A New Hyracodontid (Perissodactyla, Rhinocerotoidea) from the Ergilin Dzo Formation (Oligocene, Quarry 1) in Dzamyn Ude, Eastern Gobi Desert, Mongolia[1]

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ABSTRACT

A new hyracodontid, *Prohyracodon obrutschewi,* n. sp., is described on the basis of an incomplete juvenile skull from early Oligocene deposits at the Dzamyn Ude Locality in Mongolia. The problem of the classification of the Rhinocerotoidea is briefly discussed in light of the new material from Mongolia.

INTRODUCTION

Despite the widespread presence of Paleogene deposits in the vicinity of the Dzamyn Ude railway station, Mongolia, naturally occurring outcrops are restricted to only a few places. The author attempted to collect fossils from these outcrops in 1990, but was unsuccessful.

In August of 1990, during the construction of a basement for steam-heat pipes at the railway station, a molar belonging to a large *Embolotherium* was discovered, along with several unidentified mammalian fossil fragments (Dashzeveg and Mader, in prep.). The fossils were found at a depth of 3.0 m in yellow gravel. The genus *Embolotherium* is well documented from the Oligocene of Mongolia and China (Osborn, 1929; Dashzeveg, 1975).

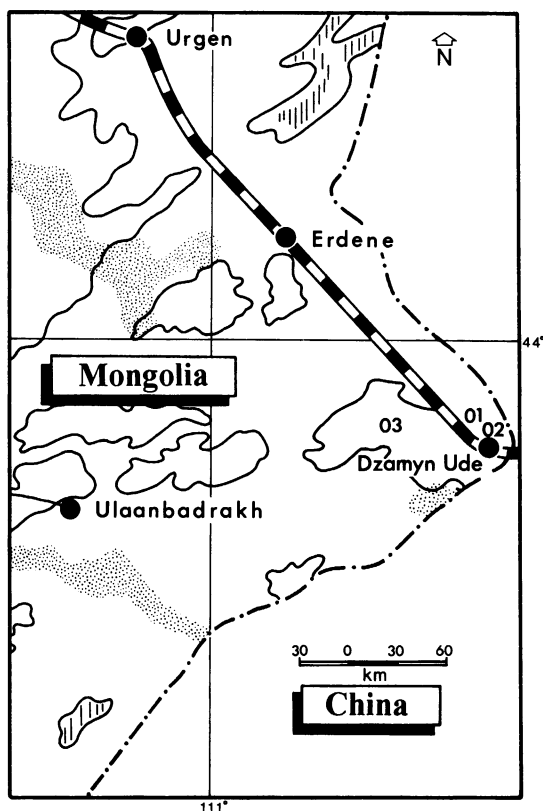In September of 1992, a field team led by the author and sponsored by the Mongolian–

Fig. 1. Map of lower Oligocene mammalian fossil localities in the Dzamyn Ude region of Mongolia. 01 Quarry 1; 02 Quarry 2; 03 Khoer Dzan.
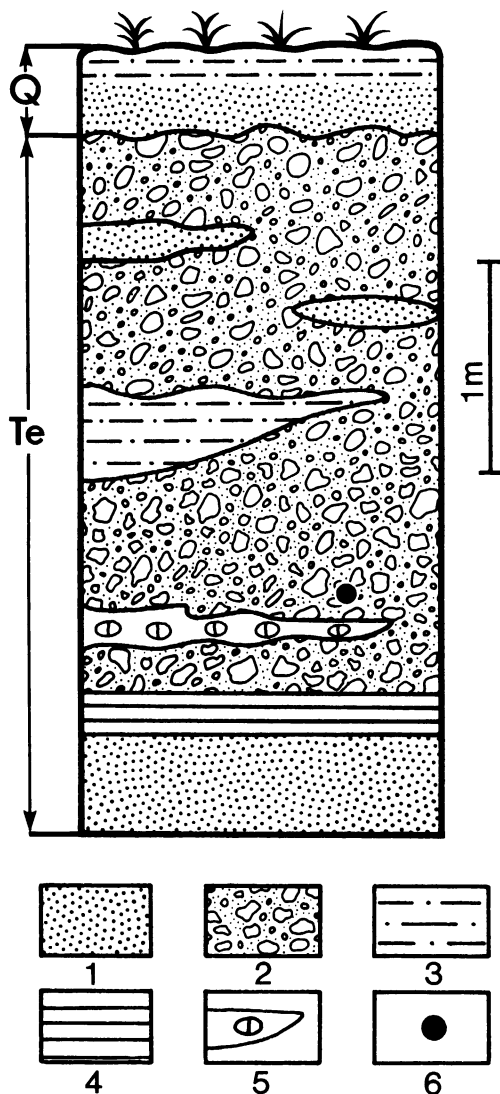

Fig. 2. Stratigraphic section of the lower Oligocene deposits (Quarry 1) in Dzamyn Ude containing the remains of *Prohyracodon obrutschewi*. Q Quaternary deposits: surface soil dark-gray, yellow sandy layer below; Te Ergilin Dzo Formation; Ergilin Member: 1 sands; 2 gravels and sands; 3 mudstone; 4 clay; 5 carbonate concretions; 6 fossil remains.

American Paleontological Expedition rediscovered two old quarries in the Dzamyn Ude area, which yielded fossil remains (fig. 1). In the early 1950s, the rocks from these quarries had been used as gravel fill for the railway station at Dzamyn Ude.

Quarry 1 is located 3 km northeast of the railway station and is situated on the east side of the railroad tracks. The quarry is 340 m long, 120 m wide, and 3.5–3.8 m deep. Quarry 2 is located 2.7 km southeast of the station and is situated on the east side of the tracks. Quarry 2 is 150 m long, 50 m wide, and 2.7 m deep. Both quarries contain lower Oligocene deposits (Ergilin Dzo Formation, Ergilin Member), which consist of yellow gravels interbedded with fine clays, with an approximate thickness of 2.7–3.0 m (fig. 2).

Among the materials collected from Quarry 1 were fragments of molars and partial jaws of *Hyaenodon* sp., *Cadurcodon ardynensis*, *Embolotherium* sp.; and the fragmentary rhinoceros skull herein designated as the holotype of the new species, *Prohyracodon obrutschewi*. Fossil remains are rare in Quarry 2; only fragmentary molars from *Cadur-*

codon ardynensis and *Embolotherium* were found.

The composition and character of the deposits at the two Dzamyn Ude quarries make it possible to identify them as analogs of the Ergilin Member of the Ergilin Dzo Formation, known from the early Oligocene Khoer Dzan section, located 70 km northwest of the Dzamyn Ude railway station (Dashzeveg, 1991). The presence of *Cadurcodon ardynensis* in both the Dzamyn Ude quarries and the Khoer Dzan section is evidence in favor of the geologic synchronicity of the deposits.

The Ergilin fauna in the Khoer Dzan and Ergilin Dzo sections is rich in fossil mammal remains. Some of these mammals are of great importance for stratigraphic correlation (Dashzeveg, 1991). The presence of such forms as *Nimravus, Ronzotherium, Entelodon,* and *Bothriodon* allows us to correlate the Ergilin fauna with the early Oligocene Ronson Marker horizon (MP21) in western Europe. Accordingly, the Ergilin fauna is regarded as being early Oligocene in age (Dashzeveg, 1991, 1993).

The nomenclature in the present paper used for ceratomorph molar morphology is taken from Gromova (1959), Prothero et al. (1986), and Prothero and Schoch (1989). The material described in this paper, which is housed at the Geological Institute of the Mongolian Academy of Sciences, was prepared by B. Namsray. Casts of *Prohyracodon meridionale* specimens housed at the Paleontological Institute of the Russian Academy of Sciences, Moscow, were used for comparative purposes. Bryn J. Mader, Luke Holbrook, Michael J. Novacek, and Malcolm C. McKenna made valuable comments on earlier versions of this paper. The author expresses his appreciation to all of them. Research at the American Museum of Natural History was supported by the Frick Laboratory Endowment in Vertebrate Paleontology, Philip McKenna Foundation, and the James Carter Fund.

Abbreviations

SYSTEMATIC PALEONTOLOGY

ORDER PERISSODACTYLA OWEN, 1848

SUBORDER CERATOMORPHA WOOD, 1937

SUPERFAMILY RHINOCEROTOIDEA GILL, 1872

FAMILY HYRACODONTIDAE COPE, 1879

SUBFAMILY HYRACODONTINAE STEINMANN AND DÖDERLEIN, 1890

Genus *Prohyracodon* Koch, 1897

TYPE SPECIES: *Prohyracodon orientale* Koch, 1897.

REVISED DIAGNOSIS: Small hyracodontid, length M1–3 approximately 51–52 mm. Dental formula: I3/3, C1/1, P3/4, M3/3. Differentiated incisors, descending in size from I1 to I3. I1-2 adapted for shearing. Lateralmost incisor (I3) and canine about equal in size. Skull comparatively elongated with a relatively short rostrum. Posterior margin of lateral nasal incision at level of P2. Molars subhypsodont, antecrochet weakly developed. Third through fourth upper and lower premolars submolariform. M3 with a persistent small metacone. *Prohyracodon* differs from *Ardynia* (the most closely related genus in the subfamily) in having a retracted nasal incision, which extends back to the level of the P2, and a shorter diastema between C and P2.

INCLUDED SPECIES: *P. orientale, P. meridionale, P.? parvus, P. obrutschewi,* n. sp.

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION: Middle? and late Eocene to early Oligocene, Asia and eastern Europe.

Prohyracodon obrutschewi, new species
Figures 3–5, Tables 1, 2

ETYMOLOGY: Named in honor of the Russian geologist, V. A. Obrutschev.

HOLOTYPE: PSS no. 42/1, an incomplete juvenile skull with I1, I2 (left only), I3 (right only), canine alveoli, and cheek teeth (dP1-M3) from the right side.

MATERIAL: Holotype only.

TYPE LOCALITY AND AGE: Quarry 1, near Dzamyn Ude, eastern Gobi Desert, Mon-
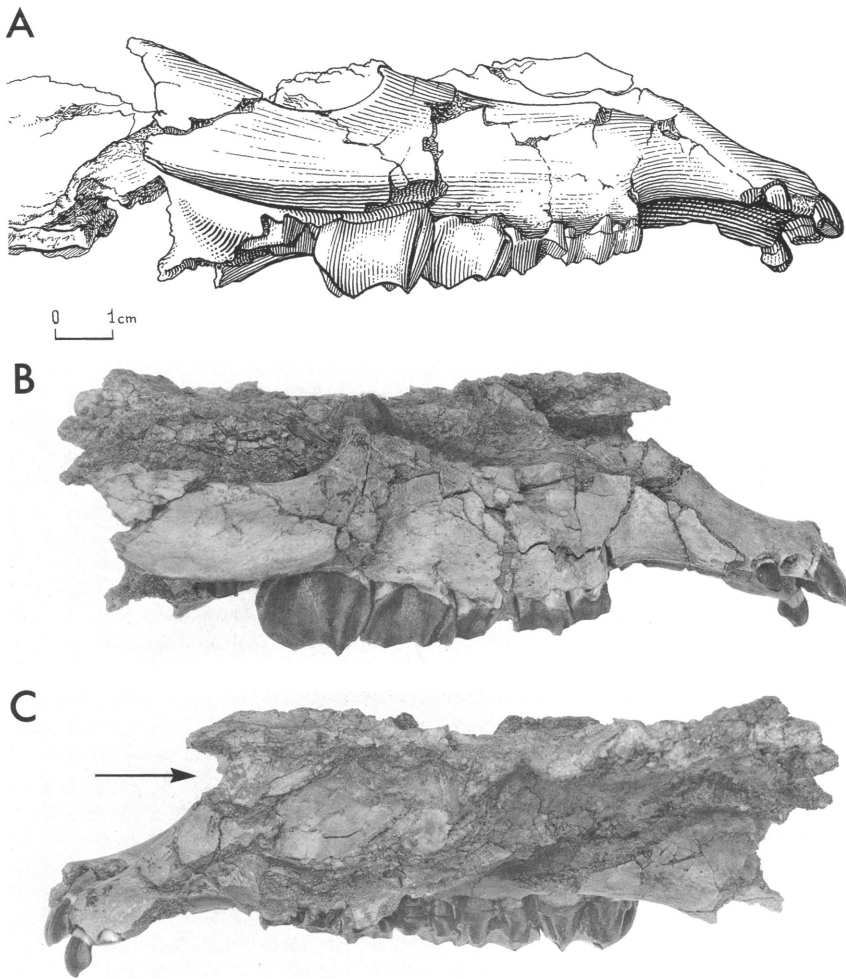
Fig. 3. Lateral views of *Prohyracodon obrutschewi,* n. sp., type specimen, PSS no. 42/1, incomplete skull and upper dentition. **A,** line drawing, right lateral view; **B,** photograph of same; **C,** photograph, left lateral view. Arrow indicates nasal incision.

golia. Ergilin Member, Ergilin Dzo Formation (early Oligocene).

DIAGNOSIS: Incisors spatulate, increasing in size anteriorly. Differs from all other species of *Prohyracodon* in having small metacone M3, strongly expressed parastyle fold on M1-2, and by the lack of a lingual cingulum on M1-M3.

DESCRIPTION: The skull is elongated and narrow, with a short face. The orbit is positioned low over the molars (16 mm over M2), and its anterior edge is located above the M3 parastyle.

The nasal bones are mediolaterally compressed, short, and their anterior edges prob-

ably did not extend further forward than P2. The posterior margin of the lateral nasal incision is located above P2.

The premaxillae are unfused, elongated, and paired. Each bears three incisors along its anterior margin. All the anterior teeth (incisors and canines) are immediately adjacent to one another. There is evidence of three pairs of incisors. The right and left I1, left I2, and right I3 are preserved intact, while the other incisors are represented by the roots only. The left canine tusk is missing, but the alveolus for this tooth is located immediately adjacent to the root of the left I3, behind the maxillary-premaxillary suture.
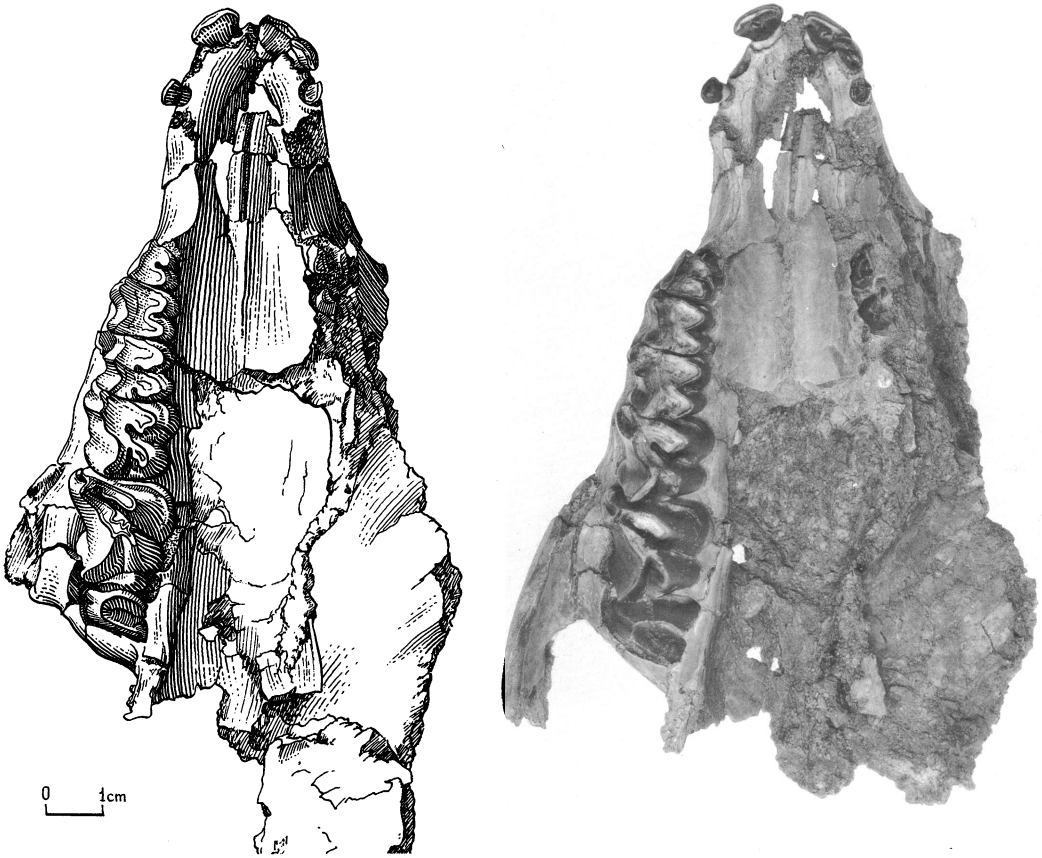
Fig. 4. Palatal view of *Prohyracodon obrutschewi*, n. sp., type specimen, PSS no. 42/1.

The first and second incisors are located along the rim of the premaxilla and are closely grouped together, as is typically the case in the Hyracodontidae. The incisors are clearly differentiated in size: I1 is considerably larger than either I2 or I3. The crown of I1 is almond-shaped, spatulate, and has a shearing profile. The transverse diameter at the base of I1 slightly exceeds the anteroposterior diameter. The anterior surface of the crown on I1 is more concave than the posterior surface.

The crown of I2 has an irregular triangular shape with a sharp occlusal surface for shearing.

I3 is chisel-shaped and much smaller than I1. Although the canine is lacking, it is possible to determine from the alveolus that the canine and I3 were approximately the same size. Both teeth probably also shared a similar form.

The canine alveolus is roughly elliptical in shape and the mesial-distal length is 2.9 mm, which is considerably reduced from the primitive hyracodontid condition. The diastema between the canine and dP2 is 14.0 mm.

dP2 is shaped like a trapezoid, although the lingual edge is rounded.

The third and fourth deciduous premolars are low-crowned teeth and are similar in form to the molars. The parastyle is the highest part of the triturating surface. A cingulum is present only on the anterior and posterior sides of the crown.

M1 is shaped like a trapezoid and is slightly narrowed posteriorly. The parastyle is distinct with the groove behind it on the buccal surface almost extending to the base of the
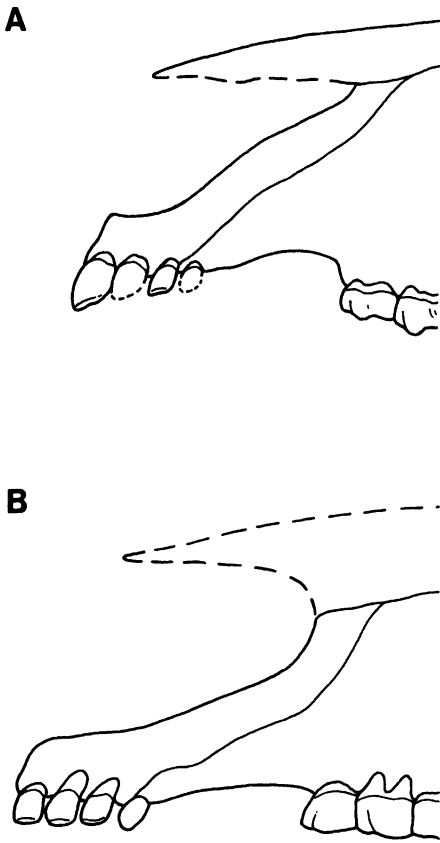
A

B

Fig. 5. Anterior portion of skull of two representatives of Hyracodontidae to show difference in nasal incision enlargement. Not to scale. A, *Prohyracodon obrutschewi*, n. sp.; **B**, *Ardynia praecox* (after Radinsky, 1966).

TABLE 1

Dental Measurements (mm) of *Prohyracodon obrutschewi*, new species

Tooth	Anteroposterior	Transverse
I1	4.4	7.1
I2	3.4	5.1
I3	2.8	3.6
C	2.9	3.7
P2	7.5	8.8
dP3	8.2	11.1
dP4	10.0	13.8
M1	13.3	15.9
M2	16.6	18.2

crown. The paracone is small, but distinct. The metacone is displaced lingually relative to the paracone. The trigon basin is open and comparatively narrow with a weak antecrochet.

M2 is larger than M1 and is less worn. The parastyle is considerably reduced, but its external rib is clearly defined. The paracone is the highest part of the tooth and takes the form of a conical tubercle. The protoloph and metaloph run almost parallel to each other. The trigon basin is deep and its labial perimeter almost reaches the parastyle.

M3, which was in the process of erupting, is partially contained in its crypt. There is a distinct metacone. Dental measurements for *Prohyracodon obrutschewi*, n. sp., are presented in table 1.

COMPARISONS: The size and structure of the upper molars of *Prohyracodon obrutschewi* are very similar to those of *P. orientale* and *P. meridionale*. An exact comparison of diagnostic characters is impeded, however, because the type of *P. obrutschewi*, and specimens of *P. orientale* (as described by Wood, 1929) and *P. meridionale* (as described by Chow and Xu, 1961) are in different states of wear. Despite these difficulties, there are some clear differences that distinguish the taxa. *Prohyracodon obrutschewi* differs from *P. orientale* and *P. meridionale* in the greater hypsodonty of M1 and M2 and the absence of a cingulum on the lingual side of the upper molars. Furthermore, the paracone of *Prohyracodon obrutschewi* is larger than that of the other two species.

Prohyracodon obrutschewi differs from *Prohyracodon* ? *parvus* from the late Eocene of Khoer Dzan, Mongolia, in the larger size of the first two molars and the narrower crowns of these teeth.

The preceding comparisons of *Prohyracodon* species from the Paleogene of Eurasia are a preliminary assessment that will suffice until better preserved material is available for study. In my opinion, however, the subhypsodonty of M1-2 in *Prohyracodon obrutschewi* clearly distinguishes this Mongolian form from the two well-known species from the late Eocene of Romania and China, respectively.

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION OF *PROHYRACODON*

To date, the genus *Prohyracodon* has been little studied. There is enough information

TABLE 2

Geographical and Geological Distribution of *Prohyracodon* and Associates

Age	Formation	Member	Mongolia, Eastern Gobi Desert		China, Yan-nan Province			Romania, Cluj
			Khoer Dzan	Dzamyn Ude	Lu-nan Basin	An-yen-cun Xiao-sha-he area	Qu-jing (Chuchung) Basin	Andrashaza
Lower	Ergilin Dzo	Ergilin	Indricotherium sp. (or Urtin-otherium) Gigantamyno-don giganteus Bothriodon chowi Entelodon orientalis Ronzotherium orientalis	Prohyracodon obrutschewi Cadurcodon ardynensis			Prohyracodon sp. Indricotheruim sp. Cadurcodon ardynensis Cadurcodon sp. Gigantamy-nodon cessa-tor (= G. giganteus) Bothriodon chowi	
Upper	Ergilin Dzo	Serkhul	Prohyracodon meridionale Amynodontopsis lunanensis Eoentelodon trofimovi			Prohyracodon meridionale Indricotherium parvus Eoentelodon yunnanense		Prohyracodon orientale Brachydias-tematherium transylvani-cum
Middle	Ergilin Dzo	Serkhul			Prohyracodon sp. (Lu-tei-yi Formation)			

available, however, to provide a general idea of its stratigraphic distribution within Eurasia.

As can be seen from table 2, *Prohyracodon* sp. from the middle Eocene or early late Eocene deposits in the Yunnan Province of China is one of the oldest occurrences of this genus (Zhang et al., 1978; Zheng et al., 1978). *Prohyracodon meridionale* from the An-yen-cun fauna of Yunnan Province has been dated as late Eocene (Chow and Xu, 1961; Chow et al., 1974).

The Qi-jing (sometimes Chuchung) fauna, also of Yunnan Province, is younger than the Lunan fauna. *Prohyracodon* sp. has been identified from the Chuchung fauna, as well as *Indricotherium intermedium, Cadurcodon ardynensis, Cadurcodon* sp., *Gigantamyno-don cessator* (= *G. giganteus*), *Bothriodon chowi, Bothriodon* sp., and *Entelodon* sp. (Chow and Xu, 1961; Wang and Zhang, 1983;

Li and Ting, 1983; Russell and Zhai, 1987; Zheng et al., 1978).

The known occurrence of *Prohyracodon* in Mongolia is limited, at present, to two localities in the eastern Gobi desert: Khoer Dzan and Quarry 1 near Dzamyn Ude. Specimens referred to *Prohyracodon meridionale* were collected by the author in light-gray sands from the Sevkhul Member of the Ergilin Dzo Formation, in the western part of the Khoer Dzan locality (Dashzeveg, 1991). *Mongo-lestes hadrodens, Pterodon exploratas, Pter-odon* sp., *Teleolophus magnus, Amynodon-topsis* (= *Amynodon*) *lunanensis, Eoentelo-don trofimovi,* and *Lophiomeryx* sp. are also known from this locality (Dashzeveg, 1991, 1993).

The Eocene/Oligocene boundary in the Khoer Dzan and Ergilin Dzo sections is placed at the base of the Ergilin Member of the Er-gilin Dzo Formation (Dashzeveg, 1991,

1993). Chow and Xu (1961) compared the deposits containing *Prohyracodon meridionale* and associated taxa (An-yen-cun fauna) with the fauna from the Shara Murun Formation of Inner Mongolia. The An-yen-cun fauna, however, is likely younger than the Ulan Usu fauna of the Shara Murun Formation and, instead, is comparable to the fauna from the Sevkhul Member of the Ergilin Dzo Formation at the Khoer Dzan locality. In addition to *P. meridionale,* these two faunas also share very similar forms of *Eoentelodon* (table 2).

I am inclined to correlate the Sevkhul Member of the Ergilin Dzo Formation with the Middle White Beds of the Ulan Gochu Formation of Inner Mongolia because of the shared presence of *Desmatalagus vetustus, Mongolestes hadrodens,* and *Teleolophus magnus.* I have dated the Sevkhul Member as Late Eocene (Dashzeveg, 1991).

The Qu-jing assemblage from Yunnan Province is faunistically and chronologically equivalent to the Ergilin fauna of Mongolia. Both faunas share the taxa *Cadurcodon ardynensis Giganamynodon cessator,* and similar forms of *Entelodon* and *Bothriodon.*

As stated above, the Dzamyn Ude gravel beds containing *Prohyracodon obrutschewi* can be correlated with the Ergilin Member of the Ergilin Dzo Formation at two key sections: Khoer Dzan and and Ergilin Dzo. *P. obrutschewi* is regarded as being early Oligocene in age.

The stratigraphic range of *Prohyracodon* in Asia, thus, extends from the middle Eocene (or perhaps, the early late Eocene) to the early Oligocene.

Prohyracodon orientale was first described from the Eocene deposits of Rumania in Transylvania, Siebenbürgen, and Andrashaza (Koch, 1897). The age of the deposits was originally regarded as being middle Eocene (Koch, 1897; Wood, 1929). Radinsky (1967), however, suggested that the deposits containing *P. orientale* were late Eocene in age, based on the progressive dental morphology of that species (molarization of the premolars and loss of the metacone on M3).

DISCUSSION

Radinsky (1966) demonstrated the importance of incisor morphology in the system-atics and classification of the Rhinocerotoidea. For almost 30 years, nothing more was added to our knowledge of rhinoceros incisor morphology, but recently, several papers have provided new information about the anterior dentition of the Rhinocerotoidea (Tanner and Martin, 1976; Russell, 1982; Prothero et al., 1986; Hanson, 1989; Dashzeveg, 1991). New hyracodontid material and recent literature permit refinement of the classification of the Rhinocerotoidea.

The principal criterion for the division of the Rhinocerotoidea into large taxonomic groups, in Radinsky's (1966) opinion, is the type of specialization of the incisors. Using this approach, the superfamily Rhinocerotoidea can be divided into four main family groups: Hyracodontidae, Indricotheriidae, Rhinocerotidae, and Amynodontidae. The Hyracodontidae is dentally characterized by unspecialized incisors, the Indricotheriidae has specialized I2/i1, and the Rhinocerotidae has specialized I1/i2. The Amynodontidae differs from all other members of the Rhinocerotoidea in the extreme development of the canine tusks (Radinsky, 1966; Prothero et al., 1986; Heissig, 1989b).

The Hyracodontidae is the basal Rhinocerotid group, but it is specialized in having a cursorial foot structure. These animals are hornless and have spatulate or pointed incisors approximately equal-sized or increasing in size anteriorly. Their premolars are premolariform to molariform. M3 is roughly triangular, with or without a small, lingually deflected vestige of the metacone (Radinsky, 1966; Prothero et al., 1986). Although highly specialized incisor morphologies do not occur in this family, some taxa show some specialization of the I1-2/i2-3 complexes.

The Hyracodontidae can be divided into two subfamilies: the Hyracodontinae and the possibly paraphyletic "Alloceropinae" (Heissig, 1989a). In early hyracodontines the dental morphology is rather primitive: undifferentiated incisors; small canines separated from the incisors by a very short diastema; premolariform premolars; conical parastyles, distinct metacones, and metastyles on M1-2.

Certain hyracondontine taxa show some differentiation of the anterior teeth, particularly the incisors. In *Prohyracodon* the incisors descend in size from I1 to I3. I1 is a relatively large, shearing tooth, while I3 is

much reduced. The canine is slightly smaller than I3.

A similar morphology occurs in the Oligocene hyracodontine *Ardynia,* in which the I1 and I2 are enlarged, while I3 and the canine are reduced in size and exhibit a similar morphology. On the lower incisors, i2 is noticeably enlarged (Radinsky, 1966: fig. 2D).

The possibly paraphyletic "Alloceropinae" are characterized, on the whole, by medium sized, unspecialized incisors, and large canine tusks (Heissig, 1989a; Reshetov et al., 1993). I include within the subfamily the genera *Forsterocooperia, Juxia, Armania, Eggysodon,* and *Tenisia.* Incisor morphology and degree of incisor differentiation vary among different alloceropine species (Radinsky, 1966, 1967). The incisors of *Armania asiana,* from the late Eocene and early Oligocene of Mongolia, are clearly differentiated: I1 is very small in size, I2 larger than both I1 and I3, and the canine tusks larger than all of the incisors (Dashzeveg, 1991).

The Indricotheriidae are characterized by two very large, tusklike upper incisors (I2) directed downward, and two very large lower incisors (i1) directed forward. It is unclear which incisors were preserved in *Indricotherium transouralicum.*

Osborn (1923) regarded the upper tusks in Mongolian indricotheres as representing I2. The lower incisors, closely approached in their morphology by those of all giant rhinoceroses, are identified by most authors as I1 (Borissiak, 1923; Gromova, 1959). The small alveoli for a second pair of incisors (i2) is preserved in one specimen of *Indricotherium transouralicum* from the Oligocene of Kazakhstan (Pavlova, 1922). Gromova (1959), who studied the giant rhinoceroses of Kazakhstan and Mongolia, identified the incisors of *Indricotherium transouralicum* as I2 and i1.

It should be noted that in *Urtinotherium,* i1 is the only functional tooth in the front of the mandible, i2, i3, and the canine being progressively smaller (Chow and Chiu, 1963). Thus I2 and i1 are the large incisors in *Indricotherium transouralicum.* Canines are present only in the upper jaw in this species. They are rudimentary and are shed early (Osborn, 1923; Gromova, 1959).

Borissiak (1923) initially grouped giant rhinoceroses at the subfamily level (subfamily Indricotheriinae) within the family Rhinocerotidae. Later, however, Borissiak (1939) concluded that indricotheres could be placed in their own family, the Indricotheriidae.

Radinsky (1967) included the Indricotheriinae in the family Hyracodontidae. There is some disagreement among systematists concerning the family-group taxonomy of giant rhinoceroses within the Rhinocerotoidea (Lucas et al., 1981; Prothero et al., 1986; Lucas and Sobus, 1989; Heissig, 1989b). In my opinion, indricotheres should be recognized at the family, rather than subfamily level, because the high degree of specialization of I2 and i1 sharply distinguish them from all other rhinocerotoid groups. The recognition of family rank is correct because of their fundamental and ancient separation from the general branch of Rhinocerotoidea, and quite sharply expressed direction of a specialization of incisors I2/I1, in the early phylogenesis of Rhinocerotoidea.

The Rhinocerotidae, or so-called true rhinoceroses, represent the largest and most diverse rhinocerotoid lineage. The evolutionary development of the group was rather complicated and lengthy compared to that of other ceratomorphs. In this group, I1 and i2 are specialized and form large tusks.

Of great significance in the early history of the family was *Teletaceras radinskyi,* which possessed incisors I1 and i2, highly specialized for shearing (Hanson, 1989). *Subhyracodon* and *Trigonias* from the late Eocene and Oligocene in North America both exhibit similar specialization of the incisors (Lucas, 1900; Russell, 1982). The high degree of specialization of I1/i2 in *Teletaceras* in the late Eocene, places the evolutionary appearance of rhinocerotids much further back in time than had been previously accepted.

COMMENTS ON THE EOCENE/OLIGOCENE
BOUNDARY IN CENTRAL ASIA

The conclusions concerning the geochronologic range of *Prohyracodon* and the age of various localities from the Tertiary of Mongolia must be considered in light of the current debate concerning the Eocene/Oligocene boundary (Martin et al., 1986). Revised radiometric dates based on single-crystal ^{40}Ar/^{39}Ar analysis and correlation with the magnetostratigraphy has prompted a shift of the

Eocene/Oligocene boundary to the end of the Chadronian in the North American record (Swisher and Prothero, 1990). However, the relevant continental strata in Mongolia are not in contact with datable rocks. Radiometrics therefore cannot be applied to the boundary problem in the Mongolian sequence. Moreover, the high degree of endemism in the Central Asian fauna makes correlation with the North American faunas for the purpose of identifying the boundary very difficult. The Asian contribution is less significant to the North American fauna than it is to the western European record. The mixing of the Asian and North American faunas actually began in the late Eocene, and the faunal break at the Eocene/Oligocene boundary is accordingly less marked than is the major faunal change indicated by the "Grande Coupure" in western Europe. Finally, the position of the boundary in western Europe is ambiguous due to contradictory evidence from various components of marine and continental faunas (Brunet, 1979; Martin et al., 1986).

The marked appearance (arrival) of Asian mammals in western Europe has generally been viewed as an early Oligocene event (Brunet, 1979; Brunet and Vianey-Liaud, 1987; Russell et al., 1982). In Mongolia and northern China, the lower Oligocene boundary has been recognized primarily on the ba-

sis of the appearance of *Entelodon, Bothriodon, Ronzotherium,* and *Nimravus.* In Central Asia, these taxa are restricted to a fairly narrow stratigraphic range but have a widespread geographic distribution, making them useful for broader-scale continental correlation.

Elsewhere, the author related the Ergilin Dzo fauna of Mongolia to the Oligocene standard sequence of Europe (Dashzeveg, 1991). For example, *Entelodon orientalis* from the Ergilin Member is very similar to *E. magnum* from Ronzon in western Europe. Similar relationships apply for Asian and European species of *Bothriodon.* The co-occurrence of *Nimravus mongoliensis,* and *Stenoplesictis* sp. with *Ronzotherium orientalis* in the Ergilin Dzo and Khoer Dzan localities of Mongolia allows assignment of the Ergilin Member to the base of the lower Oligocene and to the base of the reference level MP21 (Soumailles) of western Europe. The Asian carnivores *Nimravus mongoliensis, Stenoplesictis elegans,* and *Paleoprionodon gracilis* are more primitive than closely related western European forms from reference level M23 (Itardies). This is consistent with an earlier age for the Mongolian faunas. In conclusion, an early Oligocene age for the Ergilin fauna is recognized in this paper (see also Dashzeveg, 1991; Dashzeveg and Russell, 1992).

REFERENCES

Borissiak, A.
  1923. O rode *Indricotherium* n.g. (sem. Rhinocerotidae). Zap. PAN, OFM, ser. 35, 8(6): 1–128.
  1939. O novom predstavitele sem. Indricotheriidae. *In* V. A. Obrutschewy (ed.), Academiku, k 50-letiu nauchnoi i pedagogicheskoi deyatelnosti. Moscow, 2: 271–276.
Brunet, M.
  1979. Les grand mammifères chefs de file l'immigration Oligocene et le problème de la limite Eocene-Oligocene in Europe. Paris: Editions Fondation Singer-Plognac, 281 pp.
Brunet, M., and M. Vianey-Liaud
  1987. Mammalian reference levels MP21-30. *In* N. Schmidt Kittler (ed.), International symposium on mammalian biostratigraphy and paleoecology of the Eu-

ropean Paleogene, Mainz, February 18–21, 1987. Munchen Geowiss. Abh. 10(A): 1–32.
Chow, M., and C. Chiu
  1963. New genus of giant rhinoceros from the Oligocene of Inner Mongolia. Vertebr. PalAsiatica 8(3): 266–267.
Chow, M., and Y. Xu
  1961. New primitive true rhinoceros from the Eocene of J. Liang, Yunnan. Vertebr. PalAsiatica 5(4): 291–305. [In Chinese, English summary]
Chow, M., Y. P. Chang, and S. Y. Ting
  1974. Some early Tertiary perissodactyls from Lunan Basin, East Yunnan. Vertebr. PalAsiatica 12(4): 262–278. [In Chinese, English summary]
Dashzeveg, D.
  1975. A new representative of the genus *Embolotherium* from the Oligocene of

Mongolia. Paleontol. J. 2: 150–152. [In Russian]

1991. Hyracodontids and rhinocerotids (Mammalia, Perissodactyla, Rhinocerotidae) from the Paleogene of Mongolia. Palaeovertebrata 21(1, 2): 1–84.

1993. Asynchronism of the main mammalian faunal events near the Eocene-Oligocene boundary. Tertiary Res. Spec. Pop. 14(4): 141–149.

Dashzeveg, D., and D. E. Russell
1992. Extension of the dyspterine Pantolestidae (Mammalia, Cimolesta) in the Early Oligocene of Mongolia. Geobios 25(5): 647–650.

Gromova, V.
1959. Giant rhinoceros. Trudy PIN AN SSSR, 71: 1–164. [In Russian]

Hanson, C. B.
1989. Teletaceras radinskyi, a new primitive rhinocerotoid from the Late Eocene Clarno Formation of Oregon. In D. R. Prothero and R. M. Schoch (eds.), The evolution of perissodactyls, pp. 379–398. New York: Oxford Univ. Press.

Heissig, K.
1989a. The Alloceropinae hyracodonts. In D. R. Prothero and R. M. Schoch (eds.), The evolution of perissodactyls, pp. 355–357. New York: Oxford University Press.

1989b. The Rhinocerotidae. In D. R. Prothero and R. M. Schoch (eds.), The evolution of perissodactyls, pp. 399–417. New York: Oxford Univ. Press.

Koch, A.
1897. Prohyracodon orientale, ein neues Uräugether aus den Mitteleocänen Schichten Siebenbürgens Termezetrajii Füzetek 20: 490–500.

Li, C., and S. Ting
1983. The Paleogene mammals of China. Bull. Carnegie Mus. Nat. Hist. 21: 1–97.

Lucas, F. A.
1900. A new rhinoceros, Trigonias osborni, from the Miocene of South Dakota. U.S. Natl. Mus. Proc. 23: 221–227.

Lucas, S. G., and J. Sobus
1989. The systematics of indricotheres. In D. R. Prothero and R. M. Schoch (eds.), The evolution of perissodactyls, pp. 358–378. New York: Oxford Univ. Press.

Lucas, S. G., R. W. Schoch, and E. Manning
1981. The systematics of Forstercooperia, a middle to late Eocene hyracodontoid (Perissodactyla, Rhinocerotoidea) from Asia and western North America. J. Paleontol. 55(4): 826–841.

Martin, E., V. Fahlbush, and H. Hagn
1986. The Eocene/Oligocene boundary and the Latdorfian (Lower Oligocene). Newsl. Stratigr. 17(1): 37–43.

Osborn, H. F.
1923. Baluchitherium grangeri, a giant hornless rhinoceros from Mongolia. Am. Mus. Novitates 78: 15 pp.

1929. Embolotherium gen. nov. of the Ulan Gochu, Mongolia. Am. Mus. Novitates 353: 20 pp.

Pavlova, M. V.
1922. Indricotherium transouralicum n. sp. provenant du district de Tourgay. Bull. Moskovskogo obshestva ispitatelei Prirody, nov. ser., geol., 31: 95–116.

Prothero, D. R., E. Manning, and C. B. Hanson
1986. The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). J. Linn. Soc. London Zool. 87: 341–366.

Prothero, D. R., and R.M. Schoch
1989. The origin and evolution of perissodactyls: summary and synthesis. In D. R. Prothero and R. M. Schoch (eds.), The evolution of perissodactyls, pp. 504–529. New York: Oxford Univ. Press.

Radinsky, L. B.
1966. The families of the Rhinocerotoidea (Mammalia, Perissodactyla). J. Mammal. 47(4): 631–639.

1967. A review of the rhinocerotoid family Hyracodontidae (Perissodactyla). Bull. Am. Mus. Nat. Hist. 136: 1–46.

Reshetov, V., N. Spassov, and B. Baishashov
1993. Tenisia gen. nov.: taxonomic re-evaluation on the Asian Oligocene rhinocerotoid Eggysodon turgaicum (Borissiak, 1915) (Mammalia, Perissodactyla, Hyracodontidae). Geobios 26(6): 715–722.

Russell, L. S.
1982. Tertiary mammals of Saskatchewan, part VI: the Oligocene rhinoceros. Royal Ontario Mus. Life Sci. Contrib. 133: 1–58.

Russell, D. E., and R. J. Zhai
1987. The Paleogene of Asia: mammals and stratigraphy. Mus. Natl. Hist. Nat. (Paris) Mem., Science de la Terre, 52: 1–488.

Russell, D. E., I.-L. Hartenberger, C. Pomerol, S. Sen, N. Schmidt-Kittler, and M. Vianey-Liaud
1982. Mammals and stratigraphy: the Paleogene of Europe. Palaeovert. Mem. Extraord.: 1–77.

Swisher, C., and D. R. Prothero
1990. Single crystal ^{40}Ar/^{39}Ar dating of the

Eocene-Oligocene transition of North America. Science 249: 760–762.

Tanner, L. G., and L. D. Martin
1976. New rhinocerotoid from the Oligocene of Nebraska. *In* C. S. Churcher (ed.), Athlon: essays in paleontology in honor of Loris Shang Russell, Royal Ontario Mus. Life Sci., Misc. Publ., pp. 210–219.

Wang, B. Y., and Y. P. Zhang
1983. New finds of fossil from Paleogene of Qujing, Yunnan. Vertebr. PalAsiatica 21/2: 119–128. [In Chinese, English summary]

Wood, H. F.
1929. *Prohyracodon orientale* Koch, the old-est known true rhinoceros. Am. Mus. Novitates 395: 17 pp.

Xu, Y. X.
1961. Some Oligocene mammals from Chuching, Yunnan. Vertebr. Pal-Asiatica 5/4: 316–329. [In Chinese, English summary]

Zhang, Y. P., Y. Z. You, H. X. Ji, and S. Y. Ding
1978. Cenozoic stratigraphy of Yunnan. Prof. Pap. Stratigr. Paleontol. 7: 1–21. [In Chinese, English summary]

Zheng, J. J., Y. J. Tang, R. J. Zhai, S. Y. Ting, and X. S. Huang
1978. Early Tertiary strata of Lunnan Basin, Yunnan. Prof. Pap. Stratigr. Paleontol. 7: 22–29. [In Chinese]