averianov & Potapova 1996, fig. 1) also is identical to that of *Sharamynodon* (Fig. 5).

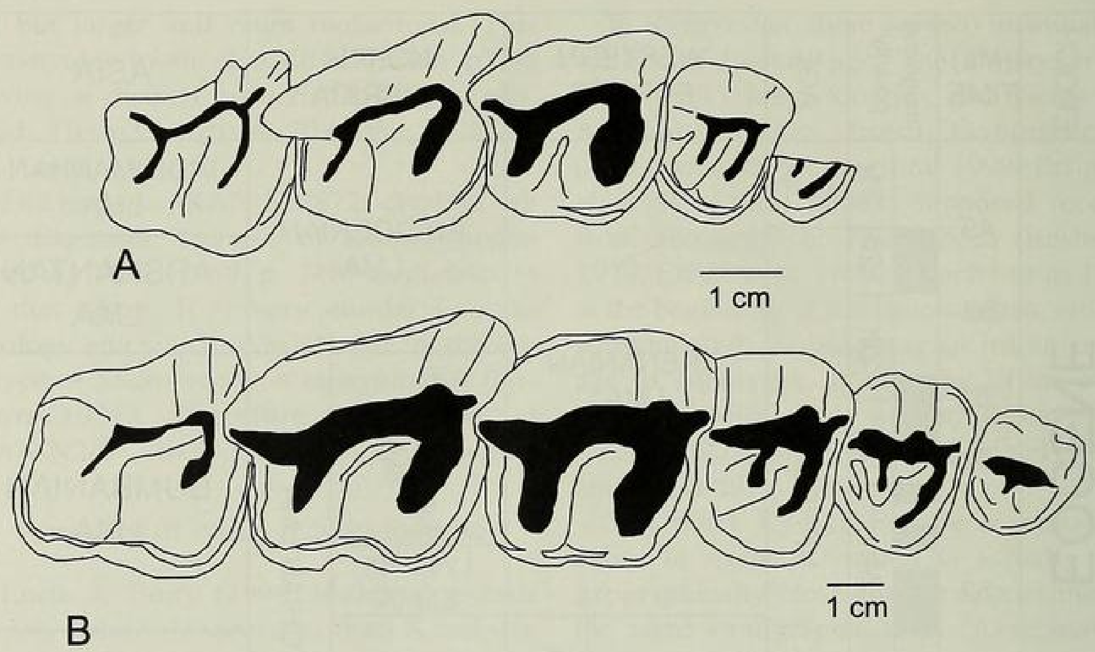

Fig. 5. Occlusal views of upper cheek teeth of "*Andarakodon*" *kirghisensis* (above, after Averianov & Potapova 1996) compared to those of *Sharamynodon mongoliensis* (below, after Osborn 1936).

Therefore, we regard *Andarakodon* as a junior subjective synonym of *Sharamynodon.* The Kyrgyz material of *Sharamynodon* is smaller than *S. mongoliensis,* but about the same size as Chinese *S. meichiapuensis.* However, pending further study, we regard the Kyrgyz species *S. kirghisensis* as valid.

Averianov & Udovichenko (1993) argued that the Andarak localities are of early Eocene (late Ypresian) age. They based this on selachian taxa from the marginal marine Andarak localities that have an upper Ypresian (nannoplankton zone NP 12) stratigraphic range in Western Europe. However, whether or not these stratigraphic ranges can be directly applied to correlation in Middle Asia is open to question.

If an Ypresian age is accepted for Andarak this suggests that at least part of Irdinmanhan time is Ypresian. This is possible, but unlikely given mammal-based correlation of the Irdinmanhan to the North American Bridgerian (Fig. 4). Nevertheless, despite any uncertainty about the marine cross-correlation of the Irdinmanhan lma, there is no evidence that Andarak is older than any other Irdinmanhan locality. This means that the Andarak amynodontid is not the oldest amynodontid. It is, within resolution, no older than any other Asian records, which indicate an Asian FAD of amynodontids at the beginning of the Irdinmanahan lma.

Acknowledgments

The National Geographic Society and the Charles D. Walcott Fund of the Smithsonian Institution supported this research. We thank W. Wall and an anonymous reviewer for their helpful remarks.

Literature Cited

Agadjanian, A. K. & P. E. Kondrashov. 1999. *Gobiatherium* (Dinocerata, Mammalia) from Kyrgyzstan: morphology and taxonomic position.—Paleontological Journal 33:308–320.

Averianov, A., & M. Godinot. 1998. A report on the Eocene Andarak fauna of Kyrgyzstan.—Bulletin of Carnegie Museum of Natural History 34: 210–219.

———, & O. Potapova. 1996. The oldest known amynodontid (Perissodactyla, Ceratomorpha), from the early Eocene of Kyrgyzstan.—Compte Rendus Academie Science Paris Série IIA 323: 1059–1065.

———, & N. I. Udovichenko. 1993. Vozrast pozvonochynykh mestonakhozhdeniya Andarak (yuzhnaya Fergana).—Stratigrafiya Geologicheskaya Korrelyatsiya 1993:139–141.

Beliayeva, E. I. 1971. Novye dannye po aminodontam SSSR.—Akademiya Nauk SSSR Trudy Paleontologicheskiy Institut 130:39–61.

Chow, M., & Y. Xu. 1965. Amynodonts from the upper Eocene of Honan and Shansi.—Vertebrata PalAsiatica 9:190–203.

Emry, R. J., S. G. Lucas, & B. U. Bayshashov. 1997. Brontothere bone bed in the Eocene of eastern Kazakstan.—Journal of Vertebrate Paleontology 17(3):44A.

Erfurt, J., A. Averianov, J. Buchantschenko & A. B. Fortuna. 1999. Rediscovery of the Eocene mammal site Toru Ajgyr (Kyrgyzstan).—Hallesches Jahrbuch Geowissenschaften B21:107–127.

Holroyd, P. A., & R. L. Ciochon. 1994. Relative ages of Eocene primate-bearing deposits of Asia. Pp. 123–141 *in* J. F. Fleagle & R. F. Kay, eds., Anthropoid origins. Plenum Press, 323 pp.

Kretzoi, M. 1942. Auslandische Saugetierfossilien der Ungarischen Museum.—Foldtony Kozlony 72: 139–148.

Lucas, S. G. 1998. Fossil mammals and the Paleocene/Eocene Series boundary in Europe, North America, and Asia. Pp. 451–500 *in* M-P. Aubry, S. G. Lucas, & W. A. Berggren, eds., Late Paleocene-early Eocene climatic and biotic events in the marine and terrestrial records. Columbia University Press, 513 pp.

———. 2000. *Gobiatherium* (Mammalia: Dinocerata) from the middle Eocene of Asia: Taxonomy and biochronological significance.—Paläontologische Zeitschrift, in press.

———, & R. J. Emry. 1996. Biochronological significance of Amynodontidae (Mammalia, Perissodactyla) from the Paleogene of Kazakhstan.—Journal of Paleontology 70:691–696.

———, ———, & B. U. Bayshashov. 1996. *Zaisanamynodon,* a late Eocene amynodontid (Mammalia, Perssodactyla) from Kazakhstan and China.—Tertiary Research 17:51–58.

———, B. U. Bayshashov, L. A. Tyutkova, A. K. Zhamangara, & B. Z. Aubekerov. 1997. Mammalian biochronology of the Paleogene-Neogene boundary at Aktau Mountain, eastern Kazakhstan.—Paläontologische Zeitschrift 71:305–314.

Osborn, H. F. 1936. *Amynodon mongoliensis* from the upper Eocene of Mongolia.—American Museum Novitates 859:1–9.

Pilgrim, G. E. 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab.—Paleontologia Indica new series, 4(2):1–83.

Raza, S. M., & G. E. Meyer. 1984. Early Miocene geology and paleontology of the Bugti Hills, Pakistan.—Memoirs of the Geological Survery of Pakistan 11:43–63.

Reshetov, V. J. 1979. Rannetretichnyie tapiroobrazniye Mongolii i SSSR.—Trudy Sovmestnaya Sovyetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya 11:1–144.

Russell, D. E., & R. Zhai. 1987. The Paleogene of Asia: mammals and stratigraphy.—Memoires du Museum National d'Histoire Naturelle 52:1–488.

Scott, W. B., & H. F. Osborn. 1883. On the skull of the Eocene rhinoceros *Orthocynodon,* and the relation of the genus to other members of the group.—Contributions E. M. Museum Geology and Archeology Princeton College Bulletin 3: 1–22.

Ting, S. 1998. Paleocene and early Eocene land mammal ages of Asia.—Bulletin Carnegie Museum of Natural History 34:124–147.

Tong, Y., S. Zheng, & Z. Qiu. 1995. Cenozoic mammal ages of China.—Vertebrata PalAsiatica 33:290–314.

Wall, W. P. 1982. Evolution and biogeography of the Amynodontidae (Perissodactyla, Rhinocerotoidea).—Third North American Paleontological Convention Proceedings 2:563–567.

———. 1989. The phylogenetic history and adaptive radiation of the Amynodontidae. Pp. 341–354 *in* D. R. Prothero & R. M. Schoch, eds., The evolution of perissodactyls. Oxford University Press, 537 pp.

Xu, Y. 1966. Amynodonts of Inner Mongolia.—Vertebrata PalAsiatica 10:123–190.