HYRACODONTIDS AND RHINOCEROTIDS (MAMMALIA, PERISSODACTYLA, RHINOCEROTOIDEA) FROM THE PALEOGENE OF MONGOLIA

by

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CONTENTS

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ABSTRACT

Two families are reviewed (Hyracodontidae and Rhinocerotidae) from the Paleogene of Mongolia. The following taxa are described from the former family: *Triplopus? mergenensis* sp. nov., *Prohyracodon meridionale* CHOW, *Prohyracodon? parvus* sp. nov., *Forstercooperia ergiliinensis* GABUNIA & DASHZEVEG, *Ardynia praecox* MATTHEW & GRANGER, *A. mongoliensis* (BELIAYEVA), *Ardynia* sp., *Urtinotherium* sp. (or *Indricotherium*) and *Armania asiana* GABUNIA & DASHZEVEG. All of them are from the Paleogene of the eastern Gobi Desert. The hyracodontid *Pataecops parvus* RADINSKY is described from a new locality, Menkhen-Teg (Middle Eocene), in the Valley of Lakes.

In the second family, a new species of *Ronzotherium*, *R. orientale* sp. nov. has been recognized from the Oligocene of Ergilin Dzo and Khoer Dzan of the eastern Gobi Desert. *Ronzotherium* sp. and *Allacerops* sp. have been described from the Oligocene of Khoer Dzan. The genus *Ronzotherium*, formerly known from the Oligocene of eastern Europe, has been reliably established in the Oligocene fauna of Mongolia. The genus *Symphysorrachis* BELIAYEVA, 1954, previously believed to be a junior synonym of *Ronzotherium*, is here resurrected.

Descriptions are provided for key localities in the Eocene and Oligocene of Mongolia and the adjacent territories of northern China, containing fossil Hyracodontidae and Rhinocerotidae. In addition, the question of the Eocene-Oligocene boundary in these Mongolian and Chinese sections is discussed. Paleontological evidence has been used to correlate Eocene-Oligocene boundary layers in the eastern Gobi Desert (Mongolia) and Inner Mongolia (China). A brief discussion is provided on the phylogenetic affinities of the genera within the family Hyracodontidae.

RESUME

Deux familles de périssodactyles (Hyracodontidae et Rhinocerotidae) du paléogène de Mongolie sont revues. En ce qui concerne les Hyracodontidae, les taxons suivants sont décrits: *Triplopus? mergenensis* sp. nov., *Prohyracodon meridionale* CHOW, *Prohyracodon? parvus* sp. nov., *Forstercooperia ergiliinensis* GABUNIA & DASHZEVEG, *Ardynia praecox* MATTHEW & GRANGER, *A. mongoliensis* (BELIAYEVA), *Ardynia* sp., *Urtinotherium* sp. (or *Indricotherium*) and *Armania asiana* GABUNIA & DASHZEVEG. Toutes ces formes proviennent du Paléogène du Désert de Gobi oriental. L'hyracodontidé *Pataecops parvus* RADINSKY a été identifié dans un nouveau gisement d'âge éocène moyen, Menkhen-Teg, dans la Vallée des Lacs.

En ce qui concerne les Rhinocerotidae, une nouvelle espèce du genre *Ronzotherium*, *R. orientale* nov. sp., a été identifiée dans l'Oligocène d'Ergilin Dzo et Khoer Dzan (Désert de Gobi oriental). *Ronzotherium* sp. et *Allacerops* sp. sont décrits dans l'Oligocène de Khoer Dzan. La présence du genre *Ronzotherium*, auparavant connu dans l'Oligocène d'Europe de l'Est, est maintenant bien établie dans la faune oligocène de Mongolie. Le genre *Symphysorrachis* BELIAYEVA, 1954, longtemps considéré comme un synonyme junior de *Ronzotherium*, est revalidé dans ce travail.

Les localités les plus riches en Hyracodontidae et Rhinocerotidae de l'Eocène et de l'Oligocène de Mongolie, ainsi que des territoires adjacents (Chine du Nord) sont décrites. En outre, la question de la situation de la limite Eocène-Oligocène dans ces coupes de Mongolie et des territoires adjacents du nord de la Chine est discutée. Les corrélations entre les différents niveaux situés autour de cette limite Eocène-Oligocène dans ces régions (Désert de Gobi oriental en Mongolie et Mongolie Intérieure en Chine) ont été établies sur la base de données paléontologiques.

INTRODUCTION

A major role in the history of Paleogene mammals, both in the Old and New World, was played by the family Hyracodontidae. It must have played a similar role in the mammalian history of Mongolia. Despite certain achievements in the study of Tertiary mammals of Mongolia in recent years, Mongolian fossil rhinoceroses still need further work.

The first collections of early Tertiary Hyracodontidae from Mongolia and Northern China were amassed by the Central Asian Expedition of the American Museum of Natural History in the late 1920's. The material collected from these regions was then briefly described in some small papers (Matthew & Granger, 1923; 1925, a and b; Osborn, 1923). Wood (1938, 1963) described in detail two new forms of Hyracodontidae from the Eocene localities of Irdin Manha and Camp Margetts in Inner Mongolia. Granger and Gregory (1936) devoted their study to the morphology of the giant rhinoceros from the Oligocene of Urtyn Obo and other North Chinese localities.

The material collected in Mongolia on the Mongolian Paleontological Expedition in 1948-1949 by I.A. Efremov and his colleagues included fossil Hyracodontidae from the Paleogene locality of Ergilin Dzo. They are of special interest since they shed light on the early history of this group.

A whole series of papers by Beliayeva (1952, 1954) has been devoted to the systematic description of primitive rhinoceroses. Hyracodontidae from the Paleogene of Ergilin Dzo: a new genus, *Symphysorrachis*, was established, together with a more precise definition of *Ardynia*. Gromova (1952) described a new genus, *Ergilia*, from the above named locality.

A large collection of hyracodontids collected by the Central Asian Expedition is stored at the American Museum of Natural History in New York. Radinsky (1967) who studied hyracodontids from the Paleogene of Asia, made a comprehensive study of the morphology, systematics and phylogeny of the group.

The Soviet-Chinese Paleontological Expedition which worked in Inner Mongolia amassed hyracodontid material. Chow and Chiu (1963, 1964) described new specimens of the giant rhinoceroses (*Juxia* and *Urtinotherium*) from the samples collected by the expedition. Separate finds of hyracodontids from the Paleogene of East and Central Asia are described in papers by Soviet, Mongolian and Chinese researchers (Gabunia & Dashzeveg, 1974; Beliayeva, 1979). The recent paper by Lucas *et al.* (1981) describes a new species, *Forstercooperia minuta*, from the Eocene locality of Camp Margetts (China) and provides a more precise diagnosis of the family. This concludes the summary of published work on hyracodontids of Central Asia.

The present paper describes hyracodontids from the Paleogene of the eastern Gobi Desert on the basis of the material collected by the author over the last 20 years. The sampling of *Forstercooperia*, *Prohyracodon* and other taxa was carried out by a paleontological team of the Mongolian Academy of Sciences led by the author in 1964-1966. The other collections were amassed by the author during the field work of the Joint Soviet-Mongolian Paleontological Expedition in 1981-1983 at the Ergilin Dzo and Khoer Dzan localities in the eastern Gobi Desert.

The illustrations in the paper have been made by V.D. Kalganov and Kh. Tzogtbaatar, and specimen preparation was carried out by B. Namsray. The author expresses his sincere gratitude for the services done. The author is also glad to have an opportunity of expressing his gratitude to Dr. B.A. Trofimov, head of the laboratory of mammals at the Paleontological Institute, U.S.S.R. Academy of Sciences, who provided the necessary material for comparison; and to Academician L.K. Gabunia for invaluable comments.

Dr. M. Brunet was kind enough to supply me with material of *Ronzotherium* from the Oligocene of eastern Europe, which has made it possible for me to compare Mongolian forms with east European ones. The author expresses his most sincere gratitude to Dr. Brunet for his assistance.

The author thanks Drs. J.J. Hooker and D.E. Russell, for their useful remarks and corrections regarding the manuscript of this paper.

Dental terminology follows the usage of V. Gromova (1959) (fig. 1). The measurements are in millimeters, and the indices in percentages. The length and width measurements of the teeth were taken at the base of the crown. The widths were measured at the positions of the transverse ridges: at the protoloph and metaloph for upper teeth, and on the metalophid and hypolophid for the lower ones. The dental height index follows Radinsky (1967). Crown height is measured only on unworn or slightly worn teeth. The height index shows the ratio of height to length at the base of the crown as this is the most reliable.

The following abbreviations have been used throughout the paper:

AMNH - American Museum of Natural History
MPE - Mongolin Paleontological Expedition of the U.S.S.R. Acad. Sci.
PIN - Paleontological Institute of the U.S.S.R. Acad. Sci.

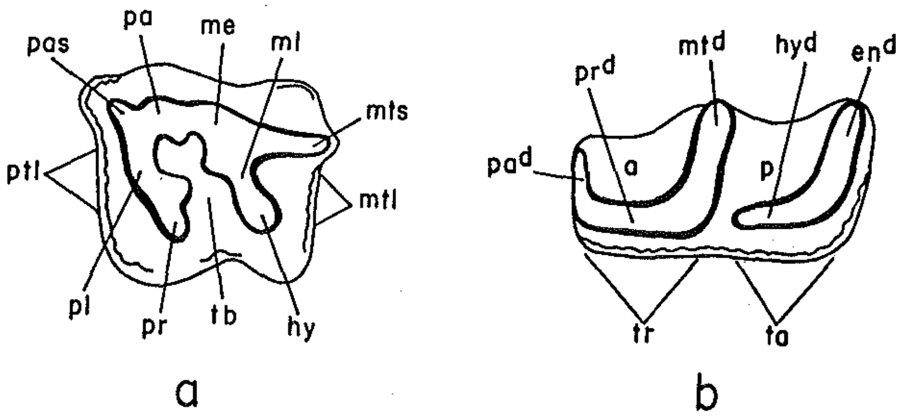

Fig. 1.— The following symbols have been used to describe the teeth:
a: upper molar; **pa**: paracone; **me**: metacone; **pr**: protocone; **hy**: hypocone; **ptl**: protoloph; **mtl**: metaloph; **pl**: protoconule; **ml**: metaconule; **pas**: parastyle; **mes**: mesostyle; **mts**: metastyle; **t.b.**: the trigon basin.
b: lower molar; **prd**: protoconid; **hyd**: hypoconid; **pad**: paraconid; **mtd**: metaconid; **msd**: metastylid; **end**: entoconid; **tr**: trigonid; **td**: talonid; **e**: the outer basin; **a**: the trigonid basin; **p**: the talonid basin

PMPE - Polish-Mongolian Paleontological Expedition
PMUU - Paleontological Museum of Upsala University
PSS - Paleontologo-stratigraphic section of the Geological Institute of the Mongolian Acad Sci.
IPP - Institute of Paleontology and Paleo-Anthropology of the Chinese Acad. Sci.
SCPE - Soviet-Chinese Paleontological Expedition
JSMPE - Joint Soviet-Mongolian Paleontological Expedition
CAE AMNH - Central Asian Expedition of the American Museum of Natural History

THE KEY LOCALITIES OF THE PALEOGENE OF MONGOLIA AND ADJACENT TERRITORIES OF NORTHERN CHINA WITH FOSSIL HYRACODONTIDS AND RHINOCEROTIDS

MONGOLIA

The Hyracodontidae and Rhinocerotidae fossils described in the present paper are from Paleogene localities in two Mongolian regions: the eastern Gobi Desert and the Valley of Lakes.

Eastern Gobi Desert

(Fig. 2, 3)

Mergen

The locality is situated 23 km northwest of the frontier station of Dzamyn Ude, on the southeastern limb of the Doloodoi Lake Basin. The Mergen Eocene sequence may be subdivided into two parts. The lower part has not yet been described in terms of the fossil fauna. It is 8.5 m thick and in the composition and colour of the rocks resembles the Arshanto Formation in the Iren Dabasu Lake Basin in the adjacent Inner Mongolian territory (China). The upper part of the section is composed of grey sandy-clay sediments which rest unconformably on theLower Red beds. They contain fossils of vertebrates. The thickness is 15 m. Mammalian fossils have been found at two levels. From the first one the teeth of a tapiroid, *Lophialetes? minutus*, are known. The second level has been shown to contain more abundant material comprising *Harpagolestes* cf. *orientalis*, *Yuomys* sp., *Lophialetes? minutus*, *L. expeditus*, *Triplopus? mergenensis* sp. nov. and *Gobiohyus* sp. In addition to the mammals, the fauna contains remains of a bird, *Eogrus* sp.

The above determinations give a mid-Eocene date to sequences in the Doloodoi Lake Basin. Mergen is the earliest reliable Eocene locality of vertebrates in the eastern Gobi Desert, important for the general stratigraphy of the Paleogene of this vast area.

Ergilin Dzo

The locality is an extensive area of badlands near Khatan Bulak in the Eastern Gobi district. It extends from the east to the west for over 50 km. All the major cliffs at the locality face north, and grade above into a vast plateau. The locality was discovered by an

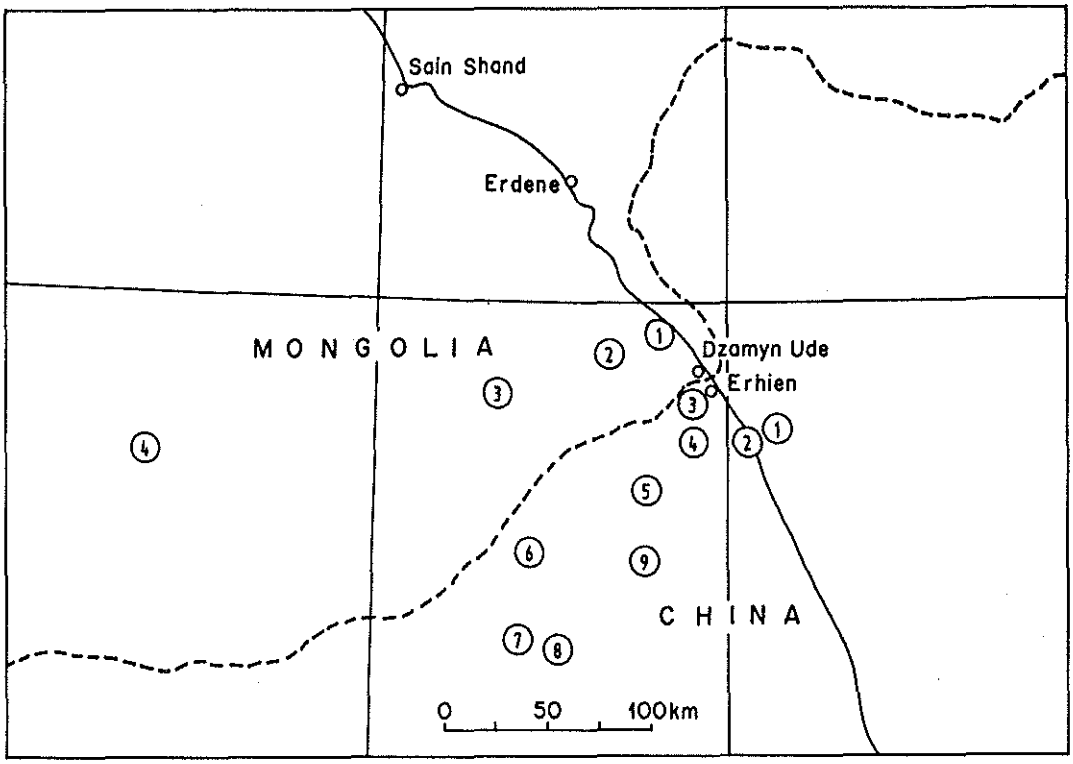

Fig. 2.— Sketch map of Eocene and Oligocene Mammalian fossil localities in Mongolia (Eastern Gobi Desert) and North China. Mongolia – 1: Mergen; 2: Khoer Dzan; 3: Alag Tsav; 4: Ergilin Dzo. North China – 1: Arshanto; 2: Irdin Manha; 3: Houldjin; 4: Camp Margetts; 5: Nom Khong Shire; 6: Ulan Shire; 7: Ula Usu; 8: Baron Sog; 9: Urtyn Obo.

	Age	Species	Note
Ergilin Dzo suite	Ergilin Member	*Ronzotherium orientale* sp. nov.	collected by Dashzeveg, 1982
		Symphysorrachis brevirostris	Beliayeva, 1954
		Forstercooperia ergilinensis	Gabunia & dashzeveg, 1974
		Armania asiana	collected by Dashzeveg, 1982
		Ardynia mongoliensis	Matthew & Granger, 1923, 1925
		Ardynia praecox	Beliayeva, 1952, 1954
		Indricotheriinae gen.?	Gromova, 1952, 1959; Radinsky, 1967
	Sevkhul Member	*Ardynia mongoliensis*	Determination by the author

Table 1.— List of Hyracodontidae and Rhinocerotidae from the Ergilin Dzo Group.

	Age	Species	Note
Ergilin Dzo suite	Ergilin Member	*Ronzotherium orientale* sp. nov.	collected by the author, 1982
		Urtinotherium (or *Indricotherium*) sp.	collected by the author, 1971
		Prohyracodon meridionale	Dashzeveg, 1982
		Ardynia mongoliensis	collected 1981-1982
		Allacerops	determination by the author
	Sevkhul Member	*Prohyracodon meridionale*	
		Armania asiana	
		Ardynia mongoliensis	collected by the author, 1981-1982
		Prohyracodon? parvus sp. nov.	
	Dzangut Member	*Prohyracodon? parvus* sp. nov.	collected by the author, 1982

Table 2.— List of Hyracodontidae and Rhinocerotidae from the Khoer Dzan locality.

American paleontological expedition in 1922 and given the name of Ardyn Obo. Specimens of hyracodontids were collected from here (Matthew & Granger, 1923, 1925).

In 1946-1949, the MPE worked here and made additional collections of rhinoceros remains (Beliayeva, 1952, 1954; Gromova, 1952, 1960). In 1962, *Forstercooperia* and other fossils were collected by the author in the western ranges of the locality (Dashzeveg, 1964; Gabunia & Dashzeveg, 1974). The author worked in the JSMPE (1981-1983) at Ergilin Dzo where new and interesting material of hyracodontids was obtained.

Hyracodontid fossils in Ergilin Dzo sections are known from two stratigraphic levels of the Ergilin Dzo Group (Tab. 1).

The locality is dated as Upper Eocene-Lower Oligocene. The Eocene-Oligocene boundary is traced at the base of the Ergilin Member.

Khoer Dzan

The locality is situated 65 km northwest of the railway station Dzamyn Ude, and is second to Ergilin Dzo in its extent within the eastern Gobi Desert. I discovered it in 1962. It is from here that *Entelodon orientalis* was first described (Dashzeveg, 1965).

Separate outcrops of the Ergilin Dzo suite are well exposed in the vicinity of Ikh Dzan in the western part of the locality. Concentrations of bones occur in light grey sands (Sevkhul Member) and yellow gravels and sandstones (Ergilin Member) in the Ikh Dzan cliffs. Fossils of hyracodontids have been established at three stratigraphic levels (Tab. 2).

The age of the Khoer Dzan locality ranges from Upper Eocene to Lower Oligocene.

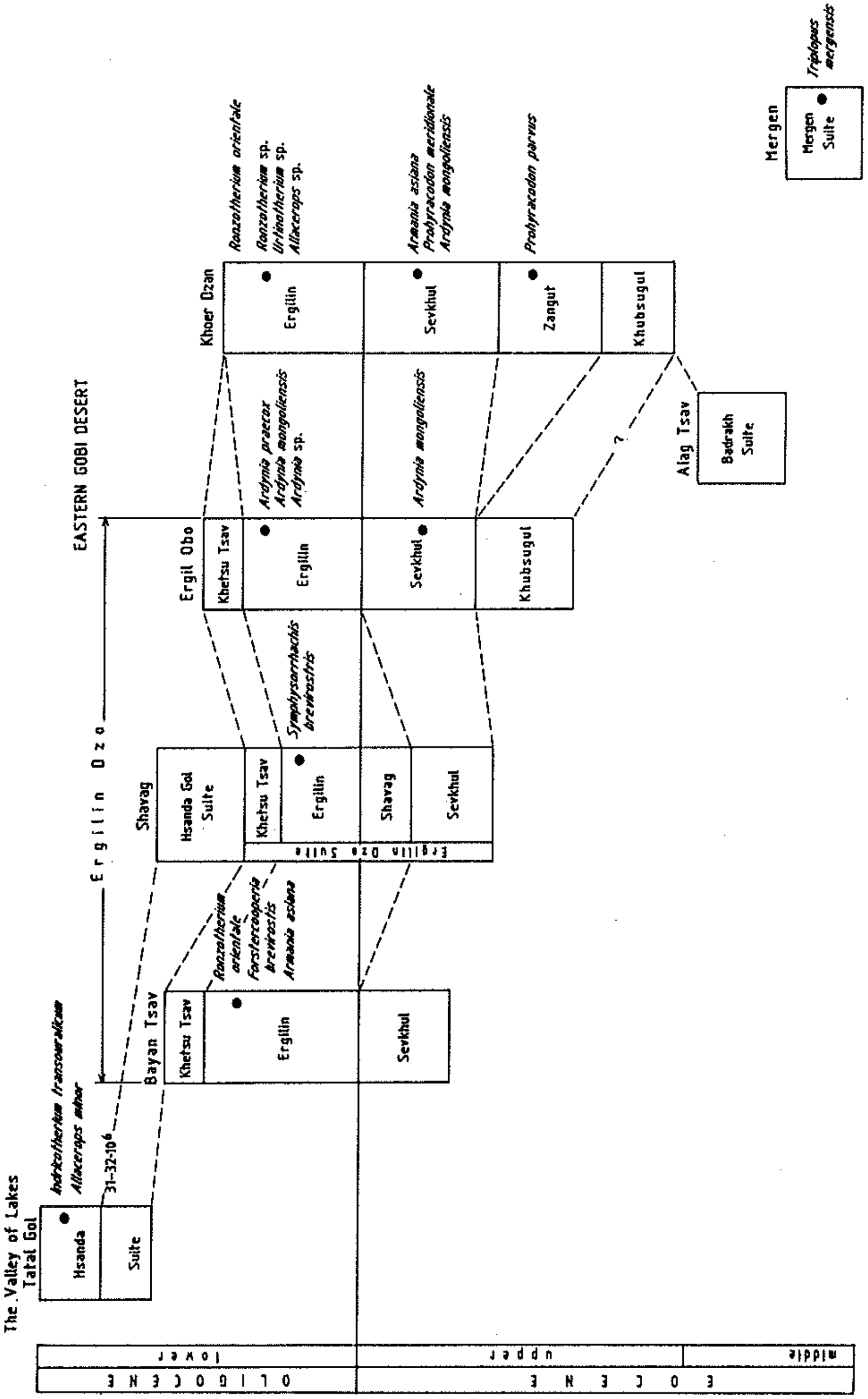

Fig. 3.— Stratigraphical distribution of hyracodonts and rhinocerotids in the Paleogene of Mongolia.

The Valley of Lakes
(Fig. 4, 5)

Tsagan Khutel

The locality was found by the CAE AMNH and given the name of Kholobolchi. It is situated 1.5 km east of the Bogd village center at the estuary of the Tui River. This locality is a more promising one in comparison to others since the bone-containing layers are exposed here over a bigger area and are thicker. Of the Hyracodontidae, *Pataecops parvus* Radinsky is known from here (Radinsky, 1967). The locality is Middle Eocene in age.

Menkhen Teg

The locality is situated 37 km northwest of Tsagan Khutel. It has been mentioned in papers by American authors (Berkey *et al.*, 1929). In 1971-1972, I collected fragments of *Pataecops parvus* from two levels, which suggest a mid-Eocene age for the included sequence, and the previous localities likewise.

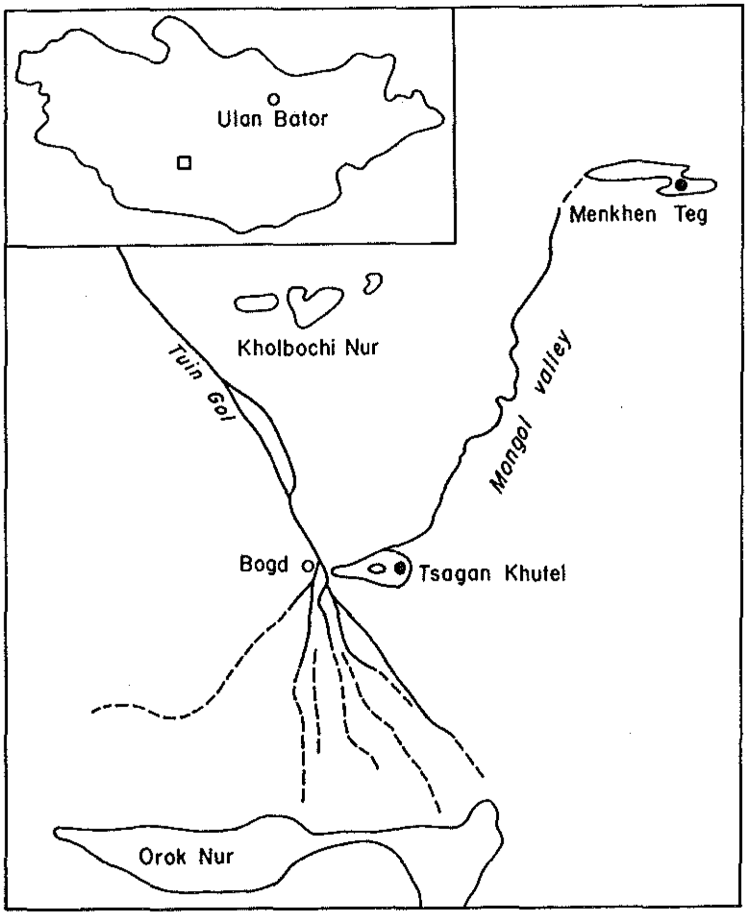

Fig. 4.— Sketch map of Middle Eocene mammalian fossil localities in the Valley of Lakes in Mongolia.

Tatal Gol

The locality has been known since the research by the American expedition under the name of the Grand Canyon. A basaltic layer divides the Red beds of the Hsanda Gol suite into two. The lower, subbasaltic, unit is represented by red-brown clay about 10 m thick. No fossils have been detected in the subbasaltic unit, which is composed mostly of red-orange, 25 m thick, sandy clays. In contrast to the lower unit, the upper one is highly carbonatized.

Large collections amassed in Tatal Gol by the American and Soviet expeditions are from the surface of the exposure, and have no precise stratigraphic level recorded.

The tentative results of our field work in 1982 suggest two bone-bearing levels in the supra-basaltic unit. The lower level is associated with lenses of green sandy clays at the base of the unit. The lenses are rich in bones and teeth of small mammals. They are likely to yield rich material after processing of the sediment. The thickness of the lenses is from 1.8-2.0 m. *Palaeoscaptor acridens*, *Sinolagomys tatalgolicus*, *Tataromys sigmodon*, *Karakoromys plicidens*, *Didymoconus colgatei*, *Amphicynodon* sp., *Palaeogale ulysses* and *Palaeogale parvula* have been determined from here.

The upper bone-bearing level is represented largely by brown clayey sandstones with marl concretions in the uppermost part of the section. *Tachyoryctoides obruschewi* and the enamel from *Allacerops turgaica minor* teeth have been found here (Beliayeva, 1954). The PMPE has collected materials of *Allacerops* at the Oligocene locality of Ulan Gang of the Trans-Altai Gobi Desert (Borsuk -Bialynicka, 1968).

Finds of *Indricotherium transouralicum* might be confined to this layer of the section.

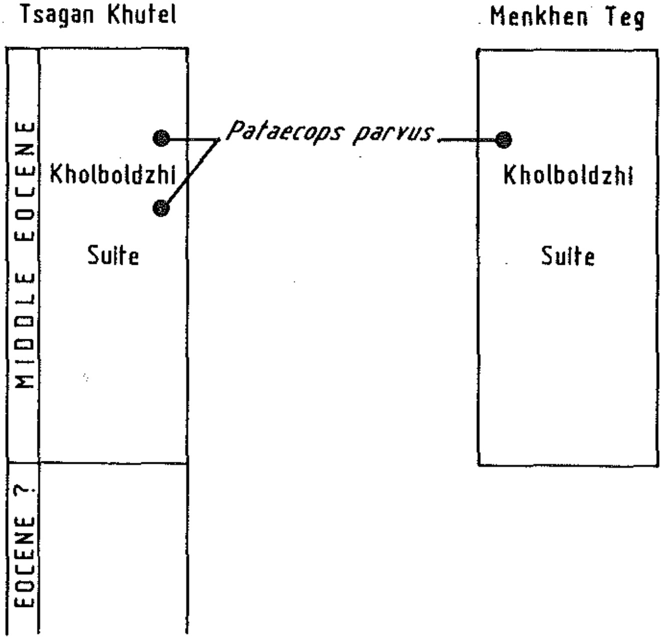

Fig. 5.— Stratigraphical position of finds of *Pataecops parvus*in sections at Tsagan Khutel and Menkhen Teg.

The absolute age of the above mentioned basalts is 31.0-32.0 MY (Evernden *et al.*, 1964). The locality is dated on paleontological evidence as uppermost Lower Oligocene.

NORTHERN CHINA: INNER MONGOLIA

(Fig. 2, 6)

Within the adjoining territory, the fossils of Hyracodontidae are known from two regions of Inner Mongolia (Li & Ting, 1983).

The Basin of Iren Dabasu

Irdin Manha

The locality is situated 35 km south-southwest of Erhlien station and was discovered by the CAE AMNH in 1922. The Hyracodontidae discovered were *Triplopus proficiens*, *Forstercooperia totadentata* and *Forstercooperia confluens* (Radinsky, 1967; Qi, 1979; Li & Ting, 1983). The locality is referred to the Middle Eocene (Dashzeveg, in prep.).

Camp Margetts

The locality is to be found 40 km southwest of the Erhlien station and 20 km east of the Iren Nur commune. It was discovered by the CAE AMNH in 1923. Abundant mammalian fossils were collected by the Americans in 1930 (Radinsky, 1964).

According to the Chinese data (Qi, 1979, 1980), the Camp Margetts section may be divided into three parts. The lower one, the Bayan Ulan Member (Lower Eocene) contains relics of *Mongolotherium efremovi*, *?Heptodon* sp., etc. The middle part, the Arshanto Member (Middle Eocene) comprises 35 mammal species, 27 of which are new. The Hyracodontidae are represented here by newly appearing forms: *Forstercooperia huhebolensis*, *F.? grandis*, *F. elongata* and *?Urtinotherium minor* (Qi, 1979). The upper part is the Irdin Manha Member (uppermost Middle Eocene). *Forstercooperia confluens* is known from this part (Wood, 1963; Qi, 1979).

Houldjin

The locality is 25 km southwest of the Erhlien station, represented by beds of pebbles and gravel covering the rugged surface of older rocks. The locality was discovered in 1892 by V.A. Obruchev (1948) who found amid gravels fragments of vertebrate teeth and took them for teeth of sharks from the Tertiary Khan Khai Sea. E. Suess (1899) devoted a separate paper to this find which he referred instead to *Rhinoceros* or *Aceratherium*. The Central Asian Expedition collected here fragmentary remains of mammals (Matthew & Granger, 1923). Of the Hyracodontidae, there occurs *Indricotherium* sp. (= *Baluchitherium*).

I have dated the Houldjin gravels with *Indricotherium* sp., *Cadurcodon* sp. and *Entelodon dirus* and others as Lower Oligocene (Dashzeveg, 1976). Note that many researchers followed Berkey and Morris (1927) and made the mistake of dating the Houldjin gravel fossil fauna as Middle Oligocene.

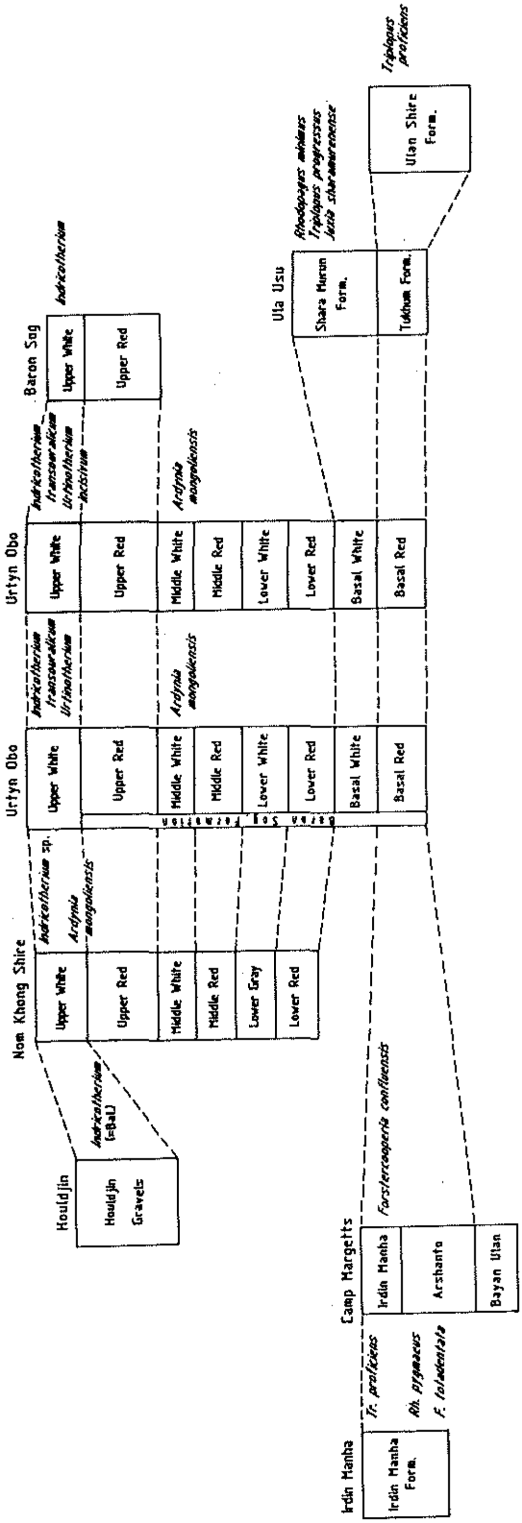

Fig. 6.— Stratigraphical distribution of hyracodontids in the Paleogene of North China.

The Valley of the Shara Murun River

Ulan Shire

The locality is 35 km north of the Baron Sog Lamasery within the North Mesa system of exposures. Many fossil bones were collected by the Central Asian Expedition between 1925 and 1928 north of the Tukhum Lamasery in the Chimney Butte outcrops. Hyracodontidae are represented here by the species *Triplopus proficiens*. The locality is dated as Middle Eocene.

Ula Usu

The locality is 24 km northwest of the Baron Sog Lamasery on the western limb of Baron Sog Mesa. It was also originally examined by the Central Asian expedition in 1922 (Radinsky, 1964). The SCPE which visited the exposure in 1959 collected some fossils (Chow & Rozhdestvensky, 1960). The Hyracodontidae described are *Triplopus progressus* and *Juxia sharamurunense* (Radinsky, 1967; Chow & Chiu, 1964). The mammal fauna of the Ula Usu locality indicates an Upper Eocene age (Osborn, 1929; Radinsky, 1964; Li & Ting, 1983).

Urtyn Obo (fig. 7)

It is located on the eastern flank of the Shara Murun valley in the East Mesa system of exposures, 40 km northeast of the Baron Sog Lamasery. It was discovered by the Central Asian Expedition in 1928 (Radinsky, 1964). The locality was visited by the SCPE in 1959 (Chow & Rozhdestvensky, 1960). Hyracodontidae are represented in the collections of these expeditions by the species *Urtinotherium incisivum* and *Indricotherium transouralicum* (Granger & Gregory, 1936; Gromova, 1959; Chow & Chiu, 1964). The age of the Baron Sog Formation in this locality is determined as Early Oligocene (Dashzeveg, 1976; Li & Ting, 1983).

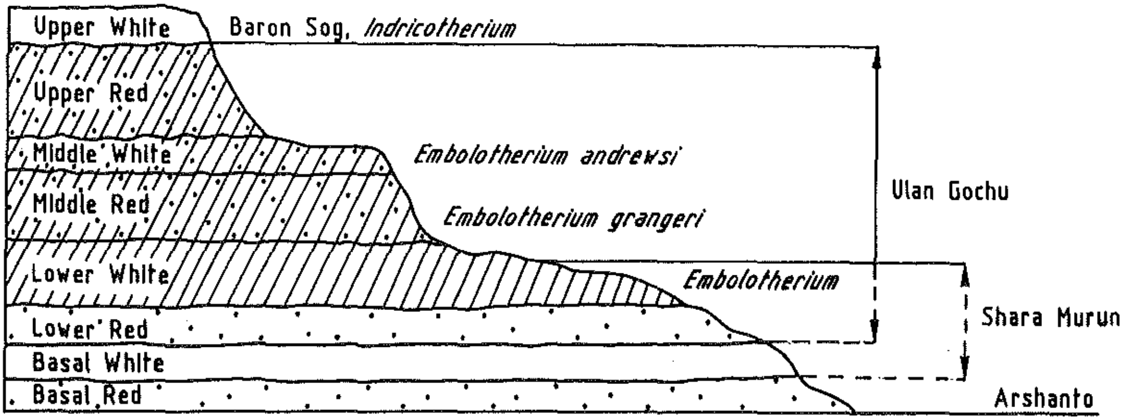

Fig. 7.— Section at Urtyn Obo, Baluchithere Camp (from Osborn, 1929).

Nom Khong Shire (= Nom Kong Obo)

The locality is situated approximately 25 km northwest of the Baluchitherium Camp within North Mesa. It was discovered by the Central Asian Expedition in 1928 (fig. 8).

The Nom Khong Shire section exposes Upper Eocene and Lower Oligocene strata (Osborn, 1929). The presence of the Shara Murun deposits has not been proved paleontologically. From the Ulan Gochu Formation, the locality contains *Schizotherium* sp. (Colbert, 1934). In the Baron Sog strata, *Ardynia mongoliensis* (= *A. kazachstanensis*) and *Indricotherium* sp. (= *Baluchitherium grangeri*) are known (Radinsky, 1967; Granger & Gregory, 1936).

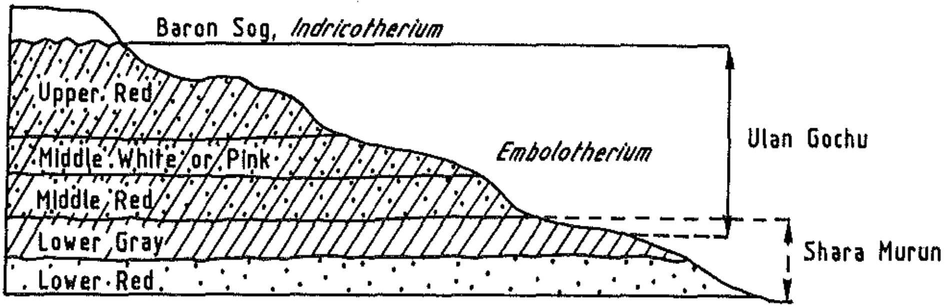

Fig. 8.— Section at Nom Khong Shire Holy Mesa Camp (from Osborn, 1929).

THE EOCENE/OLIGOCENE BOUNDARY IN MONGOLIA AND NORTHERN CHINA

Essential to the Eocene/Oligocene boundary in Central Asian continental strata are biostratigraphic data of the West European Paleogene. The virtue of the continental Paleogene in Western Europe is the successive system of marker horizons identified by various mammal groups (Brunet, 1977).

Throughout the Eocene, Asia and Europe were isolated from each other. Evolution of land mammals on the two continents took place separately, in isolation, which makes correlation of the Eocene of Eurasia on the basis of mammals impossible.

Rapid evolution of the mammals and their widespread migration from Asia to Western Europe early in the Oligocene have allowed this group to be used for stratigraphic and correlation purposes. Guide species and genera of the mammals have provided a system of successive marker horizons for the Oligocene of Western Europe. These marker horizons have helped to specify the position of the Eocene/Oligocene boundary on the West European standard scale (Cavelier, 1979). At the base of the Oligocene in the Paris Basin, the Ronzon marker is established, with its age equivalents in the rest of Western Europe well characterized by the early immigrants of the "Grande Coupure". The major role belongs to Asian immigrants, *Eucricetodon*, *Steneofiber*, *Entelodon*, *Bothriodon*, etc., which appear at the base and in lower horizons of the Oligocene (fig. 9).

Some researchers believe that Early Oligocene east-west migration of the mammals was asynchronous in various European provinces and that this paleobiogeographical event could not be accepted as the basis of the Eocene/Oligocene boundary (Sigé & Vianey-Liaud, 1979). It should be noted that in large basins of France (Paris and Aquitaine Basins), England (Hampshire) and Belgium, basal Oligocene horizons are characterized by early guide elements of the "Grande Coupure". This fact proves unambiguously the validity of mammals as biostratigraphic substantiators of the lower Oligocene boundary (Russell *et al.*, 1982). In fact, it is hard to correlate definitely and directly the lower horizon of the continental Oligocene (containing early immigrants of the "Grande Coupure") with zone NP 21 of marine strata. Although there is some discrepancy between the lower Oligocene boundaries in sequences belonging to different facies, age discrepancies are considered insignificant.

The most important genera for the substantiation of the lower Oligocene boundary in Mongolia and China are *Entelodon*, *Bothriodon*, *Ronzotherium* and *Nimravus*. Their stratigraphic value has been verified in the standard sections of the West European Oligocene. In Central Asia, they are restricted to a relatively narrow stratigraphic interval and yet have a wide geographic distribution. This is important for stratigraphic correlation.

MONGOLIA: EASTERN GOBI DESERT

Upper Eocene and Lower Oligocene strata with rich faunas are well known in the eastern Gobi Desert (fig. 9).

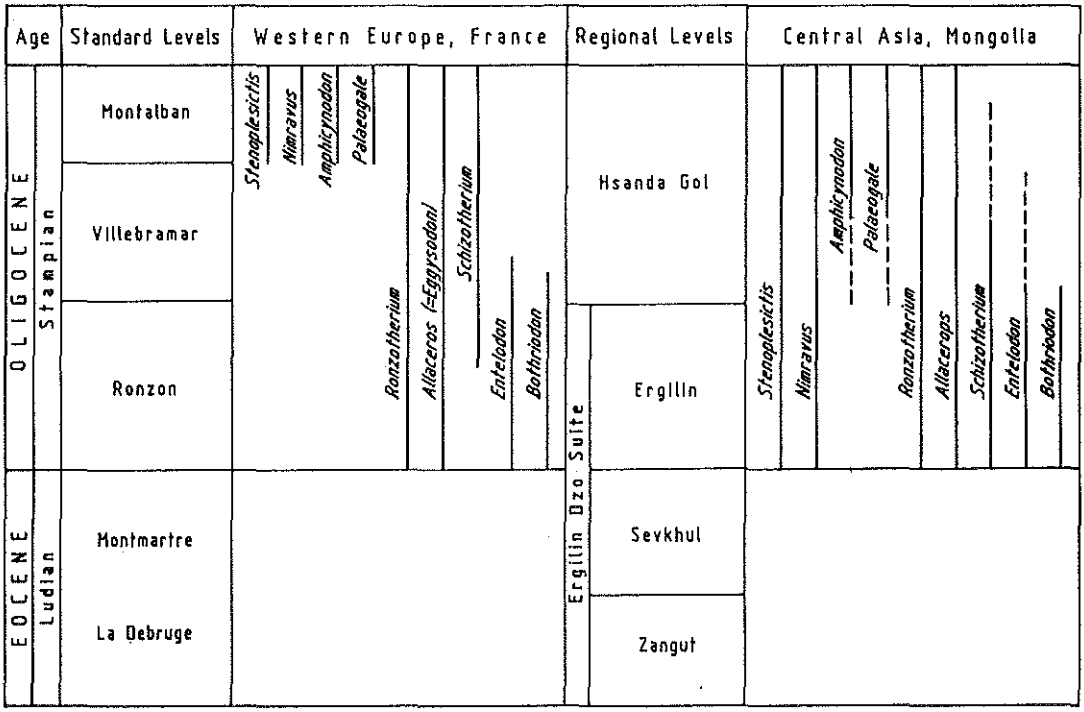

Fig. 9.— Correlation of the Oligocene deposits in Central Asia (Mongolia) and Western Europe (France).

Ergilin Dzo

This is a classic locality for Late Eocene and Early Oligocene mammals in Asia. Its section is to be considered as a key one for the Eocene/Oligocene boundary in continental sequences. The question of the age of the Ergilin Dzo sequences has long been the centre of discussion. Yanovskaya, Kurochkin and Devyatkin (1977) have used lithological and paleontological data to regard the whole of the Ergilin Dzo as a single Lower Oligocene complex.

Mammalian fossils are known mostly from two members (Sevkhul and Ergilin) of the Ergilin Dzo suite (Dashzeveg & Devyatkin, 1986). The presence of *Amynodon*, *Teleolophus*, *Epimanteoceras*, *Parabrontops*, etc. in the Sevkhul fauna makes it in general archaic. This fauna is an extension of the typical Eocene fauna of Shara Murun. On the other hand, such genera as *Pterodon*, *Hyaenodon*, *Schizotherium*, *Ardynia* and *Lophiomeryx* have a wide stratigraphic range and are thus practically useless for precise dating of the enclosing sequences. It should be remembered that *Teleophus*, *Amynodon* and some brontotheriids (*Epimanteoceras*, *Parabrontops* and *Protembolotherium*) entirely disappear at the boundary between the Sevkhul and Ergilin Members.

This boundary has a clear ecosystematic nature. It marks a change in the ecological dominants. Thus, inhabitants of marsh or humid plains and coasts give way to more progressive representatives, such as *Bothriodon*, *Gigantamymodon* and *Embolotherium ergiliense*. At this time landscapes of semi-open and open interstream areas were predominant. Open savanna-like spaces were inhabited by *Entelodon*, *Ronzotherium* and *Indricotherium*. In more open, woodless biotopes fossorial rodents such as *Ardynomys* lived.

Ecostratigraphy is known to stress the importance of the ecological nature of stratigraphic boundaries. These are interpreted as traces of events in the geobiological record, but not as entry levels or disappearance of separate species or features. The Eocene-Oligocene boundary in the Ergilin Dzo sections is traced at the base of the Ergilin Member. Consequently, the Ergilin Dzo suite falls within the interval of the Upper Eocene to Lower Oligocene.

Khoer Dzan

This locality adds significantly to the data on the stratigraphy and paleontology of the Ergilin Dzo suite. The largest number of vertebrate fossils are known from the Sevkhul and Ergilin Members (fig. 3). A radical change in the ecological dominants is also registered here at the boundary between the two members. At this boundary, *Mongolonyx*, *Metahapalodectes*, *Pterodon?*, *Teleolophus*, *Amynodon* and *Eoentelodon* disappear entirely while *Ronzotherium*, *Indricotherium* (or *Urtinotherium*) sp., *Nimravus*, *Entelodon* and *Bothriodon* appear. *Hyaenodon gigas* and *Embolotherium andrewsi* accompanying *Entelodon* and *Bothriodon* help to identify the Lower Oligocene horizons in the Khoer Dzan sections. Thus, the lower horizons of the Ergilin Dzo suite, Dzangut and Sevkhul, are dated as Upper Eocene, while the Ergilin Member is dated as Lower Oligocene.

Continuous series of Upper Paleogene strata are most extensive in the Shara Murun Valley where they are well characterized by fossils.

Urtyn Obo

This is the most complete and promising section in terms of the Eocene-Oligocene boundary within northern China. The lower part of the section shows outcrops of Basal Red beds, Basal White and Lower Red beds that still lack paleontological data (fig. 7). The Urtyn Obo exposure shows well the succession of beds that compose the Ulan Gochu and Baron Sog Formations. These sequences are exposed also in the Twin Obo and Djama Obo localities on the western flank of the East Mesa.

Remains of *Teleolophus magnus* (Deperetellidae) have been found in the middle Red beds of Urtyn Obo (Radinsky, 1965). From this level, a large brontothere, *Embolotherium grangeri* is known, while *Embolotherium andrewsi* has been described from the Middle White beds (Osborn, 1929). Osborn mentions relics of *Embolotherium* of uncertain systematic position from the Lower White beds. The capping Upper Red layers of the Ulan Gochu Formation, some 28.5 m thick, have no fossils.

It should be noted that the Ula Usu locality (Shara Murun Formation) on the western flank of Baron Sog Mesa (stratigraphicaly lower than the Ula Usu locality [Shara Murun Formation], the stratotype of the Ulan Gochu Formation) is known to contain a comparatively progressive form of *Deperetella cristata*. This gave Radinsky strong doubts as to whether *T. magnus* really belonged to the Middle Red beds of the Ulan Gochu Formation. He concluded therefore that field labels of this find had been mixed up. Radinsky admits three possible alternatives to explain the appearance of *T. magnus* in higher levels than the one with *Deperetella cristata*:

- Fossils of *T. magnus* might have been collected in the so-called Shara Murun sequences or older strata of Urtyn Obo that were misnamed as Ulan Gochu;
- "Ulan Gochu" sequences in the vicinity of Urtyn Obo are stratigraphically lower than the type sections of Ulan Gochu in the system of Baron Sog Mesa exposures;
- *T. magnus* is a relatively large but primitive, later form of the *Teleolophus* lineage which survived the extinction (at least, in this area) of *Deperetella cristata.*

Radinsky noted that remains of deperetellids from Shara Murun and "Ulan Gochu" are practically identical in terms of preservation. It is difficult therefore to judge the validity of the first supposition. In relation to the second alternative the author stressed that correlation of "Ulan Gochu" sequences in Urtyn Obo and Ulan Gochu in the stratotypical section of the Shara Murun Valley was based on studies of all the faunas collected. As for the last alternative, Radinsky argues that morphologically *T. magnus* occupies an intermediate position between *T. medium* from Irdin Manha and *D. cristata* from Shara Murun (Radinsky, 1965).

To clarify the stratigraphic position of *T. magnus*, a new find of this species in the neighbouring Mongolian localities of Khoer Dzan and Ergilin Dzo should be mentioned. Most of the finds of this species are derived from light grey sands of the Sevkhul Member in the so-called "western field" of the Khoer Dzan locality. These localities were found to contain, apart from *T. magnus*, *Colodon inceptus*, *Pterodon exploratus*, *Lophiomeryx*, *Eoentelodon trofimovi*, etc.

In western ridges of Ergilin Dzo, I have found jaws with M_1-M_3 of *T. magnus* in light grey Sevkhul sands. At this level, remains of a large *Embolotherium* have been discovered.

Thus, the most reliable finds of the tapiroid *T. magnus* in Khoer Dzan and Ergilin Dzo belong almost to the same stratigraphic level of the Sevkhul Member.

These data may suggest the following answers to the question raised by Radinsky:

1: Association of the *T. magnus* finds with the base of the Middle Red member of the "Ulan Gochu" Formation is certain. Thus, Granger's field label is to be considered correct.

2: Sequences of the Ulan Gochu type developed in Urtyn Obo sections are time equivalents of the type section of the Ulan Gochu Formation, north of the buddhist monastery, Baron Sog Sum. These sequences are most fully exposed in the Eastern Mesa area, especially in the Twin Obo and Djama Obo localities where they have a good paleontological record.

3: It should be stated that morphological transformations and rates of evolution in the genera *Deperetella* and *Teleolophus* were entirely independent and asynchronous.

The Urtyn Obo section is capped by the so-called Upper White or Grey sequences (Baron Sog Formation), only 6.5 m thick. The mammals found in the Baron Sog Formation are stratigraphically dominated by *Entelodon* sp. (= *Archaeotherium ordosius*, see Dashzeveg, 1977; Brunet, 1979) and *Indricotherium transouralicum* (= *I. grangeri*), etc.

It can be argued therefore that the Urtyn Obo section in China is similar to the Khoer Dzan and Ergilin Dzo sections in Mongolia. The Lower Oligocene boundary in Urtyn Obo is traced beneath the Baron Sog Formation.

EOCENE AND OLIGOCENE CORRELATION IN THE EASTERN GOBI DESERT (MONGOLIA) AND NORTH CHINA

Tapiroids in the Mergen fauna are represented by two well known species, *Lophialetes? minutus* and *L. expeditus*. Both were described earlier from the Eocene of Irdin Manha. Remains of *L. expeditus* have been reported also from the Camp Margetts and Ulan Shire localities (Matthew & Granger, 1925; Radinsky, 1965). These data suggested reliable correlation of the upper Mergen section with the Irdin Manha and Ulan Shire Formations of Northern China. Collections from Mergen contain isolated teeth of *Harpagolestes* (family Mesonychidae). Examination of Mesonychidae from Mergen shows that they may be referred to the species *Harpagolestes orientalis*, previously known from Chimney Butte in the Ulan Shire locality (Li & Ting, 1983). Apart from the above named forms, the fauna comprises rodents of the genus *Yuomys*. The latter are represented by isolated upper teeth which, in contrast to those of *Yuomys cavioides* from the Upper Eocene of Ula Usu (China), have a less well developed hypocone and a less distinct fold between the protocone and the hypocone.

As for the fossil birds of the genus *Eogrus* from Mergen, they have been described earlier from the Eocene of Irdin Manha on the materials collected by the Central Asian Expedition in the late 1920's (Wetmore, 1934). The cited paleontological evidence proves the existence of Middle and Upper Eocene sequences in the Doloodoi Lake Basin.

The time equivalent of the Ula Usu fauna of Inner Mongolia is the Alag Tsav locality situated 35 km west of Khoer Dzan (Dashzeveg, 1985). Fossils of vertebrates have been discovered in clayey sandstone in the mid-section. The finds of *Archaeomeryx* and a *Gigantamynodon* in the section permit the Alag Tsav locality to be dated as Upper Eocene and to be correlated with the Ula Usu locality (Shara Murun Formation) of Northern China.

Sections of Ergilin Dzo and Khoer Dzan in Mongolia are in general very similar to those of Ulan Gochu and Baron Sog of Inner Mongolia, China (fig. 10). This is confirmed by the identical succession, composition and colour of their beds, as well as the character of the fauna. Owing to the similarity of lithology and coloration, the Khubsugul beds (from the Ergilin Dzo suite) are correlated conventionally with the Lower Red layers of the Ulan Gochu Formation in the Urtyn Obo exposures. These parts of the Upper Eocene sections of Mongolia and China have not yet been faunistically characterized.

The Dzangut Member, with *Embolotherium* sp., *Prohyracodon*, *Hyaenodon* sp. and others, that directly overlies the Khubsugul Member in the Khoer Dzan series

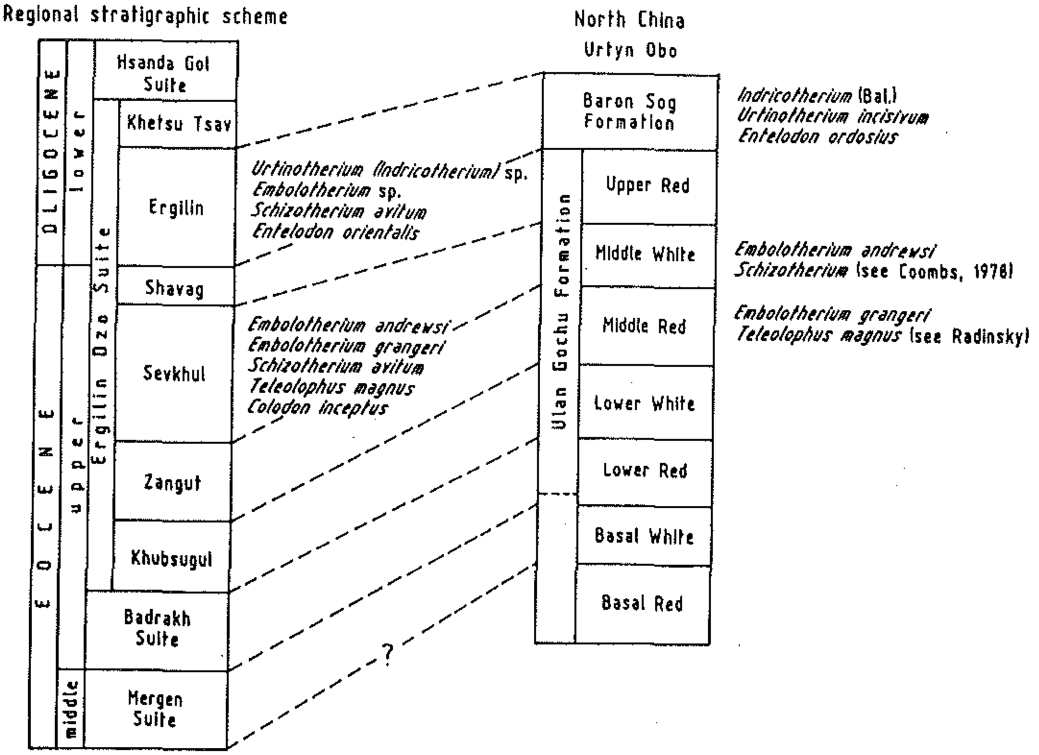

Fig. 10.— Correlation of Eocene-Oligocene sequences in Mongolia and North China.

correlates conventionally with the Lower White layers of the Ulan Gochu Formation. Osborn (1929) reported his find of *Embolotherium* in the Lower White layer of the Urtyn Obo outcrop. The next, Sevkhul Member, which is very distinct in the key Paleogene sections of the eastern Gobi Desert is correlated with more confidence with the upper part of the Ulan Gochu Formation, including the MiddleRed and White layers that outcrop in the system of the East Mesa.

Correlation of these sequences is controlled by big animals such as *Embolotherium*, etc. *Embolotherium grangeri* occurs in White sands of the Sevkhul Member in the Khoer Dzan locality. *Colodon inceptus*, *Amynodon lunanense*, *Schizotherium avitum*, *Eoentelodon trofimovi*, *Teleolophus magnus*, etc. are known from this level. According to American data (Osborn, 1929; Granger & Gregory, 1943), *E. grangeri* was discovered at the base of the Middle Red bed, while *E. andrewsi* was discovered in the Middle White layer of the Urtyn Obo locality. Fossils of *T. magnus*, judging by their field labels, have been derived from the base of the Middle Red layer (Ulan Gochu Formation) of the Urtyn Obo locality (Radinsky, 1965). I have recently found this species in the Sevkhul Member in the western ridges of Ergilin Dzo. In the Ergilin Dzo and Khoer Dzan sections of Mongolia, lithological equivalents of the Middle Red bed of the Ulan Gochu Formation, must be missing. The Sevkhul Member in these Mongolian localities can be correlated paleontologically with the Middle Red and Middle White layers of the Ulan Gochu Formation (fig. 10).

N. M. Yanovskaya (1980) mentioned her finds of *E. andrewsi* in Ergilin Dzo where this species is found in the Sevkhul and Ergilin Members, i.e. passing from the Eocene into the Oligocene. The author's reference of skeletal remains from the Oligocene of Khoer Dzan to *E. andrewsi* is considered ill-founded. Firstly, *E. andrewsi* is known exclusively by its skull. Secondly, the genus now includes three species known from close stratigraphic levels in Mongolia and China. It should be remembered that *E. ultimum* from the Baron Sog Formation scarcely differs from *E. andrewsi*, being a possible synonym of the latter. In this case, *E. andrewsi* in Inner Mongolian sections has a long stratigraphic range, from the Ulan Gochu Formation (Middle White layer) through the Baron Sog Formation. Hence, *E. andrewsi* is of little use for detailed correlation.

Apart from Urtyn Obo, sections of the Ulan Gochu type are well known in Twin Obo and Djama Obo on the east side of the Shara Murun Valley. Bone-bearing layers of the Sevkhul Member (Ergilin Dzo suite) correlate with the "Ulan Gochu" sequences in Twin Obo and Djama Obo sections, as evidenced by finds of *E. grangeri*, *Metatitan progressus* and *Mongolestes* cf. *hadrodens* in light grey sands of the Sevkhul Member in the Khoer Dzan locality.

Dawson (1968) who studied remains of *Ardynomys* from Djama Obo and Ulan Gochu noticed that they did not differ from the forms from Ergilin Dzo (= Ardyn Obo). *Ardynomys* occurs in Ergilin Dzo and Khoer Dzan, found in the first case in the upper part of the Sevkhul Member and in the lowermost Ergilin Member, and in the second case, in the yellow gravels of the Ergilin Member. Hence, *Ardynomys* in Mongolian sections ranges from the Late Eocene into the Early Oligocene.

Burke (1941) used his studies of Leporidae to conclude that the Ulan Gochu Formation was older than that of Ergilin Dzo though he dated both of them as Lower Oligocene.

It should be remembered that *Desmatolagus* in Ergilin Dzo is derived fro mtwo stratigraphic levels: from the Sevkhul Member where I have found remains of the species *Desmatolagus vetustus*, first described from Twin Obo (Burke, 1941), in the locality Shavag 30 km west of Ergil Obo; and from the Ergilin Member, where *D. gobiensis* was found, known also in the Hsanda Gol fauna of the Valley of Lakes (Gureev, 1964). Thus, Burke's conclusion is supported by additional data, and the Ulan Gochu layers from Twin Obo and Djama Obo are older than the upper beds of Ergilin Dzo (Ergilin Member) and correlate well with the Sevkhul Member of the Ergilin Dzo suite.

The Shavag Member from the Ergilin Dzo suite of Mongolia is correlated conventionally with the Upper Red layer of the Ulan Gochu Formation in the Shara Murun area. The upper horizons of the Ergilin Dzo suite (Ergilin and Khetsu Tsav Members) correlate with the Baron Sog Formation of Inner Mongolia. The Baron Sog Formation stratotype is poorly characterized, as the American expedition collections are still uninterpreted. Note that in 1924-1925 the American expedition found remains of *Entelodon, Indricotherium*, predators and other mammals in this formation 7 km north of the Baron Sog Lamasery (Osborn, 1929).

Of major importance for the correlation of the Baron Sog Formation are Urtyn Obo sections in the system of East Mesa exposures. The Urtyn Obo Formation was dated as Middle Oligocene (Berkey & Morris, 1927; Granger & Gregory, 1943). Such a date is clearly too recent. A tendency by American authors to give younger than normal ages for Tertiary sequences existed also in the works of the American Asian expedition. It can be well illustrated by the "*Baluchitherium* layers" of Mongolia and China. The Hsanda Gol fauna had first been thought to be Miocene, while the Houldjin gravel and the Urtyn Obo Formation, because of the "*Baluchitherium*" finds in them, were dated as Middle (or even Upper) Oligocene. This may be accounted for by the fact that remains of giant rhinoceros from the named localities were referred to the genus *Baluchitherium*, previously known from Bugti Hills in Pakistan (Osborn, 1923; Granger & Gregory, 1936). The Bugti fauna was believed to be Late Oligocene or Early Miocene (Pilgrim, 1932).

Until recently, the Urtyn Obo locality, in contrast to Ergilin Dzo, was characterized by the presence of *Indricotherium* (= *Baluchitherium grangeri*) *transouralicum*. In recent years, *Indricotherium* remains have been found in the upper horizons of Ergilin Dzo and Khoer Dzan. The gap thus gradually became narrower.

The upper layers of the Urtyn Obo and Ergilin Members shared the species *Cadurcodon ardynensis* and close or identical forms of *Schizotherium avitum*. The marsh rhinoceros *C. ardynensis* is a typical representative of the Ergilin fauna, first described as an included species from the Ergilin Dzo locality (Osborn, 1925; Gromova, 1954). Its stratigraphic range in the Mongolian sections of the eastern Gobi Desert has been firmly established. Its vertical distribution here is limited to the Sevkhul and Ergilin Members. The presence of *C. ardynensis* in the upper horizon of Urtyn Obo points to the Lower Oligocene age of the enclosing sequences.

Schizotherium in Urtyn Obo is known from two stratigraphic levels. A fragment of an upper jaw (A.M. No. 26061) was found at the base of the Upper Red or Middle White layer, and a lower jaw (A.M. No. 103336), in the Baron Sog layers (Radinsky, 1964). Radinsky was not certain about the exact position of these *Schizotherium* specimens, especially those from the Baron Sog Formation in the Urtyn Obo exposure. Coombs

(1978) having studied the *Schizotherium* from the locality tentatively referred them to *Schizotherium avitum*. Judging by the figures, the upper and lower teeth of the Urtyn Obo *Schizotherium* do not differ from the Mongolian *S. avitum*. It should be noted that the remains of *Schizotherium* in Khoer Dzan occur at two stratigraphic levels, in the Sevkhul and in the Ergilin Members. Consequently, the presence of *Schizotherium* at two Urtyn Obo levels is very likely.

Entelodon (= *Archaeotherium ordosius*) is known from the upper horizon of Urtyn Obo. The co-occurrence of *Cadurcodon ardynensis*, *Schizotherium* and *Entelodon* in Ergilin Dzo and Urtyn Obo is additional proof of the synchronous age of the upper horizons of these localities. In this paper, we accept the Lower Oligocene age for the upper Urtyn Obo horizons. The Ergilin Member of the Ergilin Dzo suite and the Baron Sog Formation have the same age.

SYSTEMATICS

Family **HYRACODONTIDAE** COPE, 1878

The diagnosis of the family is to be found in Radinsky (1967). To diagnose lower taxa, apart from my own studies, I used data from Beliayeva (1952, 1954), Wood (1927, 1938, 1969), Brunet (1979), Gromova (1959), Radinsky (1967) and Heissig (1968).

The family includes three subfamilies: Triplopodinae, Hyracodontinae and Indricotheriinae.

Subfamily **TRIPLOPODINAE** OSBORN & WORTMAN, 1892

Diagnosis: Relatively small in size. Dental formula: I 3/3, C 1/1, P 4/4, M 3/3. Incisors and canines similar in size and shape. Molars low-crowned; crown height index averaging 0.61. P^4 non-molariform, with a large protoloph. P_4 commonly strongly molarized; entoconid has the form of an isolated cuspule or rarely is fused with the hypolophid.

Included genera: *Triplopus*, *Prohyracodon*, *Rhodopagus* and *Pataecops*.

Comparison: For comparison with other subfamilies see the descriptions of the latter.

Genus *TRIPLOPUS* COPE, 1880

(Fig. 11, 12)

For synonymy, see Radinsky, 1967.

Type species: *T. cubitalis* (COPE, 1880).

Diagnosis: Small sized triplopodine hyracodontids. M^1-M^3 vary in length from 30 to 70 mm. Dental formula complete. Incisors and canines small, almost similar in shape and size. Molars low crowned; crown height index approximately 0.61. P_{3-4} strongly molarized. M^3 with a small metacone. Feet three-toed.

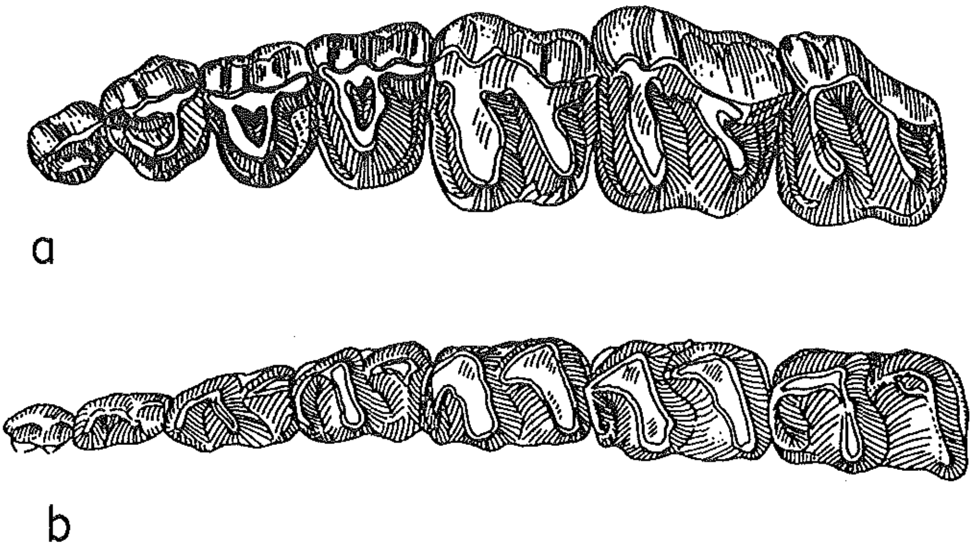

Fig. 11.—*Triplopus? proficiens* (MATTHEW & GRANGER), A.M.N.H. n° 21552, P^1-M^3; A.M.N.H. n° 26124, P_1-M_3 (from Radinsky, 1967, fig. 6); x 1.5; a, b: occlusal views.

Included species: Seven species: *T. cubitalis* (COPE, 1880), *T. implicatus* (COPE, 1873), *T. obliquidens* (SCOTT & OSBORN, 1887), *T. rhinocerinus* (WOOD, 1927); *T. proficiens* (MATTHEW & GRANGER, 1925), *T. ckhikvadzei* GABUNIA, 1984, *T.? mergenensis* sp. nov.

Discussion

In tentative reports by Matthew and Granger (Matthew & Granger, 1925, a, b), the genus *Caenolophus* was characterized exclusively by the lower jaw. Because of the paucity of material, it was hard to judge its systematic position within the Hyracodontidae. Radinsky (1967) had available more complete specimens collected by the Central Asian Expedition of the AMNH from the Eocene of Ulan Shire allowing him to conclude that the genus *Caenolophus* was synonymous with the genus *Triplopus*, previously known only from the Upper Eocene of North America. In the present paper, this synonymy is accepted.

Triplopus? mergenensis sp. nov.

(Fig. 12)

Etymology: The name is derived from the Mergen locality.

Holotype: PSS, n° 41-1, a fragment of a left lower jaw with P_2-M_3.

Material: Apart from the holotype, right P^4, PSS, n° 41-2.

Localiy and age: Mongolia, eastern Gobi Desert, Mergen (20 km northwest of the Dzamyn Ude station) Middle Eocene, Mergen suite.

Diagnosis: Medium-sized *Triplopus*. Length of M_1-M_3, 70 mm. $P_{3\text{-}4}$ considerably

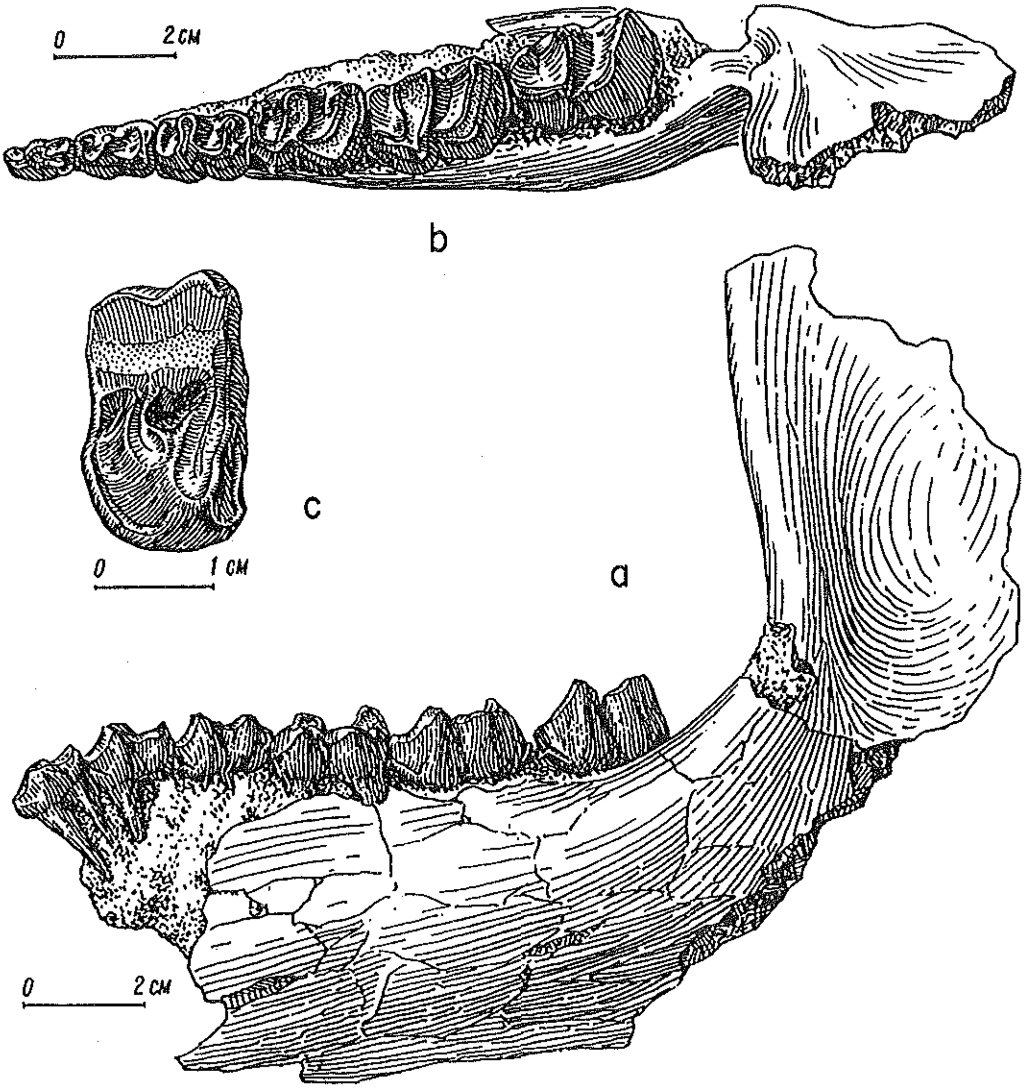

Fig. 12.— *Triplopus? mergenensis* sp. nov., PSS n° 41-1, holotype, a fragment of right lower jaw with P_2-M_3; a: labial view; b: occlusal view; c: PSS n° 41-2, a right P^4; occlusal view.

molarized; entoconid fused with the hypolophid. The hypoconulid on M_3 indistinct. The cingulum undeveloped.

Description

Judging from the lower jaw, the size is 1.5 times bigger than *T. proficiens*. The horizontal ramus of the lower jaw is apparently relatively deep; it is 44 mm deep between M_1 and M_2. There is no cingulum on the lower teeth. P_1 is not preserved, P_2 is non-molariform and double-rooted. The trigonid and its basin are simple. The talonid is slightly wider than the trigonid. The hypolophid is well developed, and the paralophid stands out. The entoconid is quite distinct and fused with the hypolophid. P_4 is more molarized than P_3

P_2	Length	10
	Trigonid width	0.6
	Talonid width	0.8
P_3	Length	12.5
	Trigonid width	
	Talonid width	12
P_4	Length	16
	Trigonid width	12.5
	Talonid width	12.5
M_1	Length	17.5
	Trigonid width	12
	Talonid width	13
M_2	Length	21.5
	Trigonid width	14
	Talonid width	15
M_3	Length	23
	Trigonid width	14.5
	Talonid width	15
P^4 (n° 41-2)	Length	16
	Width	26.5

Table 3.— Measurements of the lower cheek teeth and P^4 of *Triplopus? mergenensis* sp. nov.

and has a better developed metalophid. The metalophid and hypolophid on P_{3-4} are almost perpendicular to the horizontal dental axis.

The size of the lower molars gradually increases from M_1 to M_3. The metaconid is the highest cusp on these teeth. The trigonid basin is comparatively narrow but distinct. The M_{2-3} metalophid is perpendicular while the hypolophid is slightly inclined to the horizontal dental axis. P^4 is narrow: its breadth is 1.6 times greater than its length. The paracone is very prominent and its outer rib distinct. The parastyle fold is quite distinct. The labial fold between the paracone and metacone is thick and can be traced almost to the base of the crown. The protoloph is developed, whereas the metaloph is much shorter than the protoloph. The trigon basin is closed. The cingulum is developed and prominent at the base of the labial, anterior and posterior sides of the crown.

Comparison

It differs from *T. proficiens* from the Eocene of Inner Mongolia by its relatively larger size and more prominent hypolophid on P_{3-4}, as well as a "tapiroid" metalophid which is almost perpendicular to the long axis of P_4-M_3. It differs from *T. ckhikvadzei* from the Middle Eocene of the Zaisan Depression by a comparatively deeper ramus of the lower jaw and a more molarized P_3. No P_1 preserved in the *T.? mergenensis* holotype. Its

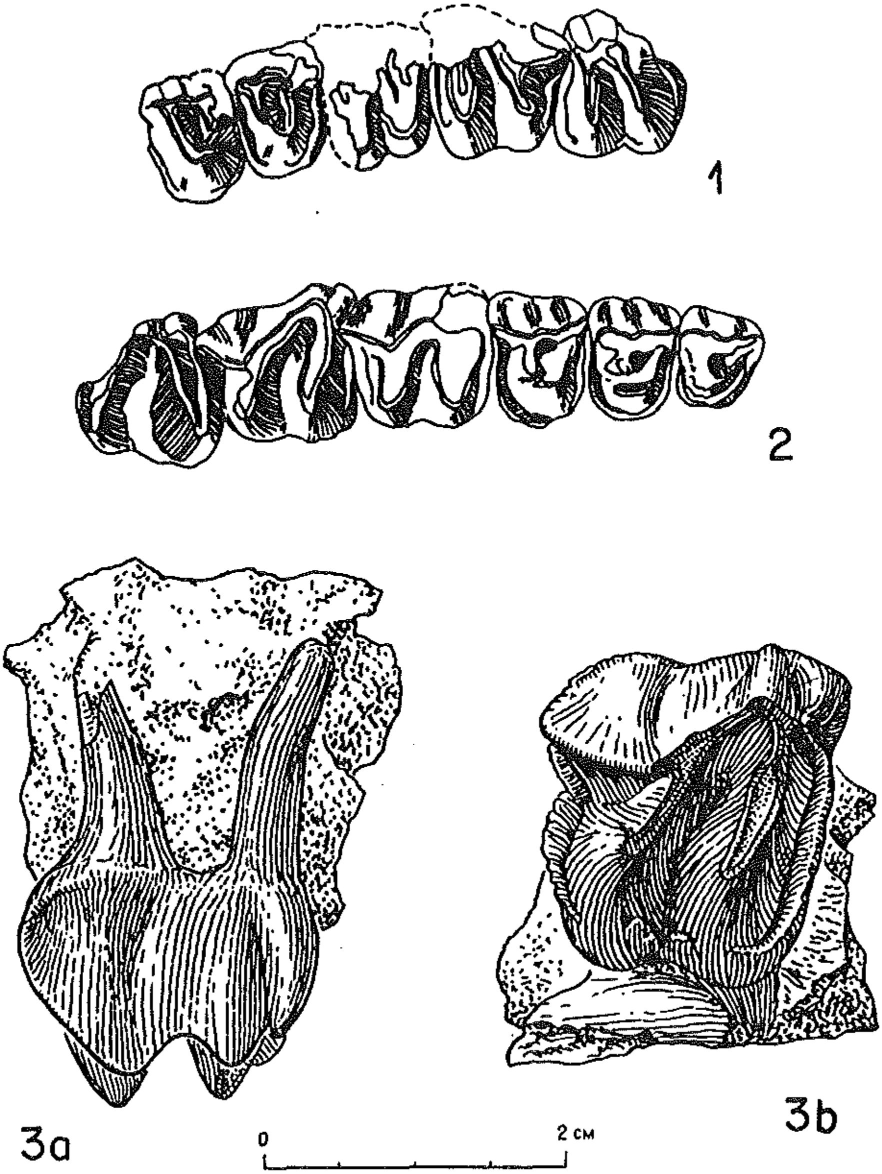

Fig. 13.— Teeth of *Prohyracodon*. **1**: *Prohyracodon orientale*, P^2-M^3; x 1 (from Wood, 1929, fig. 6). **2**: *Prohyracodon meridionale*, holotype, n° 0046, P^2-M^3; x 1 (from Chow & Xu, 1961, fig. 3). **3**: *Prohyracodon meridionale*, a right M^2, PSS n° 27-18, from Khoer Dzan beds, Mongolia; a: labial view; b: occlusal view.

presence in the jaw is suggested by a weak facet on the anterior face of P_2. P_1 of *T. ckhikvadzei* is known to be reduced (Gabunia, 1984). Note that the talonid is narrower than the trigonid of the lower teeth of the Zaisan form and slightly broader on all the molars of the Mongolian species.

It differs from the North American species *T. implicatus*, *T. rhinocerinus*, etc., by a more perpendicular position of the metalophid and a less developed protoloph on P^4.

Discussion

The species described shows distinctive features of the genus *Trilopus*: molarized P_3 and P_4, gradually increasing tooth size from P_1 to M_3, and other features. However, the described form, in contrast to the typical *Trilopus* is larger and has a tapir-like metalophid on P_1-M_3. These metalophids are almost perpendicular to the long axis of the tooth, while the hypolophid is similar in structure to previously described species of the genus *Triplopus*. Note that the P^4 index of *T.? mergenensis* is 60%, whereas that of *T. proficiens* is 76%; i.e. P^4 of the former is narrower.

Thus, there is so far no form among the known Triplopodinae identical to *T.? mergenensis*. Because of lack of evidence, the question of its generic affinity is still open.

Genus ***PROHYRACODON*** KOCH, 1897

(Fig. 13, 14, 15)

Prothyracodon: Beliayeva, 1954.

For complete synonymy, see Radinsky, 1967

Type species: *P. orientale* KOCH, 1897.

Diagnosis: Medium small-sized triplopodine hyracodontids: Length of M^1-M^3, 33-35 mm. Dental formula complete. P^2 almost quadrate in shape. P^4/P_4 submolariform; $P_{3\text{-}4}$ entoconid in the form of a separate cuspule not fused with the hypolophid; on P^4, the protoloph is robust, with an incipient separation of the hypocone on the lingual end. Metacone lost in M^3.

Included species: Four species: *P. orientale* KOCH, 1897; *P. turgaiensis* BELIAYEVA, 1954; *P. meridionale* CHOW & XU, 1961 and *P.? parvum* sp. nov.

Comparison: *Prohyracodon* differs from *Triplopus* in having a reduced metacone on M^3 and less developed hypolophids on P_4.

Discussion

Prothyracodon turgaiensis, described by E. I. Beliayeva (1954) from fragments of the lower jaw with P_4-M_3 from the Oligocene of Chelkar-Teniz (Kur Sai ravine), has the same structure as *Prohyracodon meridionale* from Mongolia. P_4 of the Turgai form is not molarized, while the entoconid is in the form of a separate cuspule which is not fused entirely with the hypolophid and does not form a transverse talonid ridge. The talonid of this form, like that of *P. meridionale*, is lower that the protoconid and forms anterior and posterior projections, the anterior one adjoining the back wall of the metalophid. $M_{1\text{-}3}$

sizes, and especially the structure of the metalophid and hypolophid of the lower molars, are typical of the genus *Prohyracodon*. The author believes that the fragments of lower jaw with P_4-M_3 described by Beliayeva (1954) from the Oligocene of Chelkar-Teniz belong to the genus *Prohyracodon*.

Prohyracodon meridionale CHOW & XU, 1961

(Fig. 13, 14)

Prohyracodon meridionale: Chow & Xu. 1961, p. 301, fig. 3, fig. 2, A.B; Radinsky, 1967, p. 26, fig. B.C.?; Li & Ting, 1983, p. 43; Chow *et al.*, 1974, p. 263, pl. II, fig. 1-8; Chow *et al.*, 1974, p. 12, pl. II, fig. 1-7.
Prohyracodon progressa: Chow & Xu, 1961, p. 303, fig. 2; Li & Ting, 1983, p. 43.

Holotype: IPP, n° 0046, a fragment of the right upper jaw with P^2-M^3; China, Yunnan, Lower Oligocene, the lower Lunan series.

Material: PSS, n° 27-18, a fragment of the right upper jaw with M^2: PSS, n° 27-44, a fragment of the left lower jaw with P_1-M_3.

Locality and age: Mongolia, eastern Gobi Desert, Khoer Dzan, Upper Eocene, Ergilin Dzo, Sevkhul Member.

Description

M^2 is slightly worn, with a quadrate crown, outline relatively low. The post-metaloph area of the ectoloph is robust, the metastyle strong. The parastyle is rather prominent. The paracone is the biggest cone on the ectoloph. The groove separating the parastyle from the paracone is quite distinct. The labial rib of the paracone is very distinct, reaching the base of the crown.

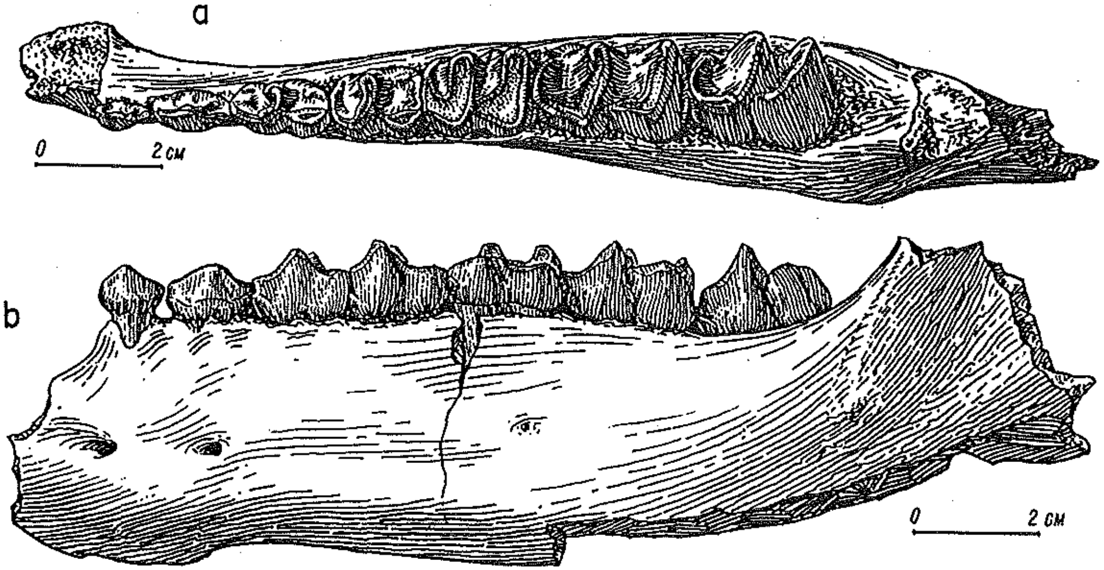

Fig. 14.— *Prohyracodon meridionale* CHOW & XU, PSS n° 27-44, a fragment of the left lower jaw with P_2-M_3 (from Khoer Dzan beds of Mongolia); a: occlusal view; b: labial view.

The horizontal ramus is relatively shallow, the lower edge almost straight. There are two mental foramina, the anterior one is 20 mm below the front edge of P_1, while the second is 18 mm below P_2. No incisors or canines are preserved. The cingulum is not developed on the lower teeth. P_1 and P_2 are not molarized at all: P_1 has a single root, P_2 has two roots which are more robust than that of P_1. P_3 and P_4 show traces of molarization: their trigonids acquire almost a triangular shape, while the talonids, in contrast to those of the molars, have an incomplete hypolophid and an isolated entoconid. P_3 has a rectangular shape in occlusal view, the hypolophid is incomplet, and the metalophid almost perpendicular to the horizontal axis of the tooth. The anterior crest, the paralophid, is quite prominent. The

Measurements and indices		n° 27-44	n° 27-21
P_1	Length	8.0	9.0
	Width	4.5	5.0
P_2	Length	10.0	12.0
	Width	6.7	8.0
P_3	Length	12.8	14.0
	Trigonid width	7.8	8.0
	Talonid width	8.0	9.0
P_4	Length	13.0	13.5
	Trigonid width	10.0	11.8
	Talonid width	10.0	12.0
M_1	Length	16.0	17.2
	Trigonid width	11.0	13.0
	Talonid width	12.0	13.8
M_2	Length	19.0	20.1
	Trigonid width	13.5	14.5
	Talonid width	14.1	15.8
M_3	Length	19.0	20.1
	Trigonid width	13.5	14.5
	Talonid width	14.1	15.8
P_1-M_3 length		104	
P_1-P_4 length		49	51
M_1-M_3 length		55	
Indices:			
P_1-P_4 length / M_1-M_3 length		89	
P_1-P_4 length / P_1-M_3 length		47.1	
Depth of the horizontal ramus at the P_1 level: 30			
Depth of the horizontal ramus at the P_4 back edge level: 33			
Thickness of the horizontal ramus at the P_1 level: 11			
Thickness of the horizontal ramus at the M_1 middle level: 15			

Table 4.— Measurements and indices of the lower cheek teeth and mandibles of *Prohyracodon meridionale*.

hypoconid is much lower than the protoconid, and its front end adjoins the protoconid. The entoconid is low and has the form of a small cuspule in the posterior-lingual region of the crown. P_4 is rectangular. The hypoconid forms anterior and inner projections. The anterior projection adjoins the back of the metalophid. The inner projections of the hypoconid on the badly worn P_4 does not reach the posterior region of the crown and is not fused with the entoconid. With deeper wear, its "hypolophid" becomes more like the hypolophid of the molars. The entoconid is isolated and situated along the lingual edge of the talonid at the front of the rear-basin.

Thus P_3 and P_4 are characterized by weak molarization and differ from the molars proper by the imperfect structure of the hypolophid.

The P_1-P_4 length accounts for 47.1% of the overall length of the cheek teeth. The molars are relatively long and narrow. Their crowns are relatively low. M_1 is more worn than P_4. The hypolophid and metalophid are parallel, the hypoconid is slightly lower than the metaconid. M_2 is a little narrower and more elongated than M_1. The trigonid basin is distinct and always open on the lingual side. The anterior transverse ridge of the metalophid is low reaching almost to the lingual side of the crown. The entoconid is slightly lower than the metaconid.

M_3 is less worn than M_2, and the hypolophid is practically intact.

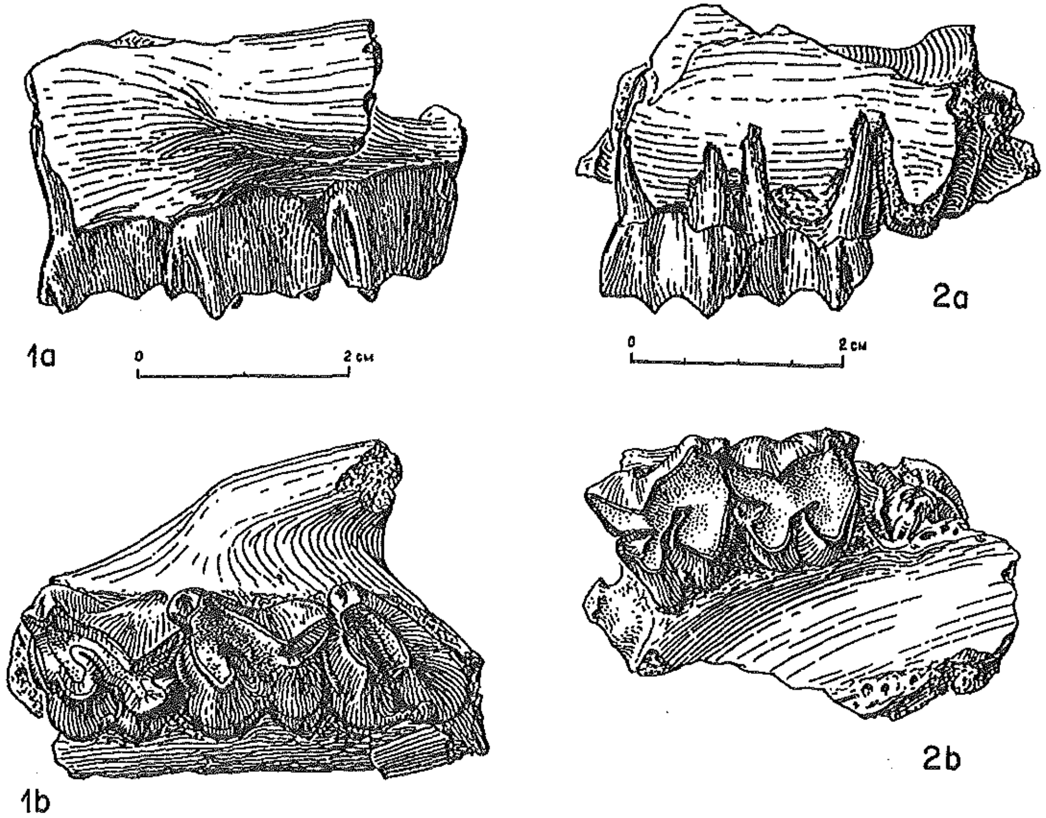

Fig. 15.— *Prohyracodon? parvum* sp. nov. **1**: PSS n° 27-14, holotype, a fragment of the left upper jaw with M^1-M^3; a: labial view; b: occlusal view. **2**: PSS n° 27-17, a fragment of the right upper jaw with P^4-M^1; a: labial view; b: occlusal view.

Comparison

Comparison of M^2 from the Oligocene of Khoer Dzan with equivalent teeth of the Hyracodontidae has shown that the described form undoubtedly belongs to the species *Prohyracodon meridionale* known from the Upper Lunan series in the Yunnan Province of China. A large paracone and a relatively low parastyle are distinctive features of *P. meridionale.* In the PIN collections from Khoer Dzan, there is a fragment of the right upper jaw with P^{1-4} with the typical structure of a *Prohyracodon.* The lingual end of the protoloph on P^{3-4} bends around the metaloph; there is a narrow fissure between the protoloph and metaloph, opening the trigon basin on the distal side. These data are significant for determination of the systematic affinity of the small rhinocerotoid from the Oligocene of Khoer Dzan.

Until recently, the genus *Prohyracodon* was known exclusively from upper molars. New finds of lower jaws with teeth of *P. meridionale* significantly reinforce its specific characters. The hypolophid on P_{3-4} of this species is always incomplete, and the entoconid remains isolated. Hence, molarization of P^{3-4} is quite apparent in the new material from the Oligocene of Mongolia.

Prohyracodon? parvum sp. nov.

(Fig. 15)

Etymology: The name of the species is derived from the Latin "parvus" = "small".

Holotype: PSS, n° 27-14, a fragment of the left upper jaw with M^{1-3}.

Material: PSS, n° 27-53, a fragment of the right upper jaw with P^{2-4}, PSS, n° 28-17, a fragment of the right upper jaw with P^4-M^1.

Locality and age: Mongolia, eastern Gobi Desert, Khoer Dzan; Upper Eocene, Ergilin Dzo suite, Dzangut-Sevkhul Member.

Diagnosis: 1.5 times smaller than *P. meridionale.* Length of M^1-M^3, 38 mm. The metaloph much shorter than the protoloph. The cingulum weak. No traces of metacone on M^3. The parastyle fold barely outlined.

Description

Small in size, approximately 1.5 times smaller than *P. meridionale*, judging by M^1-M^3. P^2 is triangular, with a distinct parastyle. The protocone is labial with respect to the hypocone. Both cuspules are quite prominent and isolated, with a narrow longitudinal notch delimiting them. P^3 is too worn for precise description. P^4 is larger than P^3. Its paracone and metacone are equal in size. The cingulum on P^{2-4} is moderately developed. M^1 is rectangular; its outer side is slightly longer than its anterior one. The parastyle is clearly distinguished. M^2 differs from M^1 by being slightly larger. The outer edge of the paracone has a strong rib reaching the base of the crown. The parastyle is smaller and lower than the paracone. The metastyle is quite prominent. The protoloph is longer than the metaloph. The medium basin on slightly worn molars reaches almost to the parastylar shelf. M^3 is triangular. Its metacone is totally reduced. The paracone is very small and the parastylar shelf distinct. The cingulum on the molars is rather underdeveloped, traced

		Holotype n° 27-14	n° 27-17	n° 27-53
P^2	Length			8.0
	Width			8.5
P^3	Length			9.0
	Width			11.5
P^4	Length		9.0	10.5
	Width		12.0	14.5
M^1	Length	12.5	13.5	
	Width	13.5	14.5	
M^2	Length	15.0		
	Width	14.5		
M^3	Length	12.5		
	Width	13.5		

Table 5.— Measurements of the upper cheek teeth of *Prohyracodon? parvus* sp. nov.

exclusively on the anterior side of the crown.

Comparison

Differs from *P. orientale* from the lower Oligocene of Romania (Wood, 1929), apart from its relatively small size, by its less developed cingulum on M^{1-3} and rather indistinct parastylar shelf. On P^{3-4} of *P. orientale*, the ligual end of the protoloph is bent considerably around the metaloph, and there is a slight separation of the hypocone from the protocone. This clearly progressive feature is not developed on P^{3-4} of the new species.

The new species differs from *P. meridionale* from the Oligocene of China and Mongolia by its smaller size and reduced parastyle on M^3.

Genus *RHODOPAGUS* RADINSKY, 1965

Rhodopagus: Radinsky, 1965, p. 207; Lucas & Schoch, 1981, p. 47; Reshetov, 1979.

Type species: *R. pygmaeus* RADINSKY, 1965.

Diagnosis: Very small triplopodine hyracodontids; length of M^1-M^3/M_1-M_3 approximately 23 mm. P_1 reduced. P_{3-4} submolariform, P^{2-4} non-molariform. The series of premolars is much shorter than that of the molars. The crown height index of the M^3 paracone averages 0.3. M_3 longer than M_1 and M_2. The symphyseal region of the lower jaw long and narrow. M^3 with a small metacone.

Included species: Three species: *R. minimus* (MATTHEW & GRANGER, 1925); *R. zdansky*

Measurements		n° 14-1
P^2	Length	4
	Width	4
P^3	Length	5
	Width	5.5
P^4	Length	5.5
	Width	7.2
M^1	Length	7
	Width	8.2
M^2	Length	7.8
	Width	9.3
M^3	Length	7
	Width	8.2

Table 6.— Measurements of the upper cheek teeth of *Pataecops parvus.*

LUCAS & SCHOCH, 1981; *R. pygmaeus* RADINSKY, 1965. The distinctness of the species *R. minutissimus* RESHETOV from the Eocene of Andarak (U.S.S.R.) is insufficiently supported.

Comparison: Differs from the genus *Triplopus* by smaller size, less molarized P_4 and a shorter series of premolars with respect to the molars.

Rhodopagus minimus (MATTHEW & GRANGER, 1921)

For synonymy, see Lucas & Schoch, 1981.

Holotype: AMNH, n° 20310, a fragment of the left ramus of the lower jaw with M_{2-3}.

Locality and age: China, Inner Mongolia, Ula Usu locality, Baron Sog Mesa; Upper Eocene, Shara Murun Formation.

Rhodopagus zdanskyi LUCAS & SCHOCH, 1981

For synonymy, see Lucas & Schoch, 1981.

Holotype: PMUU, n° 3004, a fragment of the left lower jaw with M_{2-3}; and a fragment of the left lower jaw with P_{2-3}.

Locality and age: China, Xintai County, Shandong Province; a presumably late Eocene horizon within the Guanzhuang Series at Xi Gou.

Measurements		n° 14-2	n° 14-3
P_3	Length	4.0	
	Width	3.2	
P_4	Length	5.0	
	Width	4.5	
M_1	Length	5.2	
	Width	4.8	
M_2	Length		
	Width		
M_3	Length		6.8
	Width		4.2

Table 7.— Measurements of the lower cheek teeth of *Pataecops parvus.*

Genus *PATAECOPS* RADINSKY, 1965

Pataecus: Radinsky, 1965, p. 212 (preoccupied).
Pataecops: Radinsky, 1965, p. 212.

Type species: *P. parvus* RADINSKY, 1965.

Diagnosis: Small sized triplopodine hyracodontids; length of M^1-M^3, 23 mm. Series P^1-P^4 shorter than that of M^1-M^3. The metaloph on M^{1-3} much shorter than the protoloph. The M^3 metacone much reduced. The parastylar fold well developed on the upper molars. No hypoconulid on M_3. The cingulum rather poorly developed.

Included species: Single species *P. parvus.* As for the species *P. microdon* RESHETOV, 1979 from the Eocene of Andarak in Kirgizia, its systematic position is poorly founded.

Comparison: Differs from the closest genus *Rhodopagus* from the Eocene of China by a more molariform P_4 whose hypolophid is almost complete, i.e. a small lingual cuspule, the entoconid, is fused with the hypolophid; by a more oblique position of the metalophid and hypolophid on M_{1-3} and a clearly triangular shape of M^3 due to the reduced length of the metaloph and the lingual position of the metacone.

Pataecops parvus (RADINSKY, 1965)

(Fig. 16)

Pataecus parvus: Radinsky, 1965a, p. 212, fig. 11 (genus preoccupied).
Pataecops parvus: Radinsky, 1965a; Reshetov, 1979, p. 2, 3; Lucas & Schoch, 1981 p. 50.
Rhodopagus sp.: Reshetov, 1975, p. 37, fig. 12.

Holotype: AMNH, n° 21747, a fragment of the right lower jaw with P^2-M^3 PSS, n° 14-2, a fragment of the left lower jaw with P_4-M_1; PSS, n° 14-3; a fragment of the left lower jaw with M_3; PSS, n° 14-4, a fragment of the right lower jaw with M_{1-2}.

Locality and age: Mongolia, the Valley of Lakes, the basin of the Orok Nur Lake, Menkhen Teg, 38 km northwest of the Tsagan Khutel locality; Middle Eocene, the Kholboldji suite.

Description

Small in size; length of M^1-M^3 20 mm (Tab. 6). P^2 is of regular triangular shape. P^3 is rectangular. The protoloph is distinct, the metaloph is undeveloped. The protocone is prominent. P^4 is of distinctly rectangular shape; its ectoloph is slightly drawn to one side, the parastyle is distinct. The paracone and its outer edge are well developed. There is no hypocone. The cingulum is present on the anterior and posterior sides of the crown and labially.

M^1 is trapeziform. The parastyle is well developed. The fold separating the paracone from the parastyle is quite distinct. The paracone is prominent. The metacone is much reduced and much more lingual with respect to the paracone. The metastyle is indistinct. The median basin is U-shaped. The protoloph is much stronger and longer than the metaloph. The former narrows at the junction with the parastyle. The labial extremity of the metaloph is fused with the metacone.

M^2 differs from M^1 in the more oblique position of the ectoloph. The parastyle is developed like that of M^1. It is slightly more lingual than the paracone. The parastylar shelf fold is thick, reaching to the base of the crown on the outer side. The paracone is the highest part of the tooth. The protoloph and metaloph are almost parallel and have their lingual ends slightly bent back. The trigon basin is U-shaped. The cingulum is developed like that of M^1. M^3 is distinctly triangular. The parastyle is well developed. A small depression separates the parastyle and the paracone. The metacone is distinct and the metastyle is poorly developed. The metaloph is only half the length of the protoloph. The anterior cingulum is prominent.

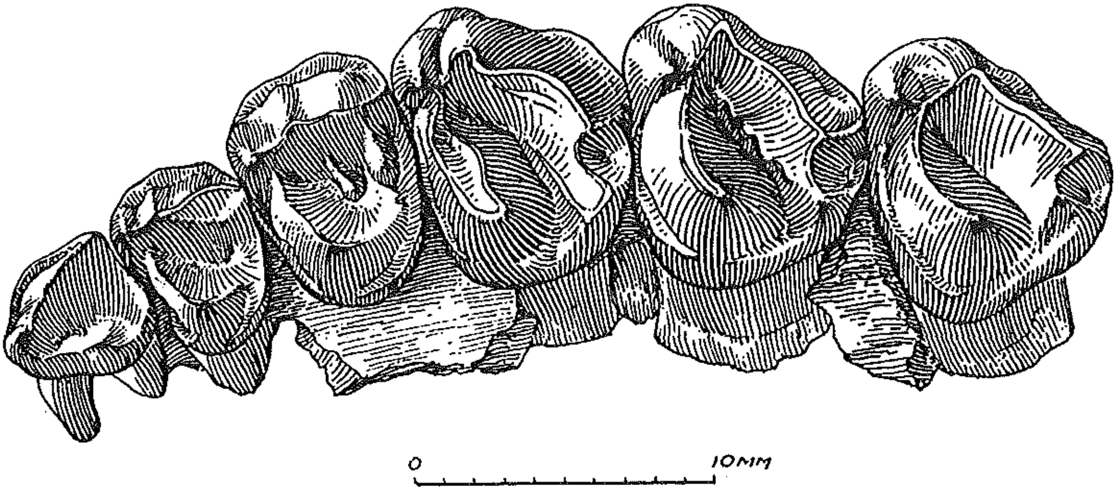

Fig. 16.— *Pataecops parvus* RADINSKY, PSS n° 14-1, a fragment of the left upper jaw with P^2-M^3; occlusal view.

Features	*Pataecops parvus*	*"Pataecops" microdon*
Ectoloph	Oblong, at angle of 25° with the horizontal axis of the tooth	Short, lingually shifted, almost parallel to protoloph
Parastyle	Well developed, not fused with protoloph	Highly fused with protoloph
Paracone	Robust and higher than parastyle	On the same level with the parastyle
Metaloph	Distinct but much reduced	Indistinct and parallel with the ectoloph
Trigon basin	Broad, U-shaped	Narrow, U-shaped
M^3 shape	Isosceles-triangular	Narrow-triangular

Table 8.— Comparison of M^3 of *Pataecops parvus* and *"Pataecops" microdon.*

P_4 is molariform. The entoconid is small and fused with the hypolophid. The paralophid is similar in size and shape to that of M_1. The hypolophid is considerably more extended in the middle than the metalophid. The entoconid is prominent and the highest among the rest of the cuspules on $M_{1\text{-}2}$. The metalophid is low. The trigonid basin on $M_{1\text{-}2}$ is narrow. The hypoconulid on $M_{1\text{-}2}$ is indistinct. M_3 is much larger than M_2 and it does not taper posteriorly. The metalophid is larger and higher than the paralophid and hypolophid. The outer wall of the trigonid forms almost a right angle with the tooth axis. The cingulum is weak and developed on the anterior and posterior sides of the crown. The hypoconulid is indistinct.

Discussion

It appears that *P. microdon*, described by Yu. Reshetov (1979) from an isolated M^3 from the Eocene of Kirgizia, does not belong either to *Pataecops* or to *Rhodopagus*. *"Pataecops" microdon* differs considerably from the specimens of the above genera in the shape of the crown, the structure of the ectoloph and some other features. However, it is extremely difficult to place this small perissodactyl within the classification of the Hyracodontidae or Tapiroidea because the material available is too scant. The most distinctive features of *"P." microdon* are the small size (M^3 length 5.2 mm) and the lingually shifted ectoloph which becomes, as a result, parallel to the protoloph (Tab. 8).

Radinsky (1965) referred, with question, *Rhodopagus* and *Pataecops* to the family Lophialetidae (Tapiroidea). Lucas *et al.* (1981) transferred them to the family Hyracodontidae (Rhinocerotoidea) guided by the following features: (1) relatively high tooth crowns: the crown height index for $M^{1\text{-}2}$ of *Rhodopagus* averaging 0.6 which is very close to the index of *Triplopus* and *Forstercooperia*; (2) a long and flat ectoloph on $M^{1\text{-}2}$ due to the elongated and lingually positioned metacone; (3) the protoloph on $M^{1\text{-}2}$ longer than the metaloph; (4) a reduced parastyle on upper molars; (5) the triangular M^3 shape due to the reduction of the metacone; (6) the labial end of the metaloph always fused with the ectoloph on M^{1-3}; (7) a relatively high paralophid and metalophid on M_{1-3}; (8) the hypolophid on M_3 not developed.

The above features are in general well seen in the PSS specimens, n° 14-1, PSS, n° 14-3, and PSS, n° 14-4 of *Pataecops parvus* from the Eocene of Menkhen Teg in the Valley of Lakes. In particular the crown height index (0.6-0.7 for M^{1-2}), a more lingual metacone and the absence of the hypoconulid on M_3, and other features are obvious in these specimens.

In spite of much similarity between *Rhodopagus* and *Pataecops*, they have certain features to distinguish them: the former has a less molariform P^4/P_4 and a more developed metacone on M^3. This makes *Rhodopagus* somewhat closer to the genus *Triplopus* than to *Pataecops*, which was shown by previous researchers (Lucas & Schoch, 1981).

It should be pointed out that the metalophid and hypolophid on M_{2-3} of *Rhodopagus* are orientated almost at a right angle to the horizontal axis of the teeth, meaning that their "tapir-like" appearance is quite obvious. However, the *Pataecops* metalophid and hypolophid are inclined with respect to the horizontal axis of the teeth; i.e., primitive "hyracodont" structural features are easily traced on M_{1-3}.

All this, together with such features as the absence of the hypoconulid from M_3, the lingual metacone on M^3 and a relatively high tooth crown, makes it possible to refer the genus *Pataecops* to the family Hyracodontidae. The author therefore shares entirely the opinion of Lucas *et al.* (1981) that *Rhodopagus* and *Pataecops* are primitive representatives of the Hyracodontidae (Rhinocerotoidea).

Subfamily HYRACODONTINAE STEINMANN & DODERLEIN, 1890

Diagnosis: Larger than Triplopodinae. Dental formula complete. Canines and incisors almost equal in size. Symphysis short; its posterior end does not reach the premolars. P^{3-4} molariform: on P^{3-4} the inner end of the protoloph bends round the metaloph, there is an incipient division between the protocone and hypocone made by an inner groove. On P_{3-4}, the entoconid is fused with the hypolophid, or rarely forms a separate, rather large cusp. The metalophid and hypolophid on M_{1-3} are more oblique than those of Triplopodinae. M^3 lacks the metacone.

Included genera: *Hyracodon* LEIDY, 1865; *Epitriplopus* WOOD, 1927; *Triplopides* RADINSKY, 1967; *Ardynia* MATTHEW & GRANGER, 1923.

Comparison: Differs from Triplopodinae by more molariform P^{3-4} and reduced metacone on M^3.

Genus *ARDYNIA* MATTHEW & GRANGER, 1923

Ardynia: Matthew & Granger, 1923, p. 1; Matthew & Granger, 1925, p. 5; Beliayeva, 1952, p. 128-131; Radinsky, 1967, p. 33-34.
Ergilia: Gromova, 1952, p. 99; Gromova, 1960, p. 82.
Parahyracodon: Beliayeva, 1952, p. 122-128, p. 19.

Type species: *A. praecox* MATTHEW & GRANGER, 1923.

Diagnosis: Medium-sized hyracodontids: length of M^1-M^3 approximately 60 mm. Crowns relatively high, the height index over 1.1. P^1/P_1 reduced, P^2/P_2 much reduced. P_{3-4} molariform. Canines very small, smaller than I^3/I_3. Incisors become smaller from I^3/I_3 to I^1/I_1. M^{1-2} relatively long and low with well developed transverse ridges.

Included species: Two species: *A. praecox* MATTHEW & GRANGER, 1923 and *A. mongoliensis* (BELIAYEVA, 1952).

Comparison: Differs from the rest of the Hyracodontinae by non-molariform P^{3-4} and a longer diastema between C and P_2. The incisors of *Ardynia*, in contrast to the North American genera, increase in size from I^3/I_3 to I^1/I_1; canines very small, less than I^3/I_3.

Discussion

The genus *Ardynia* was described by Matthew and Granger (Matthew & Granger, 1923) from fragments of the upper jaw with greatly worn P^2-M^1 from the Oligocene of Ergilin Dzo (= Ardyn Obo) in Mongolia. They also described M^3, referring it to *Ardynia praecox*. Later, Matthew & Granger (1925) were able to diagnose *A. praecox* more precisely using new collections made by the American expedition from the same locality.

E. I. Beliayeva (1952) described, in detail, apart from *A. praecox*, a new hyracodontid genus and species, *Parahyracodon mongoliensis*, from materials of the MPE, 1948-1949, from Ergilin Dzo. Simultaneously, V.I. Gromova (1952) established a new genus and species of hyracodontid, *Ergilia pachypterna*, from the Oligocene of the same locality using the collections of the same expedition.

Radinsky (1967), having summarized systematic data on Asian Hyracodontidae, included *Parahyracodon* and *Ergilia* in the synonymy of the genus *Ardynia*.

New material collected by the author in 1981-1983 from the Ergilin Dzo and Khoer Dzan localities of the eastern Gobi have made it possible to be much more precise about the characteristics of the genus *Ardynia* and its included species.

The following forms can be recognized in the genus *Ardynia*:

1: *A. praecox* MATTHEW & GRANGER, 1923 has a reduced P_1 and a well developed P_2 with two distinct roots.

2: *A. mongoliensis* (BELIAYEVA, 1952) has a reduced single rooted P_2.

3: *Ardynia* sp. In this form, in contrast to the above species, P_{1-2} are totally reduced and there is no cingulum on lower premolars or molars.

The distinctions between these *Ardynia* species have so far been made only on the premolars (P_2 and P_3) of the lower jaw. As for the upper teeth, their remnants are too fragmentary to form a basis for distinguishing the species.

Radinsky's studies (Radinsky, 1967) of the AMNH's Central Asian Expedition collections from the Oligocene of Inner Mongolia have considerably broadened the diagnosis of the genus *Ardynia*. This material has provided full knowledge of the dental formula and reduction of P^1 in *Ardynia*. Specimen n° 26039 of the AMNH from Urtyn Obo shows well the structure of incisors and canines, with the latter being very small, intermediate in size between I^1 and I^3.

Ardynia praecox MATTHEW & GRANGER, 1923
(Fig. 17)

Ardynia praecox: Matthew & Granger, 1923, p. 2, fig. 1.

Holotype: AMNH, n° 191560, a fragment of the left upper jaw with P^2-M^1.

Material: PSS, n° 27-99, a fragment of the right lower jaw with P_3-M_3.

Locality and age: Mongolia, Khoer Dzan, Upper Eocene, Ergilin suite, Sevkhul Member.

Diagnosis: P_2 with two roots. Cingulum on P_{3-4} but on M_{1-3} not developed. The index of P_3-P_4 length to M_1-M_3 length is 53%.

Description

P_1 totally reduced, P_2 not preserved. Judging by the alveolus, it was double-rooted. P_3 molariform, elongated, almost triangular and wedging forward. An anterior cristid (paralophid) of the trigonid is weakly developed. The hypolophid is more developed than the metalophid.

The structure of P_4 is similar to that of P_3; it has a long lingually bent anterior cristid of the trigonid. The tooth is more molarized than P_3. A groove separating the trigonid and talonid is found on the outer side of the crown.

M_1 and M_2 have the structure typical of the genus. The entoconid is larger and higher than the other cuspids. The hypolophid is more inclined relative to the longitudinal axis than the metalophid. M_3 is in the process of erupting. There is no cingulum on any of the lower teeth.

The depth of the horizontal ramus changes noticeably: it is 23 mm below P_2; 25 mm between P_2 and P_3; 26 mm between P_3 and P_4; 31 mm between P_4 and M_1, and 35 mm between M_1 and M_2 (Tab. 9).

Measurements		n° 27-99
P_2 (from alveolus)	Length	6
	Width	4
P_3	Length	10
	Width	6.8
P_4	Length	13
	Width	8.8
M_1	Length	16
	Width	11
M_2	Length	22
	Width	16

Table 9.— Measurements of the lower cheek teeth of *Ardynia praecox*.

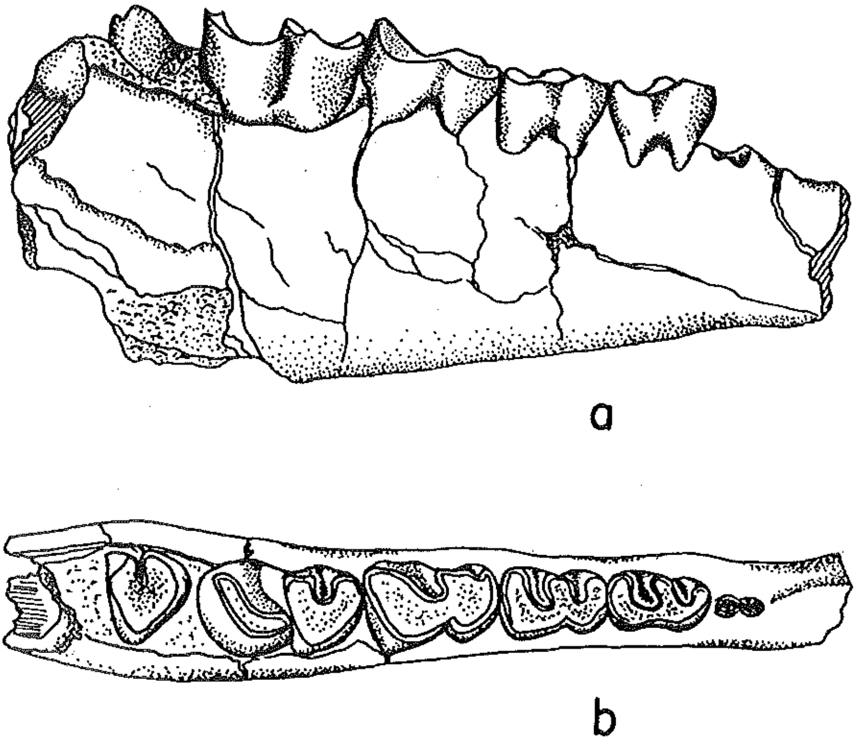

Fig. 17.—*Ardynia praecox* MATTHEW & GRANGER, PSS n° 27-99, a fragment of the right lower jaw with P_3-M_3; × 1; a: labial view; b: occlusal view.

Discussion

Matthew & Granger (1923) chose as a holotype for *A. praecox* a fragment of the left upper jaw with heavily worn P^2-M^1 from the Oligocene of Ergilin Dzo. At present, there is little information on the upper teeth and jaws of the genus *Ardynia*, which prevents correlation of the lower and upper teeth of *Ardynia*. On the basis of the holotype it is thus impossible to establish the relations between *A. praecox* with other known species of the genus *Ardynia*.

It has been pointed out above that the main distinctions of *Ardynia* reside in the structure of the front teeth of the lower jaw. To specify the characteristics of *A. praecox*, I have chosen as a hypodigm a fragment of the right lower jaw with P_3-M_2 and the double-rooted P_2 alveolus (PSS, n° 27-99) from the Upper Eocene of Khoer Dzan of Mongolia.

Ardynia mongoliensis (BELIAYEVA, 1952)

(Fig. 18, 19)

Ardynia praecox: Matthew & Granger, 1925, p. 5, fig. 6; Radinsky, 1967, p. 34, fig. 19.
Parahyracodon mongoliensis: Beliayeva, 1952, p. 122, tab. 1, fig. 1, 2; tab. 2, pl. 2, fig. 1; Beliayeva, 1954, p. 318, fig. 412.

Ardynia kazachstanensis: Beliayeva, 1952, p. 127, fig. 2, tab. 1, fig. 3; tab. 2, fig. 1; Beliayeva, 1954, p. 48; Radinsky, 1967, p. 34, fig. 19.

Holotype: PIN, n° 473-25, an incomplete lower jaw with P_2-M_3.

Material: PSS, n° 21-19, a fragment of the right lower jaw with P_2-M_3; PSS, n° 21-18, a left half of the lower jaw with P_3-M_3; PSS, n° 21-21, a fragment of the right lower jaw with P_4-M_2; PSS, n° 27-22, a fragment of the right lower jaw with P_3-M_3. PSS, n° 27-22, a fragment of the right lower jaw with P_3-M_3.

Locality and age: Mongolia, eastern Gobi Desert: I - Ergilin Dzo, Bayan Tsav cliff; Lower Oligocene, Ergilin Dzo suite, Ergilin Member; II - Khoer Dzan, Upper Eocene, Ergilin Dzo suite, Sevkul Member.

Diagnosis: The symphyseal region does not extend posteriorly to the premolars. P_2 much reduced. Canines small, much smaller than I_3. I_2 is intermediate in size between I_1 and I_3.

Description

The symphyseal region of the lower jaw is extended anteriorly, elevated and slightly broadened. The symphyseal length is only slightly more than half that of the P_2-M_3 series. The horizontal ramus is shallow, with the symphyseal region slightly elevated (around 20°) and extended forwards. The depth of the horizontal branch varies little: it is 25 mm at the anterior of P_2; 27.8 mm between P_3 and P_4, and 30 mm between M_1 and M_2. P_2 reduced and single rooted. P_3 is triangular, double rooted and molariform.

P_4 is molarized, the trigonid is V-shaped, the entoconid is quite distinct, and the hypolophid is complete.

M_1 and M_2 have similar crown shape and size. M_3 differs from M_2 by being larger and having a higher crown. The cingulum is developed exclusively on the labial side of $P_{3\text{-}4}$.

Comparison

It differs from *A. praecox* by much reduced P_2, and more developed cingulum on the labial side of $P_{3\text{-}4}$.

Discussion

The structure of the front teeth is very important for the systematics of *Ardynia*. Front teeth, especially the incisors and canines, are well seen in the specimen AMNH n° 26183 from the Nom Kong Shire locality in North Mesa of Inner Mongolia (Radinsky, 1967). Its incisors become smaller progressively from I_1 to I_3, while the lower canines are smaller than I_3. P_1 is reduced, P_2 is small and consists of a single root. New Mongolian data, in combination with the Chinese data, suggest that the specimen described by Radinsky as *A. praecox* is actually *A. mongoliensis*.

E. I. Beliayeva (1952) described a new species of a small rhinoceros from the *Indricotherium* beds of Kazakhstan, giving it the name of *Parahyracodon kazachstanensis*. *A. mongoliensis* and *P. kazachstanensis* show similar structures and sizes of P_3-M_3, reduced P_2 and molariform $P_{3\text{-}4}$. Beliayeva shows the following distinctive features of the Kazakhstan form, in contrast to the Mongolian one: (1) its cingulum is more developed on $P_{3\text{-}4}$, and (2) P_3-P_4 length is slightly more than that of M_1-M_3. As for the first

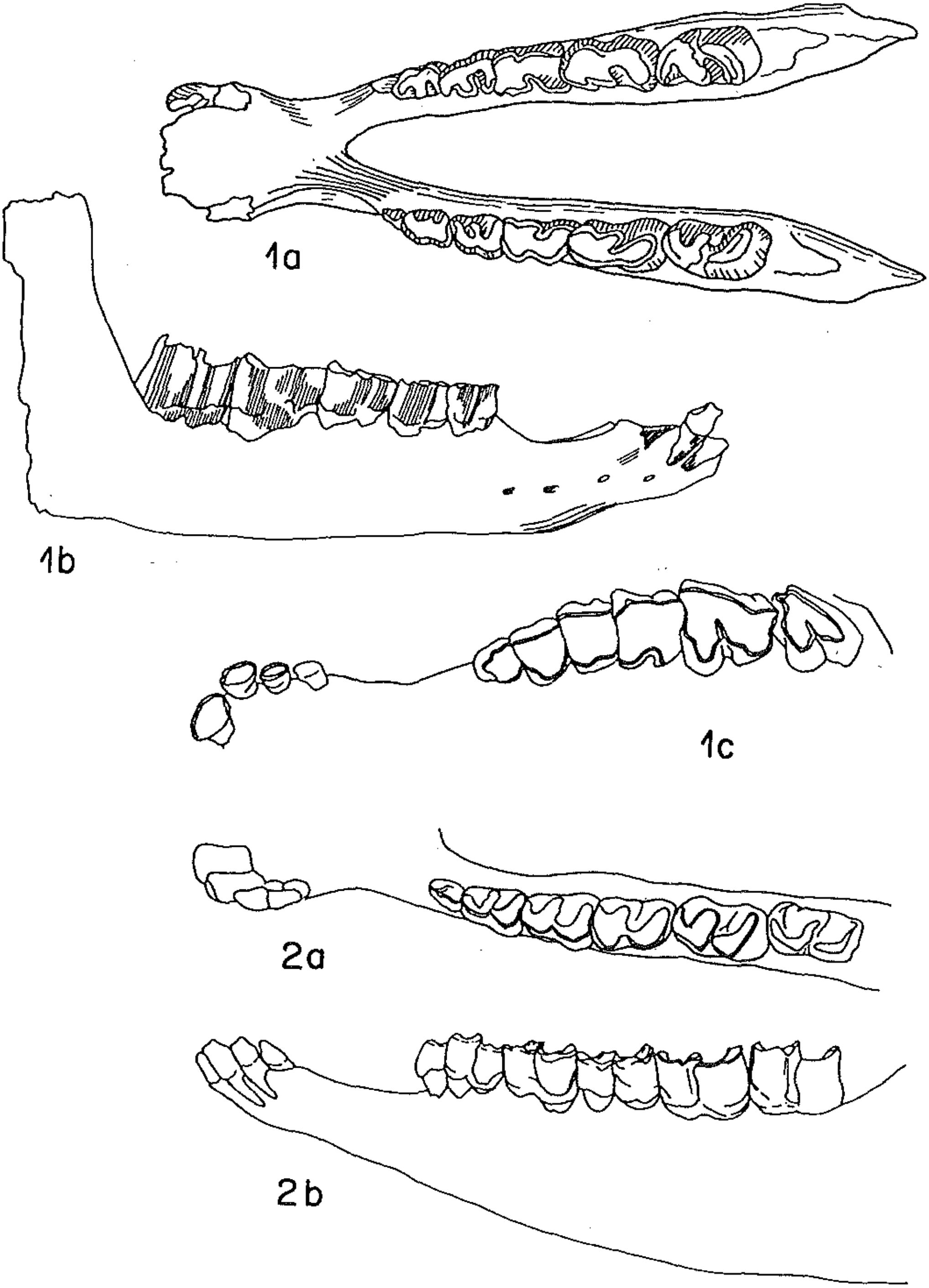

Fig. 18.— *Ardynia mongoliensis* (BELIAYEVA). **1**: PIN n° 473-25, Holotype, a incomplete lower jaw with P_2-M_3; a: occlusal view; b: labial view (from Beliayeva, 1952, fig. 1, 2); c: A.M.N.H. n° 26039, upper jaw with I^1-I^3, C, P^2-M^3; from the Ulan Gochu beds (Radinsky, 1967); x .9; occlusal view. **2**: A.M.N.H. n° 26183, lower jaw with I_1-M_3; x .9; a: occlusal view; b: labial view. (From Radinsky, 1967, fig. 19).

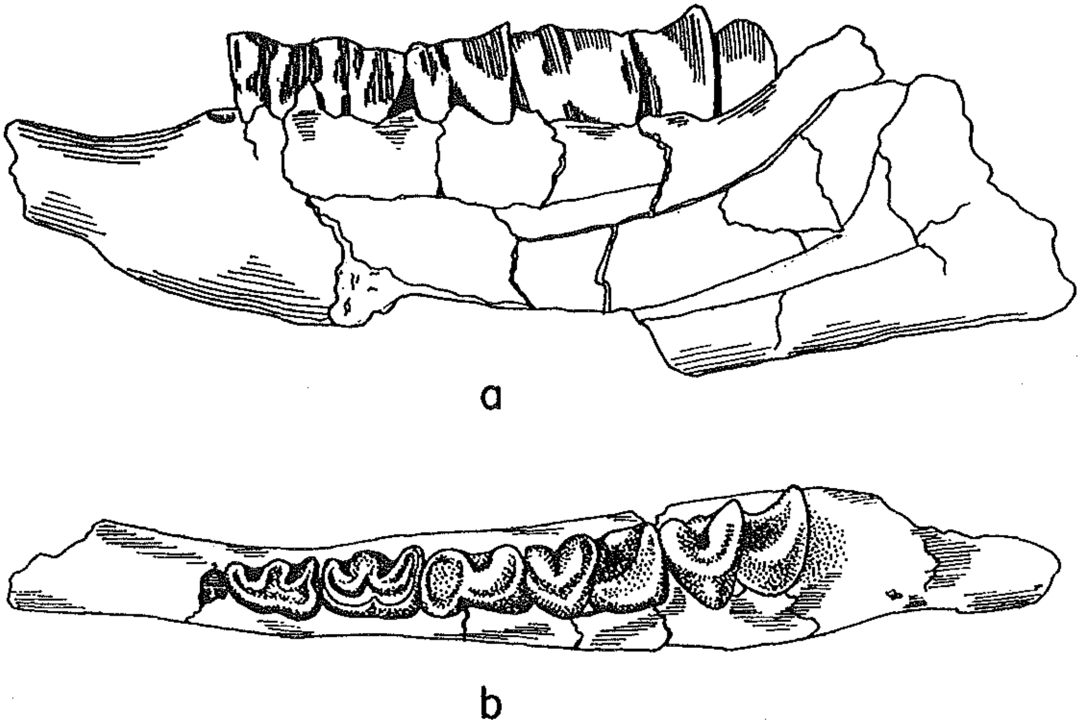

Fig. 19.— *Ardynia mongoliensis* (BELIAYEVA), PSS n° 21-19, a fragment of the right lower jaw with P_2-M_3; × .9; a: labial view; b: occlusal view.

feature, the P_{3-4} cingulum is developed also in some Mongolian specimens. This feature is apparently individual variation.

Concerning the second feature, Mongolian specimens show a widely ranging P_3-P_4/M_1-M_3 length index, from 42.4 to 54%. This index for the Turgai species therefore falls within the range of variation of *A. mongoliensis*. These data allow us to judge that the Turgai species should be considered a junior synonym of *A. mongoliensis*.

Ardynia sp.

(Fig. 20)

Material: I - PSS, n° 27-26, a fragment of the lower right jaw with P_3-M_1; II - PSS, n° 21-23, a fragment of the lower right jaw with P_3-M_1.

Locality and age: Mongolia, eastern Gobi Desert; I - Khoer Dzan; Upper Eocene, Ergilin Dzo suite, Sevkhul Member, Ergilin Member.

Description

Comparatively small *Ardynia*; length of P_3-P_4 is 24 mm. The diastema between C

Measurements and indices		PIN	PSS		PIN	
		n° 473-55 Holotype	n° 21-19	n° 21-18	n° 21-24	n° 1463-169
P_2	Length		6.0	5.0	3.0	7.5
	Width		3.8	4.5	3.8	5.0
P_3	Length	12.0	10.0	10.0	7.0	15.0
	Trigonid width	8.0	5.0	7.5	5.0	9.0
	Talonid width	9.0	8.5	8.0	5.7	10.0
P_4	Length	17.0	13.5	12.8	8.0	16.0
	Trigonid width	10.0	9.8	9.2	6.0	10.0
	Talonid width	11.5	11.0	9.5	7.0	12.0
M_1	Length	17.0	15.5	14.6	9.5	17.0
	Trigonid width	11.0	9.8	10.0	7.0	12.0
	Talonid width	12.5	11.0	11.0	8.0	13.0
M_2	Length	22.0	19.0	18.5	12.0	21.0
	Trigonid width	12.0	12.0	11.8	7.5	12.0
	Talonid width	15.0	13.0	12.5	8.4	13.0
M_3	Length	23.0	22.0	20.5	14.0	21.0
	Trigonid width	11.0	12.6	11.8	8.0	12.0
	Talonid width	14.0	13.0	13.0	8.5	12.0
P_2-M_3 length		97.0	88.0	90.0	56.0	98
P_3-M_3 length		90.5	81.0	84.0	52.0	90
P_3-P_4 length		26.3	30.0	31.0	17.0	31
M_1-M_3 length		64.3	55.0	56.0	—	59
Indices:						
P_3-P_4 length / M_1-M_3 length		42.4	52.6	55.3	54.0	52.5
M_1-M_3 length / P_3-M_3 length		71.0	65.0	66.6	64.5	65.5
P_3-P_4 length / P_3-M_3 length		29.0	34.5	34.4	35.4	34.0

Table 10.— Measurements and indices of the lower cheek teeth of *Ardynia mongoliensis*.

Measurements		n° 21-23	n° 27-26
P_3	Length	10	10
	Width	7	7
P_4	Length	14	12
	Width	8.8	8
M_1	Length	16	14.8
	Width	9.8	8.8

Table 11.— Measurements of the lower cheek teeth of *Ardynia* sp.

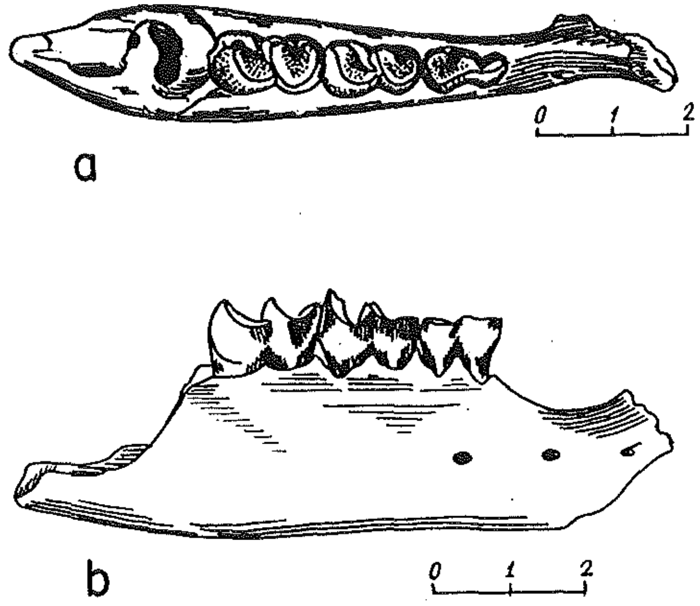

Fig. 20.—*Ardynia* sp., PSS n° 27-23, a fragment of the right lower jaw with P_3-M_1; a: occlusal view; b: labial view.

and P_3 is approximately 18 mm. In the lower jaw (PSS, n° 27-26) there are three equal mental foramina. P_1 and P_2 are reduced. P_3 is relatively long, the talonid is much wider than the trigonid; the tooth is molariform, with two distinct roots. P_4 is slightly larger and more molarized than P_3. The entoconid is higher and larger than the other cusps. M_1 has a higher crown than P_4, and a V-shaped trigonid. The talonid basin is deep. These is no distinct cingulum. The horizontal ramus depth beneath P_3 is 21 mm and 23 mm at the level between P_4 and M_1. The thickness of the horizontal ramus is 9 mm in front of P_3, and 12 mm at the level of P_4 and M_1.

Discussion

The most characteristic features of *Ardynia* sp. are as follows: (1) P_2 totally reduced; (2) the cingulum on P_{3-4} and M_1 not developed; (3) the diastema between C and P_3 is relatively short, a little shorter than the length of the diastemata of *A. praecox* and *A. mongoliensis*.

Thus, the reduction of P_2 of *Ardynia* sp. suggests that this form is more specialized than *A. mongoliensis* or *A. praecox*. E.I. Beliayeva (1952) figured a fragment of the lower jaw of *Ardynia* (PIN, n° 473-531) with P_4-M_3 and a broken double rooted P_3 from Ergilin Dzo. Its P_2 is reduced and the overall length of the dental series is 82 mm. Note that the P_3-P_4 to M_1-M_3 length index is 45%, which is definitely less than the equivalent index of *A. mongoliensis*.

For lack of consistent material, it is as yet impossible to formally name this *Ardynia* species.

Subfamily **INDRICOTHERIINAE** BORISSIAK, 1923

Diagnosis: From small to giant in size. Skull long and narrow, especially posteriorly. The sagittal crest very weak. The nasal incision extends back as far as P^4. Dental formula: I 3-1/3-1, C 1-0/1-0, P 4-3/4; M 3/3. Early forms have the complete number of incisors and canines; the canines are slightly smaller than the incisors. Indricotheriinae proper (*Indricotherium* and *Urtinotherium*) have I^2 very big, canine-like, directed downwards, or rudimentary; I_1 large, from rounded to oval in section, directed forwards; there is occasionally a rudimentary I_2. P^{3-4} are submolariform; the degree of molarization decreases from P^2 to P^4. All the limbs show three functioning toes.

Included genera: *Forstercooperia* WOOD, 1939; *Juxia* CHOW & CHIU, 1964; *Urtinotherium* CHOW & CHIU, 1963; *Indricotherium* BORISSIAK, 1915; *Paraceratherium* COOPER, 1911 and *Armania* DASHZEVEG & GABUNIA, 1988.

Comparison: Differs from other subfamilies by the larger body size, reduced incisors and almost entire absence of canines in the lower jaw.

Typical of the subfamily (and especially of *Indricotherium* and *Urtinotherium*) is also the downward-bent anterior region of the lower jaw.

Genus *FORSTERCOOPERIA* WOOD, 1939

(Fig. 21, 22, 23)

Cooperia: Wood, 1938, p. 1 (preoccupied).
Forstercooperia: Radinsky, 1967, p. 18; Gabunia & Dashzeveg, 1974, p. 497; Chow *et al.*, 1974, p. 273, pl. 1, a, b; Lucas *et al.*, 1981, p. 287.
Fortrigonias: Beliayeva, 1959, p. 83.
Pappaceras: Wood, 1963, p. 2.

Type species: *Cooperia totadentata* WOOD, 1938.

Diagnosis: Medium and small indricotheriine hyracodontids; M^1-M^3 varies in length from 70 to 150 mm. Dental formula complete. No tooth reduction observed. Canines a little larger than incisors. The crown height index averages 0.65. P^4/P_4 not molarized. Nasal incision goes back to the level of the canine. The lingual end of the protoloph on P^{2-4} clearly wraps round the lingual end of the metaloph; the hypocone and protocone are not separated. On P_{3-4} (the North American species excluded), the entoconid is not developed. The hypolophid is incomplete. The metacone is much reduced on M^3. The cingulum is well developed on P^{2-4}.

Included species: Six species: *F. grandis* (PETERSON, 1919), *F. totadentata* (WOOD, 1938) (= *F. shiwopuensis*, see Lucas *et al.*, 1981), *F. confluens* (WOOD, 1963), *F. minuta* LUCAS *et al.*, 1981, *F. borissiaki* (BELIAYEVA, 1959) and *F. ergiliinensis* GABUNIA & DASHZEVEG, 1974.

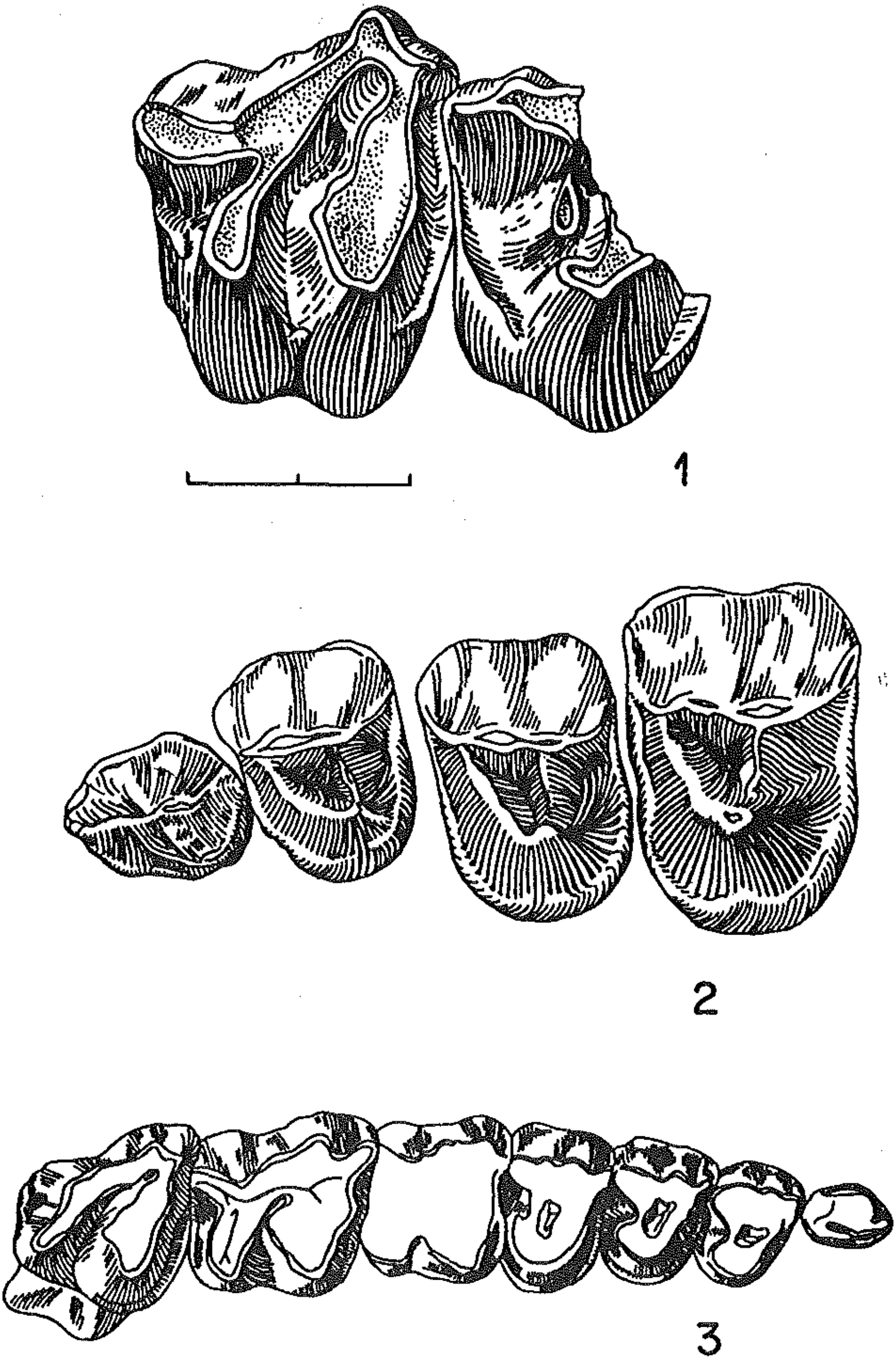

Fig. 21.— Teeth of *Forstercooperia*. **1**:*Forstercooperia borissiaki* (BELIAYEVA), PIN n° 858-71d, holotype, P^4-M^1; occlusal view (from Beliayeva, 1952, fig. 1). **2**: *Forstercooperia totadentata* WOOD, A.M.N.H. n° 20216, holotype, P^1-P^4; occlusal view (from Wood, 1938, fig. 5B). **3**: *Forstercooperia confluens* (WOOD), A.M.N.H. n° 26660, holotype, P^1-M^3; occlusal view (from Wood, 1963, fig. 2A).

Discussion

E.I. Beliayeva (1959) described a fragment of the upper jaw with P^4-M^1 of a hyracodontid from Eocene (Oligocene?) strata in a pit in Artem town near Vladivostok. She referred it to the genus *Eotrigonias* previously known from North America. Radinsky (1967) believed that this fragment belonged to the genus *Forstercooperia*, whereas Lucas & Schoch (1981) referred it to the genus *Juxia*.

Here Radinsky's point of view is accepted, with some additional evidence in his favour. *Eotrigonias borissiaki* is well distinguished from *Juxia sharamurunensis* by the triangular outline shape and less developed protoloph of P^4.

Wood (1963) believed *Fortrigonias borissiaki* a more progressive species in comparison with *F. totadentata* and *F. confluens*, since its P^4 shows an incipient

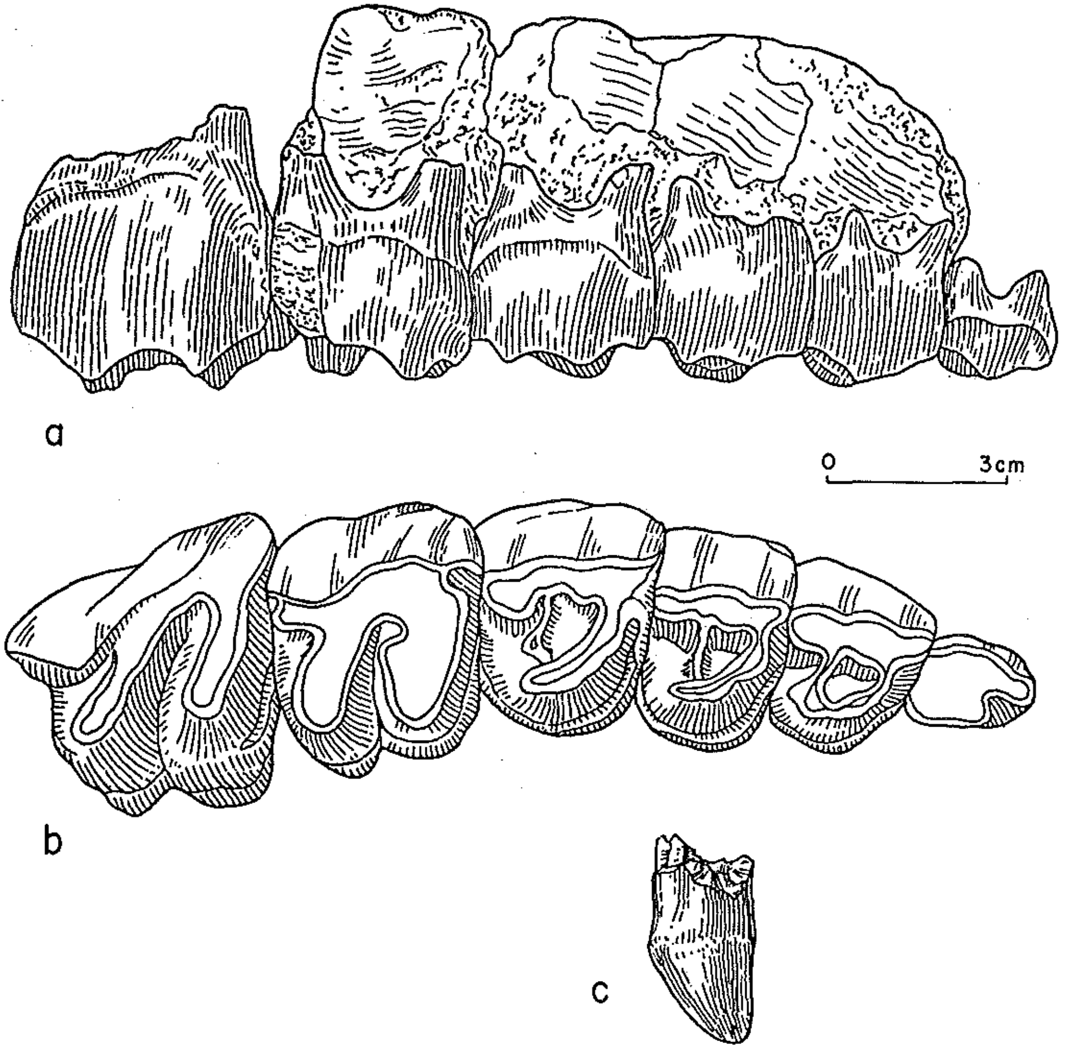

Fig. 22.— *Forstercooperia ergilinensis* DASHZEVEG & GABUNIA, a and b: PSS n° 17-1, holotype, a fragment of the upper right jaw with P^1-M^2; a: labial view; b: occlusal view; c: PSS n° 17-2, an upper C; labial view.

hypocone yet isolated from the protoloph. However, it is hard to accept Wood's conclusion. Note that the *F. confluens* holotype is represented by an old individual showing little detailed structure, in particular the presence or absence of the hypocone on P^4. On the isolated P^2 of *F. confluens*, the hypocone is distinct on the distal end of the protoloph (Wood, 1963, fig. 2, D). This suggests that it might have been present also on less worn P^3 and P^4 of *F. confluens*.

Due to extensive wear, the hypocone of *F. totadentata* is weakly represented on P^3 and is absent on P^4 (Wood, 1938, fig. 3B). Thus the fragment of the upper jaw with P^4 and M^1 described as *F. borissiaki* is more likely to belong to the genus *Forstercooperia* than to *Juxia*.

Significant for drawing distinctions between the genera *Forstercooperia* and *Juxia* is *F. ergiliinensis* from the Lower Oligocene of Mongolia. This species is characterized also by the triangular shape of the crown, the presence of a massive protoloph and well developed cingulum on P^{2-4}. The hypocone on P^{3-4} is not separated from the protoloph in this species. The very features that distinguish *F. ergiliinensis* from *Juxia sharamurenense* are typical of *Forstercooperia totadentata* and *F. confluens*. Hence, *Forstercooperia* and *Juxia* differ significantly in the structure of their premolars. As for the molars, they also show some important distinctions. M^1 and M^2 of *Juxia sharamurenense* have a structure characteristic of the specimens of the genus *Indricotherium*, and in contrast to the named *Forstercooperia* species show no antecrochet, a thick parastyle and a less distinct parastylar shelf. These data make it possible for the author to conclude that the upper jaw with P^1-M^2 of a rhinoceros from the Oligocene of Ergilin Dzo belongs to the genus *Forstercooperia* and not to the genus *Juxia*.

Forstercooperia ergiliinensis GABUNIA & DASHZEVEG, 1974

(Fig. 22)

Forstercooperia ergiliinensis: Gabunia & Dashzeveg, 1974, p. 497, fig. 1.

Holotype: PSS, n° 17-1, a fragment of the upper right jaw with P^1-M^2.

Material: Apart from the holotype, there are canines, PSS, n° 17-2.

Locality and age: Mongolia, eastern Gobi Desert, Ergilin Dzo, Bayan Tsav cliff; Lower Oligocene, Ergilin Dzo suite, Ergilin Member.

Diagnosis: Large-sized *Forstercooperia*; Length of P^{1-4}, 97mm. Protoloph robust; its distal end shows an incipient hypocone which is not separated from the protocone. The parastyle on M^2 is significantly reduced. The cingulum is well developed on the premolars.

Description

The canine is relatively small, pointed and rounded in cross section. The crown of P^1 is elongated and double rooted. Due to heavy wear it is impossible to judge its structure.

P^2 is triangular, its length being less than its width. The trigon basin is triangular and closed. P^3 has a rectangular shape. The paracone and metacone on P^3 are almost equal in size. The parastyle is well developed, and the metastyle outlined. The protoloph lingual end sharply bends around the metaloph; its highest part corresponds in position to the protocone. The hypocone is distinct but it is not isolated from the protocone. The trigon basin is deep. The metaloph is fused at its labial end with the ectoloph. Its lingual end touches the protoloph.

P^4 is subquadrate in outline shape and differs from P^3 by being larger. The protoloph is robust. The hypocone is not isolated. The highest part of the tooth (2/3rds of the protoloph's length) must be the top of the protocone. The closed trigon basin is of a triangular shape. The cingulum is well developed on all the premolars.

M^1 quadrate: its length is slightly greater than the width. The ectoloph is noticeably bent inwards, especially in the parastylar area. The parastyle is prominent and separated from the paracone by a distinct parastylar fold. The paracone is well developed, being the highest part of the ectoloph. The protoloph is a little smaller than the metaloph, but stands out lingually. The antecrochet is prominent, while the crochet is barely recognizeable. The cingulum is moderately developed; it is present on the front and rear sides of the tooth. M^2 is larger than M^1. The parastyle is much reduced though its outer edge is very distinct. The paracone is well developed; its outer rib is also prominent down to the base of the crown. No crochet or antecrochet are visible. The metaloph is shorter and more oblique to the long axis of the tooth than is the protoloph. The metastyle is noticeably bent outwards. The trigon basin is deep, reaching almost to the lingual side of the paracone.

Measurements		n° 17-1
C	Length	16.0
	Width	12.0
P^1	Length	20.1
	Width	14.0
P^2	Length	22.0
	Width	31.0
P^3	Length	26.5
	Width	37.0
P^4	Length	28.5
	Width	37.0
M^1	Length	33.0
	Width	42.5
	Length / Width	76.7
M^2	Length	40.5
	Width	45.5
	Length / Width	89.1

Table 12.— Measurements of the upper teeth of *Forstercooperia ergiliinensis*.

The cingulum is developed on the front and rear sides of the crown and is less distinct labially.

Comparison

Differs from *F. totadentata* from the Middle Eocene of China by a better developed protoloph on P^{2-4}. The distolingual end of the Mongolian species shows a distinct hypocone not present on any premolars of *F. totadentata*. Differs from *F. confluens* from the Eocene of China by a less developed parastyle on M^2. The holotype of *F. confluens* is represented by a heavily worn specimen, precluding a more detailed comparison. Differs from *F. borissiaki* from Eocene sequences of the Artem pit near Vladivostok by larger size, a robust cingulum on the premolars and a less distinct paracone on M^1.

Differs from *F. minuta* from the Eocene of China by larger size, a less developed lingual cingulum and the presence of an antecrochet on M^1 and M^2.

Differs from *F. grandis* from the Upper Eocene of North America by a more robust protoloph and a prominent parastyle on P^{3-4}.

Forstercooperia sp.

(Fig. 23)

Material: PSS, n° 21-17, a fragment of the right branch of the lower jaw with P_{2-4}.

Locality and age: Mongolia, eastern Gobi Desert, Ergilin Dzo, Bayan Tsav cliff; Lower Oligocene, Ergilin Dzo suite, Ergilin Member.

Description

A jaw of medium size, the diastema between C and P_1 is 12 mm. Judging by a partially preserved alveolus, the canine was developed. P_1 must have been much reduced

Measurements		n° 21-17
P_1	Length	7
	Width	6
P_2	Length	11
	Trigonid width	7
	Talonid width	6
P_3	Length	16
	Trigonid width	10
	Talonid width	11
P_4	Length	—
	Trigonid width	12
	Talonid width	10

Table 13.— Measurements of the lower premolars of *Forstercooperia* sp.

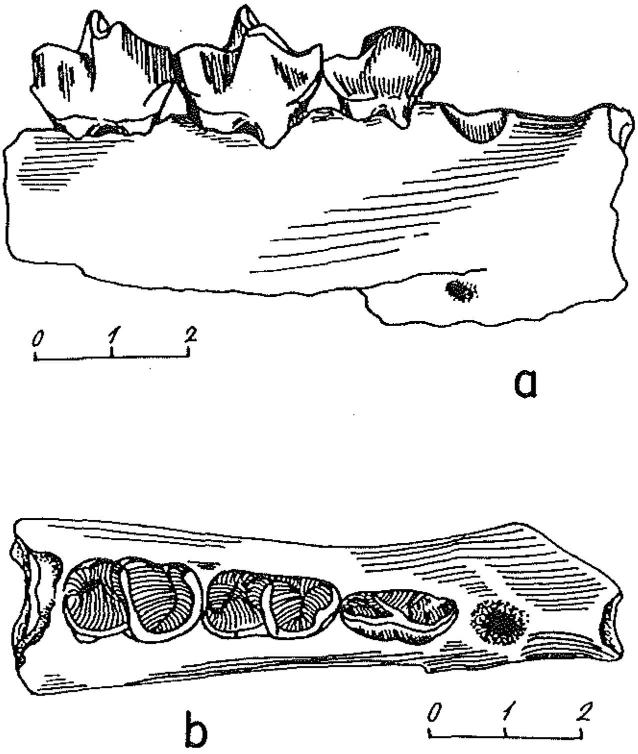

Fig. 23.— *Forstercooperia* sp., PSS n° 21-17, a fragment of the right lower jaw with P_2-P_4; a: labial view; b: occlusal view.

and had only a single root. P_2 is double rooted, completely non-molariform, and splayed forward and backward. P_3 is rectangular, with the front side slightly shorter than the back. The trigonid is clearly marked and the protoconid is higher than the other cuspids. The talonid basin is distinct. The hypoconid is well developed, the entoconid very small but distinct, while the hypolophid is incomplet. The cingulum though poorly developed is found on the front and rear of the crown. P_4 is more massive than P_3. The lingual end of the paralophid reaches the inner side of the crown. The metalophid is well developed and its forward branch is bent at a narrower angle than the hypolophid. The front end of the outer edge of the hypolophid closely adjoins the back wall of the metalophid. The entoconid is small and much lower than the hypoconid.

Notes

The structure of the premolars, in particular the incomplete hypolophid and poorly developed entoconid, permits the described form to be referred to the genus *Forstercooperia*. This form cannot be compared with *F. ergiliinensis* from the same sequences at Ergilin Dzo, since the latter species is represented entirely by upper teeth. Nevertheless, the described form differs from it by being almost half its size. Due to the fragmentary nature of the material, the specific affinity of this *Forstercooperia* remains unclear.

Genus *JUXIA* CHOW & CHIU, 1964

Juxia: Chow & Chiu, 1964, p. 266; Lucas *et al.*, 1981, p. 828.

Type species: *J. sharamurenense* CHOW & CHIU, 1964.

Diagnosis: Almost half the size of *Indricotherium transouralicum*. The skull is dolichocephalic and the brain case is long, with a relatively high nuchal region. The sagittal crest is developed, the nasal bone long. The nasal incision extends back to the level of the front of P^3. Dental formula: I 3/3, C 1/1, P 4/4, M 3/3. I^1 bigger than I^2 or I^3. P$^{2-4}$ highly molarized. Symphysis short, extending to the front of P$_1$.

Included species: One species, *J. sharamurenense* CHOW & CHIU, 1964.

Comparison: Differs from *Forstercooperia*, the closest genus, by the distinctly rectangular outline shape of P$^{2-4}$ and advanced molarization of the premolars. In addition, the nasal incision of *Juxia* is deeper; it extends back to the level of P^3.

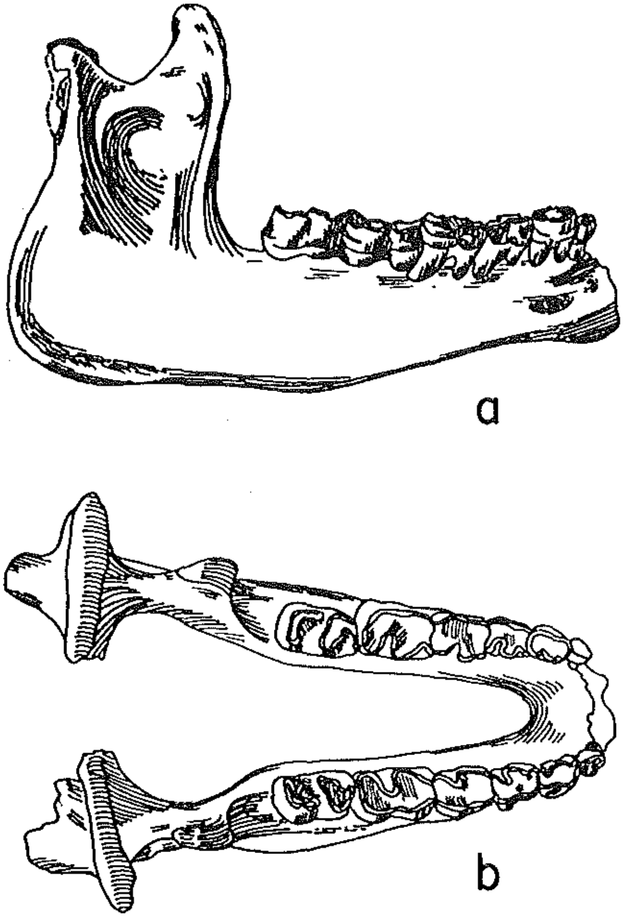

Fig. 24.—*Indricotherium* sp., A.M.N.H. n° 26172, a nearly complete lower jaw (only incisor region missing) with P$_2$-M$_3$; x 2/15; a: labial view; b: occlusal view. From Granger & Gregory (1936, fig. 4C, D).

Juxia sharamurenense CHOW & CHIU, 1964

Juxia sharamurenense: Chow & Chiu, 1964, p. 264, pl. 1, fig. 1-3; Lucas, Schoch & Manning, 1981, p. 828.

Holotype: IPP, n° 2891, a skull and a complete well preserved skeleton.

Locality and age: China, Inner Mongolia, Ula Usu locality, Baron Sog Mesa; Upper Eocene, Shara Murun Formation.

Genus *URTINOTHERIUM* CHOW & CHIU, 1963

Urtinotherium: Chow & Chiu, 1963, p. 236; Radinsky, 1966, p. 635, fig. 3b; Radinsky, 1967, p. 37.

Type species: *U. incisivum* CHOW & CHIU, 1963.

Diagnosis: Slightly smaller than *Indricotherium*. The formula of the lower permanent teeth: I /3, C /1, P /4, M /3. I_1 much larger and more robust than I_2 and I_3. The latter much reduced. P_1 double rooted. Symphysis medium sized, extending posteriorly almost to the middle of P_3.

Included species: Only the type species.

Comparison: Differs from the genera *Forstercooperia* and *Juxia* by being larger, having specialized I_1, reduced I_3 and the anterior region of the lower jaw bent downwards; differs from the closely related *Indricotherium* by the presence of $I_{2\text{-}3}$, almost total absence of the diastema between C and P_1 and a comparatively shallower horizontal ramus of the lower jaw.

Urtinotherium incisivum CHOW & CHIU, 1963

Urtinotherium incisivum:: Chow & Chiu, 1963, p. 236; fig. 1, tab. 1, 2.

Holotype: IPP, n° 2769, an almost complete lower jaw with dental series.

Locality and age: China, Inner Mongolia, Urtyn Obo locality, Eastern Mesa; Lower Oligocene, Baron Sog Formation.

Genus *INDRICOTHERIUM* BORISSIAK, 1915

Indricotherium sp.

(Fig. 24)

Baluchitherium grangeri: Granger & Gregory, 1936, p. 17 (a small form, Grade IV).

Material: AMNH, n° 26172, a nearly complete lower jaw (only the incisor region missing) with P_2-M_3.

Locality and age: China, Inner Mongolia, Nomkhong Shireh locality, Northern Mesa; Lower Oligocene, Baron Sog Formation.

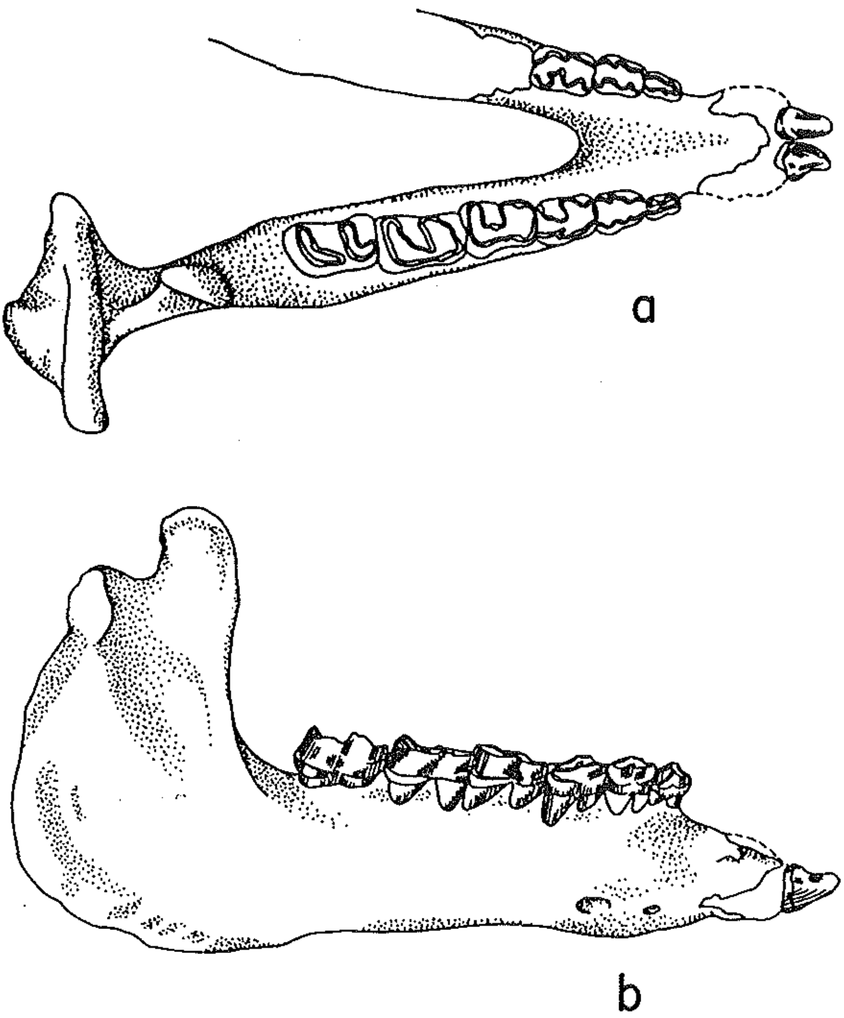

Fig. 25.— *Indricotherium transouralicum* PAVL., A.M.N.H. n° 26166, lower jaw; x 2/15; a: occlusal view; b: labial view (from Granger & Gregory, 1936, fig. 4 A, B).

Description

Lower jaw is massive, the lower edge of the horizontal ramus slightly indented in the region of M_2 and M_3. The symphysis is relatively short; its rear end is in front of P_4. One large mental foramen is under P_3 near the lower edge of the horizontal ramus.

The processus angularis of the jaw is well developed, the indentation on the lower edge barely visible. The coronoid process is relatively tall and distinctly taller than the articular process. The articular process is well distinguished, the incision between the processes very wide. P_1 must have been lacking. P_2 is much reduced and single rooted. P_3 is double rooted, weakly molarized and elongated. P_4 is strongly molarized and more robust than P_3. The hypolophid is poorly developed. The entoconid is low and wear has fused it with the hypolophid. The molars are similar with an almost quadrate crown outline. The metalophid and hypolophid are parallel, the talonid basin is always larger and wider than the trigonid basin. The cingulum is not developed on the lower teeth.

The sizes of the *Indricotherium* sp. teeth and lower jaw could not be assessed from the papers by Granger & Gregory (1936, fig. 6C, D), since these authors did not provide a scale for their figures.

Comparison

The *Indricotherium* from the Oligocene of Nomkong Shire, judging from the lower jaw, was almost a third of the size of *Indricotherium transouralicum* M. PAVLOVA and characterized by a less complete hypolophid on P_3 and P_4. Note that P_2 of the described form is single rooted, while this tooth is normally double rooted in *Indricotherium*. In addition, it has a more distinct articular process, and the incision between the lower jaw processes is much more developed than that of *I. transouralicum* (fig. 25).

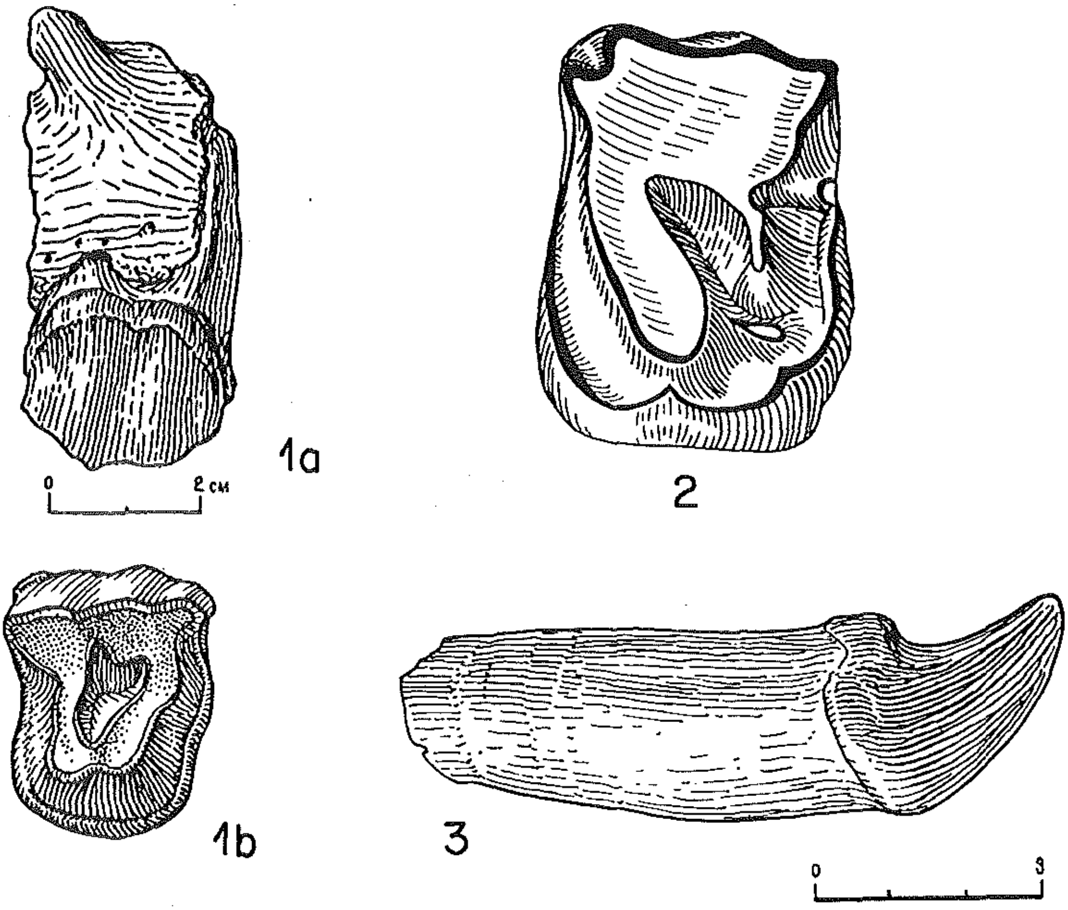

Fig. 26.— *Urtinotherium* or *Indricotherium* sp. **1**: PSS n° 27-68, left P^2; a: labial view; b: occlusal view. **2**: PSS n° 27-3, right P^4; occlusal view. **3**: PSS n° 27-100, right I^1; labial view.

Discussion

Mongolian remains of giant rhinoceroses were first described by American researchers as *Baluchitherium grangeri* from the Hsanda Gol locality in the Valley of Lakes (Osborn, 1923; Granger & Gregory, 1936). A radical revision of giant rhinoceroses based on the osteological material of Gromova (1959) provided a new approach to the generic and specific systematics of this interesting group. The comparison of *B. grangeri* with the Turgai species suggests that both forms have much in common in all their skeletal components, including the skull and lower jaws.

Therefore the above mentioned forms from the Oligocene of Mongolia, Kazakhstan and China should be referred to *Indricotherium transouralicum* M. PAVLOVA (Gromova, 1959). It should be pointed out that the recent papers by Chinese and American researchers advocate the independence of the Mongolian species *I. grangeri* (Chow & Xu, 1959; Chiu, 1962; Radinsky, 1967). At present, three species of the genus *Indricotherium* are known from China and Mongolia - they are *I. parvum, I. intermedium* and *I. grangeri.* According to Chiu (1962), all three belong to a single phyletic line and are distinctive. It is hard to accept the view of this author, however, since the systematic position of *I. intermedium* is poorly substantiated. *I. grangeri* can hardly be regarded as an independent species. It is more likely to be conspecific with *I. transouralicum.*

Urtinotherium (or *Indricotherium*) sp.

(Fig. 26)

Material: PSS: n° 27-68, left P^2; n° 27-3, right P^4, n° 27-100, right I_1.

Locality and age: Mongolia, eastern Gobi Desert, Khoer Dzan; Lower Oligocene, Ergilin Dzo suite, Ergilin Member.

Description

The incisor root is straight. The antero-posterior diameter is greater than the medio-lateral (inner-outer) throughout its length. As the end of the root is broken its overall length and proportions are unknown. The incisor crown is pointed and bent backwards. There are two distinct faces, one on the inner side gradually attenuating in the direction of the crown tip and not reaching its base. The other one, a more distinct face, is on the rear inner slope of the crown. Both faces meet at the incisor tip at an angle of 35°. The crown is oval in section (at the base). The bases of both of the lower incisors must have adjoined each other closely since there is a small facet on the inner side of the lower right incisor. The cingulum is only developed anteriorly at the base of the crown. The crown of P^2 is trapezoidal; its outer edge is longer than its inner one, while its front edge is slightly longer than its rear one. The tooth is almost fully molarized, the paracone and metacone being almost identical in size. The parastyle is quite distinct, and its shelf is well demarcated. The protoloph and metaloph are perpendicular. The lingual end of the protoloph, bent backwards, closely contacts the hypocone. The metaloph is more lingual than the protocone. The trigon basin is closed, and the crochet distinct. The cingulum is well developed anteriorly, posteriorly, and lingually. It is less well developed on the outer side of the tooth.

P^4 is rectangular in shape. The ectoloph is slightly inclined lingually. The tooth is submolariform. Its paracone is well developed and represents the tallest part of the crown. The metacone is less distinct than the paracone. The parastylar shelf is relatively deep, reaching almost the middle of the crown. The parastyle is quite distinct. The metastyle is clearly demarcated. The metaloph is incomplete. The hypocone is a low, isolated, crest-like cusp separated from the distal end of the metaloph by a fissure. The protoloph is more robust than the metaloph and is directed forward and laterally, thus obliquely with respect to the long axis of the tooth. The vertical outer groove between the para- and metacone is quite distinct almost to the middle of the crown. The trigon basin is deep and open from the distal side of the tooth. The cingulum encircles the crown with the exception of the ectoloph.

Discussion

In 1959, Gromova recorded from the upper horizon at Ergilin Dzo in Mongolia the distal end of a lateral metapodial that must have belonged to some giant rhinoceros. Because of the fragmentary nature of the material, the systematic position of this find remains unclear.

The above mentioned fragmentary materials prove the existence in some Early Oligocene faunas of a primitive *Indricotherium*. The structure of P^4, especially its size and the isolated hypocone, as well as the character of the lower right incisor are strongly suggestive of the genus *Indricotherium*.

The *Indricotherium* from Khoer Dzan is distinctly different from the type species *I. transouralicum*, apart from its smaller size, by an incomplete metaloph and a fully isolated hypocone on P^4. Comparison of this find with a Chinese *Indricotherium* specimen is impeded by the latter's more worn P^4. It is nevertheless easy to see that when P^4 of these forms is heavily worn, the isolated hypocone fuses with the metaloph, and there is some

	Measurements	
I_1	The full length of the tooth across	ca 90
	The full length of the tooth in the forward curvature	ca 113
	The alveolar length	ca 59
	The apical length	31
	Inner alveolar size across (up to the enamel)	24
	The apical width, maximum	23
P^2	Length (the base of the ectoloph length, from outside)	24.5
	The base of the inner side length	22.5
	Protoloph length	33
	Metaloph length	32.5
P^4	Length (the base of the ectoloph length)	31
	The base of the inner side length	
	Protoloph width	56.0
	Metaloph width	56.5
	Index Ectoloph length / Protoloph width	55.5

Table 14.— Measurements of the teeth of *Urtinotherium* (or *Indricotherium*) sp.

small slit between the hypocone and the incomplete metaloph.

In one of his communications, the author referred a right P^4 from Khoer Dzan to *I. parvum* CHOW, previously known from the Oligocene of China. Radinsky believed that the fragmentary material described as *I. parvum* from China actually belonged to *Urtinotherium*. The author now refrains from any definite determination through lack of material.

Any comparison with *Urtinotherium incisivum* from the Lower Oligocene of Inner Mongolia is impossible since the latter is represented by a lower jaw only. As for the right lower incisor of a big rhinoceros from Khoer Dzan, it shows a structure identical to the I_1 of *Urtinotherium*, the only difference being their absolute sizes.

It should be noticed that Granger & Gregory (1936) established, along with a giant form (*I. transouralicum* = *Baluchitherium grangeri*), a relatively small form (Grade IV) of *Indricotherium* from the Oligocene of Nomkhong Shireh in Inner Mongolia. This form was described only from the lower jaw with the incisor region missing. Note that the Mongolian form from Khoer Dzan is identical in size and geological age to the *Indricotherium* (Grade IV) from the Nomkhong Shireh.

In my opinion, this form is quite different from the type species *I. transouralicum*. The fragmentary material is insufficient to establish a distinct species of *Indricotherium* from the Oligocene of Khoer Dzan although its affinity with the genus *Indricotherium* or *Urtinotherium* is likely.

Genus *ARMANIA* GABUNIA & DASHZEVEG, 1988

Armania: Gabunia & Dashzeveg, 1988, p. 244.

Etymology: The name is derived from "Arman" (Mongolian) = "rhinoceros".

Type species: *A. asiana* DASHZEVEG & GABUNIA, 1988.

Diagnosis: Medium sized indricotheriine hyracodontids. The facial part of the skull is greatly reduced, and the front edge of the orbit is at the level of P^2. The nasal incision extends back to the middle of P^2. Dental formula: I 3/3, C 1/1, P 3/4, M 3/3. I^1 is greatly reduced, I^2 is larger than I^3. The canines are well developed and larger than the incisors. P^1 is missing, P^4 is strongly molarized: the paracone and parastylar shelf are quite distinct. The teeth are hypsodont: the height index of the paracone to the ectoloph length is 175-180 on slightly worn M^{1-2}. Upper cheek tooth crowns are clearly rectangular in shape, except for P^2. The metaloph is incomplete on P^{2-4} and M^{1-2}. Secondary folds are well developed and the cingulum is quite prominent on the upper teeth.

Included spcies: Type species only.

Comparison

The affinity of the genus *Armania* with the Hyracodontidae is beyond doubt since it shows differentiation of the incisors (I^{1-3}) which evolved within the family. In addition, the structure of the premaxillary and maxillary bones, and their ratios may also prove the affinity of the species with the Hyracodontidae. Apart from the clearly inherited features,

Tab. 15.— Comparison of features of upper jaws and teeth of Indricotheriine genera.

Features	*Armania*	*Forstercooperia*	*Juxia*	*Indricotherium*
Furthest extent of nasal incision	At the level of P^2 middle	Above C	At the level of P^3	At the level of P^4
Facial section of the skull	Much shortened; front edge of orbit level with P^2	Considerably shortened in *F. totadentata*; front edge of orbit level with P^3 (Wood, 1938, fig. 1)	Much elongated; front edge of orbit level with the back edge of P^2	Comparatively long; orbit above M^2
Incisors	I^1 strongly reduced; I^2 bigger than I^3	I^1 comparatively small; I^2 bigger than I^3	I^1 bigger than I^2 and I^3	I^1 very large, canine-like, directed downward; I^2 and I^3 reduced
Premolars	P^1 missing; $P^{2\text{-}3}$ non molariform, P^4 strongly molariform	P^1 present; molarization increases from P^2 to P^4	P^1 present; $P^{2\text{-}4}$ strongly molariform; molarization increases from P^1 to P^2	P^1 present; $P^{2\text{-}4}$ strongly molariform; molarization increases from P^4 to P^2
Hypsodonty: $\frac{\text{Height at paracone}}{\text{Ectoloph length}}$	For P^4, 162; for $M^{1\text{-}2}$, 176-180	Not developed	Not developed	Not developed
Position of protoloph and metaloph	Protoloph robust; metaloph much less developed on upper teeth	Protoloph well developed and metaloph poorly developed on $P^{2\text{-}4}$, both ridges almost identically developed on molars	The same; $P^{2\text{-}4}$ rectangular	The same
Secondary elements on teeth (folds, etc.)	Well developed on metaloph of upper teeth	Not developed	Not developed	Not developed

Armania shows a number of acquired specialized features which distinguish this genus from other hyracodontid genera (tab. 15). It differs from all the others by the much reduced facial region of the skull, well developed hypsodont teeth and by the incomplete nature of the metaloph on the upper molars. From the most primitive genus *Triplopus*, it differs in being larger, having advanced molarization of P^4 and a clearly quadrate outline shape of P^3-M^2. From *Prohyracodon* it differs, apart from larger size, by the loss of P^1 and the high crowned molars; from *Ardynia*, by a strongly reduced I^1 and a short diastema between C and P^2, non-molariform $P^{2\text{-}3}$ and the presence of secondary folds in the metaloph region of the upper molars; from *Indricotherium*, by its smaller size, the presence of three incisors in the premaxillary bone and the clearly rectangular outline of the molars. It should be pointed out that in contrast to the genus *Indricotherium*, the facial part of the *Armania* skull is shorter, and the metaloph is less developed than the protoloph on upper teeth.

From *Juxia*, *Armania* differs by a much reduced facial region of the skull and by non molariform $P^{2\text{-}3}$; from the closest genus *Forstercooperia*, by the reduced P^1, more completely molarized P^4 and the rectangular shape of the upper molar crowns. In addition, *Armania*, in contrast to *Forstercooperia*, shows a deeper nasal incision, a more reduced I^1 and better developed canines.

From the North American genera *Hyracodon*, *Triplopides*, etc., it differs by a relatively shorter facial part of the skull, non molariform $P^{2\text{-}3}$ and an imperfect metaloph on the upper molars.

Armania asiana DASHZEVEG & GABUNIA, 1988

(Fig. 27, 28)

Armania asiana: Gabunia & DDashzeveg, 1988, p. 497, fig. 1-3.

Etymology: The name is derived from "asianus" (Latin) = "Asian".

Holotype: PSS, n° 27-10, a fragment of the left uper jaw with $P^{2\text{-}4}$.

Paratype: PSS, n° 27-14, a fragment of the right upper jaw with alveoli of $I^{1\text{-}3}$, C and P.

Material: Khoer Dzan: PSS, n° 27-12, a fragment of the upper jaw with $P^{2\text{-}3}$; PSS, n° 27-13, an isolated M^1; PSS, n° 27-11, an isolated M^2; PSS, n° 27-90, an isolated M^1; PSS, n° 27-91, an isolated M^2; PSS, n° 27-92, an isolated M^2; Ergilin Dzo: PSS, n° 17-31, a fragment of the right upper jaw with $P^{3\text{-}4}$; PSS, n° 17-32, a fragment of the right upper jaw with $P^{3\text{-}4}$.

Depth of upper jaw at the level of the middle of P^2	73
Maximum depth of the incisor region of the upper jaw	40.5
Incisor width on the outer edge	66
Length of P^2-P^4	62.5
Distance from the edge of the incisor region to P^2	61.5
Diastema length from I^3 to P^2	18.5
Diastema length from I^3 to C	4.4

Table 16.— Measurements of the upper jaw of *Armania asiana*.

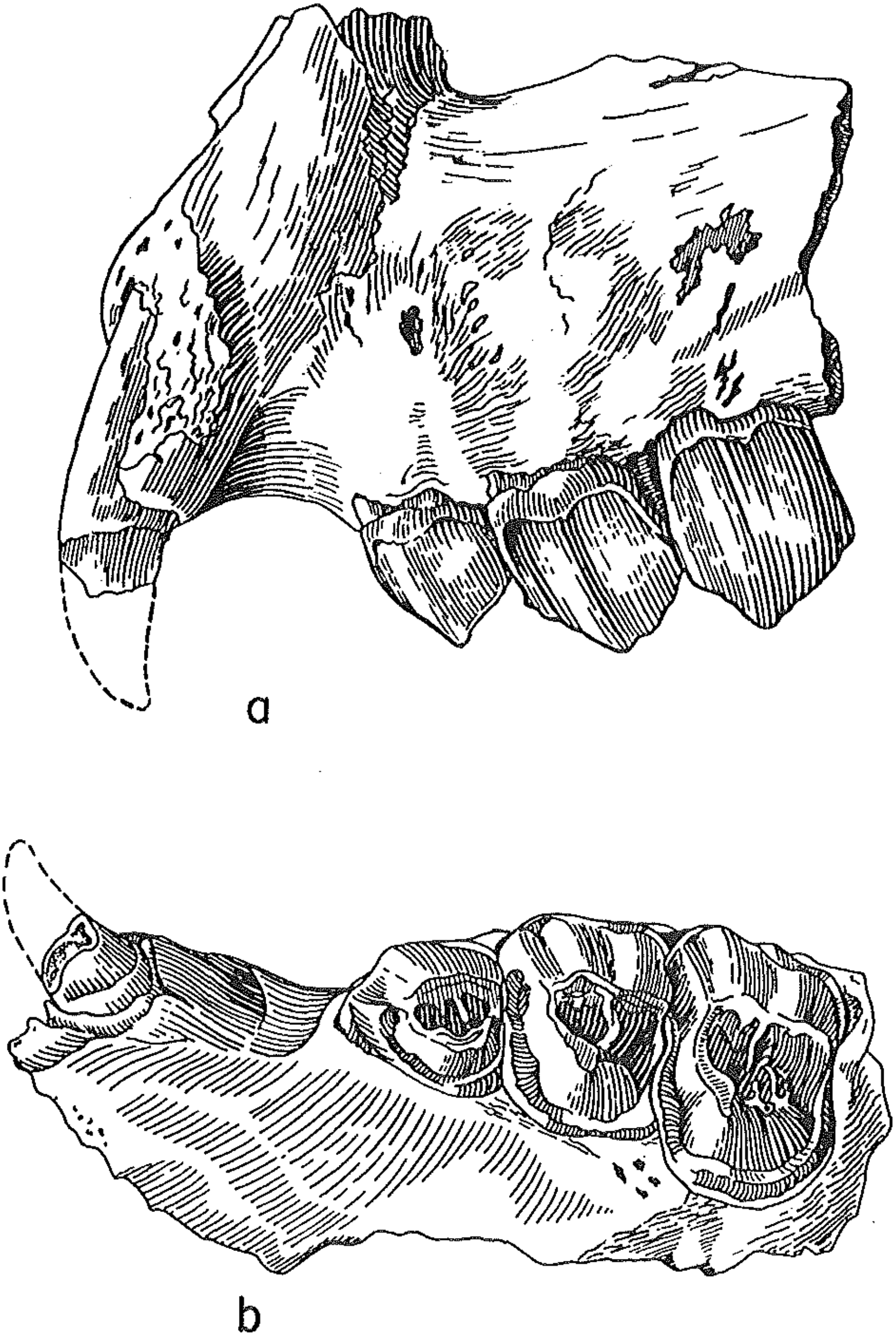

Fig. 27.—*Armania asiana* DASHZEVEG & GABUNIA, PSS n° 27-10, holotype, a fragment of the upper left jaw with P^2-P^4; x 1; a: labial view; b: occlusal view.

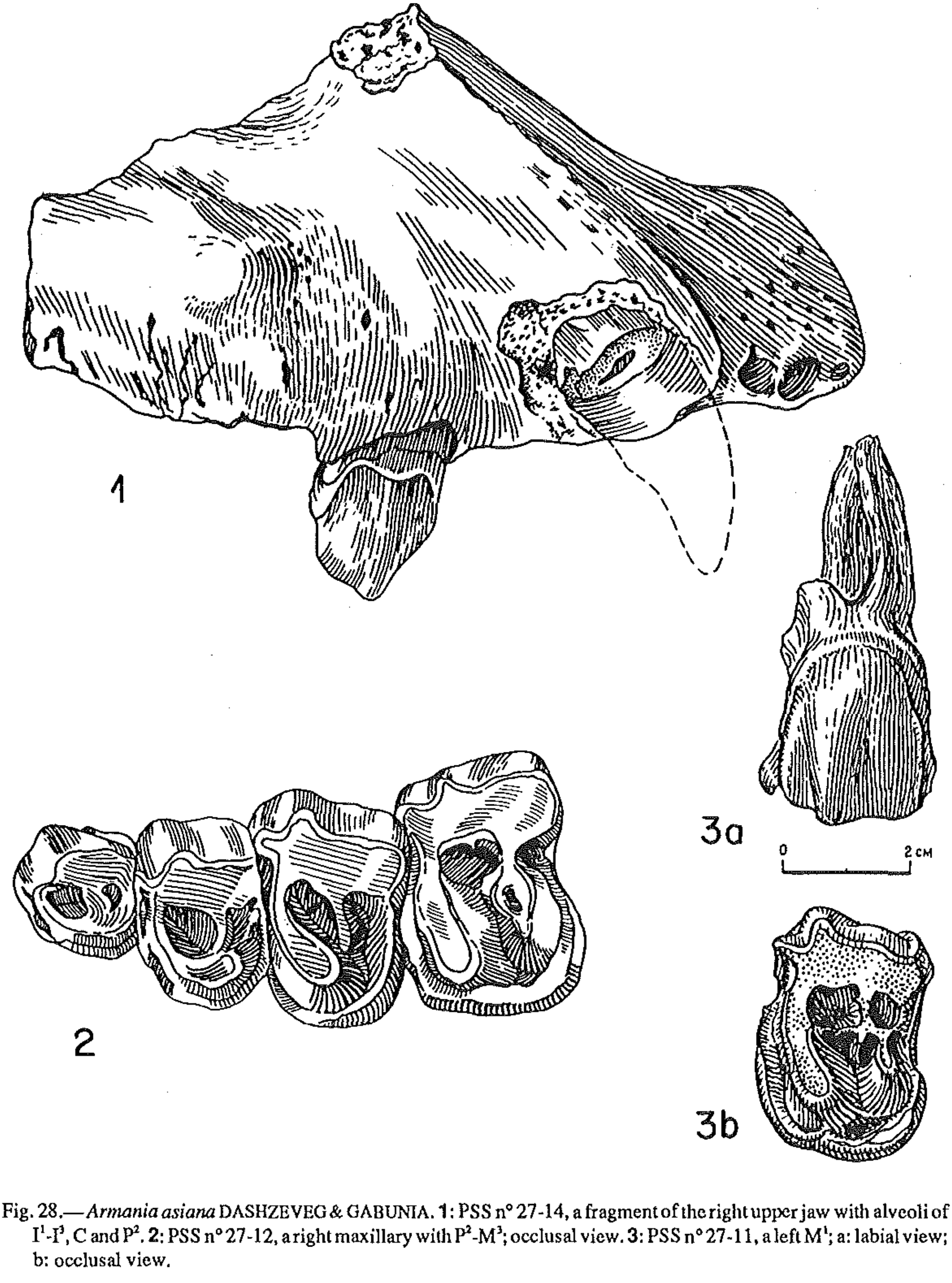

Fig. 28.—*Armania asiana* DASHZEVEG & GABUNIA. **1**: PSS n° 27-14, a fragment of the right upper jaw with alveoli of I^1-I^3, C and P^2. **2**: PSS n° 27-12, a right maxillary with P^2-M^3; occlusal view. **3**: PSS n° 27-11, a left M^1; a: labial view; b: occlusal view.

Locality and age: Mongolia, eastern Gobi Desert: Khoer Dzan. Upper Eocene; Ergilin Dzo suite, Sevkhul Member; Ergilin Dzo, Lower Oligocene, Ergilin Dzo suite, Ergilin Member.

Diagnosis: The same as for the genus.

Description

The facial part of the skull is much shortened and the front edge of the orbits is at the level of P^2. The premaxillary bone is relatively low, clearly extended. Its front part is slightly broadened and bears three unequal incisors. The premaxillaries are connected with the nasals and they wedge out posteriorly at a narrow angle between the nasal and maxillary bones above P^2. Specimen PSS n° 27-10 from the Upper Eocene of Khoer Dzan shows well the premaxilla-maxilla contact. The former is at its highest above P^2. The preserved lower front edge of the orbit is distinct and has an oval to rounded shape.

The nasal incision is shallow; its rear edge is at the level of P^2. The orbit is very close to the nasal incision. No incisors are preserved. Judging from the alveolus, I^1 is much reduced and I^2 is slightly larger than I^3. The canine is well developed and is separated from I^3 by a short diastema (3 mm). It is rounded in cross section, deeply set in the jaw and directed slightly forward and downward. The diastema between C and P^2 is 84 mm long. P^1 is missing. P^2 is oval to rounded in shape and non molariform. The outer wall is a little taller than the inner one and the cingulum is well developed on the lingual side of the crown. P^2 is distinctly rectangular in shape and tends to be molariform. The paracone is quite prominent, and its outer edge distinct. The parastylar shelf is deep, reaching almost to the base of the crown. The parastyle is distinct. The metacone is developed. The vertical groove between the paracone and metacone can easily be traced. The protoloph is developed, extending disto-lingually across the crown. The metaloph is much more

Measurements		Khoer Dzan					Ergilin Dzo	
		n° 27-10	n° 27-12	n° 27-73	n° 27-78	n° 27-13	n° 17-32	n° 17-31
C	Length	16						
	Width	13						
P^2	Length	17.5						
	Width	22						
P^3	Length	20.6	18.5	14	16		20	20
	Width	30.3	20.4	19	16		26	24
P^4	Length	23.2	20.5	19	18		21	22
	Width	37.6	26.6	23	24		36	37
M^1	Length					25		
	Width					41.4		

Table 17.— Measurements of the teeth of *Armania asiana*.

weakly developed than the protoloph. Worn specimens show the lingual end fused with the protoloph or closely adjoining it. The talon basin is deep. The cingulum is well developed at the base of the crown except for the labial side. P^4 is strongly molariform and rectangular. The ectoloph is distinct, with its major elements developed. The most prominent of them are the paracone and parastyle separated by a relatively deep vertical fold. The parastyle is low, the metacone is distinct, and its outer rib is quite prominent. The protoloph is robust, while there is no evidence of the hypocone being separated from the postero-lingual side. The metaloph is weak, its lingual end often joining the back wall of the protoloph. The cingulum is well developed and encircles the whole tooth. The crown is high: the paracone height on the unworn specimen (PSS, n° 27-10) is 34.5 mm. The height index (the paracone height to ectoloph length ratio) is 149.

The M^1 outline is rectangular: its outer edge is almost the same length as the inner one, while the anterior edge is a little longer than the posterior one; the protocone protrudes further lingually than the hypocone. The parastylar rib is strong, reaching almost to the middle of the crown (on the outside). The protoloph is nearly twice as large as the metaloph; the median valley is open from the lingual side. The metaloph has a complex structure. As the available material is scarce it has so far been impossible to establish its detailed structure. The crown is high, its index of height to length of the ectoloph on the less worn examples is 170-180. M^2 is slightly larger than M^1 and has a slightly better developed cingulum. The index of height to length is 175.

Measurements and indices	n° 27-10			n° 27-67	n° 27-90	n° 27-91	n° 27-9
	P^2	P^3	P^4	M^1	M^1	M^2	M^2
Ectoloph length at the base (1)	17.5	20.6	23.2	21	20	23	24
Protoloph length (2)	22.0	30.3	37.8	37	36	39	42
Height of paracone (3)	21.5	27.5	34.5	36	30	36	42
Height of protocone (4)				20	22	20	27
Length (2) / Length (1)	130	147	162	176	180	170	175
Height (3) / Length (1)	122	133	149	171	150	154	157
Height (4) / Length (1)				95.2	110	87	112

Table 18.— Measurements and indices the teeth of *Armania asiana.*

Family RHINOCEROTIDAE OWEN, 1883

Subfamily CAENOPINAE COPE, 1887

Diagnosis: Small to medium in size. Skull long, narrow, tapering anteriorly. Frontal bones smooth. The symphyseal region of the lower jaw narrow or slightly broadened, the angular process projects distinctly backward. Dental formula: I 2/1-2, C 0/0?, P 4/3-4, M 3/3. Upper canines not developed or small, the lower ones missing. P^{3-4}/P_{3-4} incompletely molarized. Molars low crowned, cement missing.

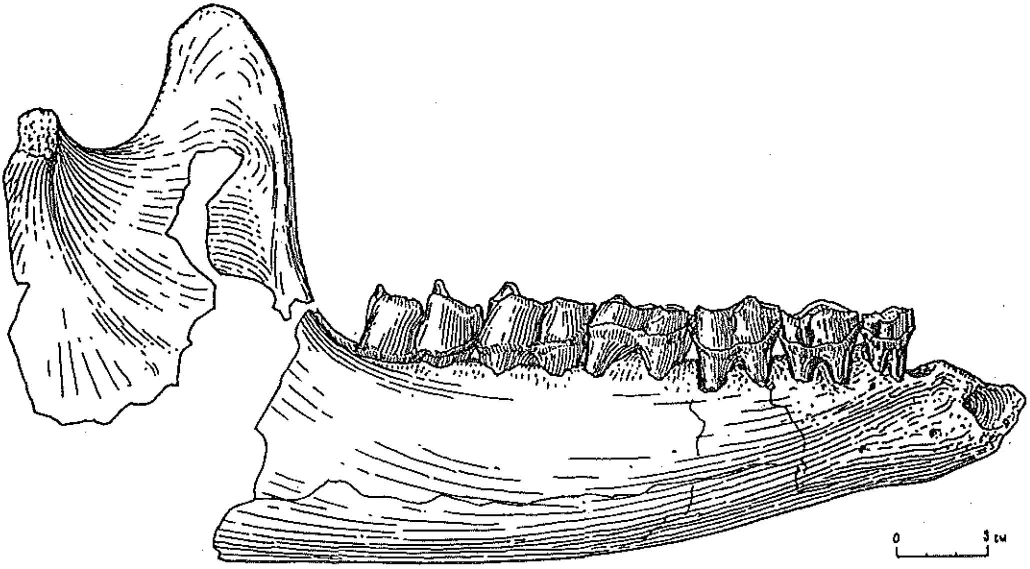

Fig. 29.— *Ronzotherium orientale* sp. nov., PSS n° 21-15, holotype, an incomplete lower jaw with I_2 (right) and P_2-M_3; labial view.

Included genera: *Ronzotherium* AYMARD, 1856 and *Symphysorrhachis* BELIAYEVA, 1954 are known in Mongolia.

Comparison: Differs from the closest subfamily Allaceropinae by the absence of lower canines, reduction of the upper canines and a better development of the incisors. The Caenopinae, in contrast to other subfamilies are characterized by the primitive structure of their dental apparatus, in particular by less distinct molarization of P^4/P_4.

Genus *RONZOTHERIUM* AYMARD, 1856

For complete synonymy, see Brunet, 1979.

Type species: *R. velaunum* (AYMARD, *in* PICTET, 1853).

Diagnosis: Medium-sized to large rhinocerotids. The symphyseal region comparatively short, extending posteriorly to the front edge of P_1. One pair of upper incisors, one or two pairs of lower ones. One of the pairs of lower incisors (I_2) is considerably larger than the upper pair (I^1). I_1 is usually rudimentary. P^4/P_4 incompletely molarized: on P^4, the hypocone is not isolated from the protoloph, and the metaloph is incomplete; the entoconid is almost fused with the hypolophid on P_4. The cingulum is strongly developed on P^{2-4}. The parastylar shelf on M^{1-2} is relatively deep. The antecrochet is present throughout, the crochet is either present or missing. The metastyle is bent outwards on M^{1-2}.

Included species: According to Heissig's data (Heissig, 1969) the genus *Ronzotherium* includes the following species and subspecies from the Oligocene of Western Europe:

R. velaunum (AYMARD, 1853),

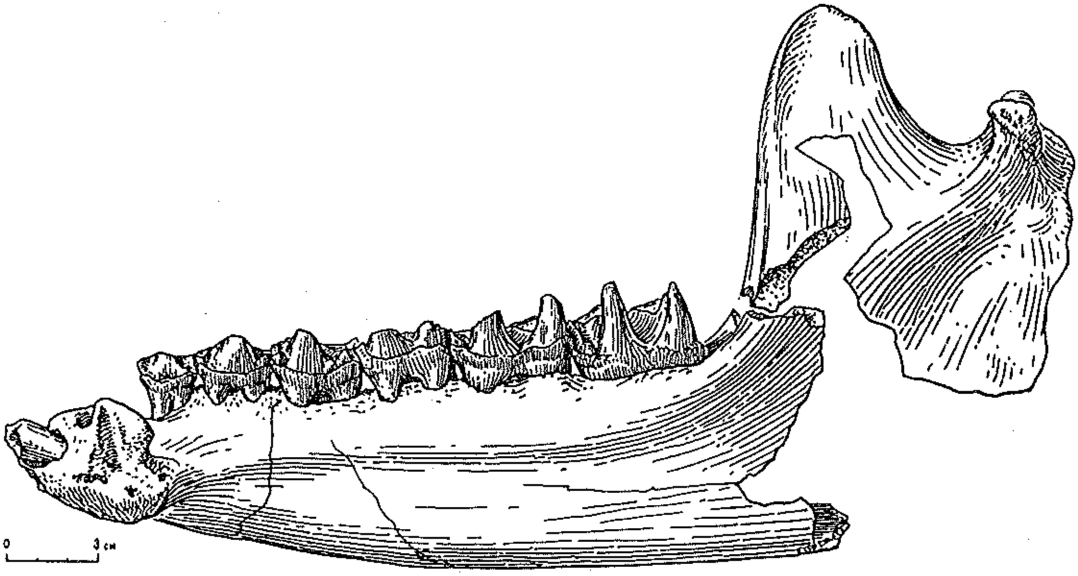

Fig. 30.— *Ronzotherium orientale* sp. nov., PSS n° 21-15, holotype, an incomplete lower jaw with I_2 (right) and P_2-M_3; lingual view.

R. filholi (OSBORN, 1900), with subspecies: *R. filholi filholi* (OSBORN, 1900),
R. filholi elongatum HEISSIG, 1969,
R. filholi romani KRETZOI, 1940,
R. kochi (KRETZOI, 1940).

A somewhat different arrangement of species is listed in Brunet (1979):

R. velaunum (AYMARD, 1853),
R. filholi (OSBORN, 1900), and
R. romani KRETZOI, 1940.

From Mongolia I add the species *R. orientale* sp. nov.

Comparison: Differs from the genus *Symphysorrhachis* from the Oligocene of Mongolia by a much reduced and narrow symphysis in the lower jaw. Note that *Symphysorrhachis* has a distinct median keel on the lower surface of the symphyseal region, and retains I_1.

Discussion

The newly described species from the Oligocene of Ergilin Dzo and Khoer Dzan has much in common with the genus *Indricotherium*. This is seen from the structure of the lower teeth, reduced symphysis and presence of one pair of incisors in the lower jaw. Together with certain similarities, there are also radical differences.

Indricotherium is distinguished by comparatively smaller size and different character and proportions of the symphysis in the lower jaw. The lower edge of its jaw anteriorly is bent downwards along with the whole incisor region (Osborn, 1923; Gromova, 1959). In addition, the *Indricotherium* from the Oligocene of Urtyn Obo (specimen n° 26166) has the jaw beneath the premolars (P_{3-4}) swollen laterally and ventrally (Granger & Gregory, 1936). A similar lower jaw swelling is also evident in *Urtinotherium* from the Oligocene of Urtyn Obo, China (Chow & Chiu, 1963).

Ronzotherium orientale sp. nov.

(Fig. 29, 30, 31, 32, 33, 34)

Etymology: The name of the species is derived from "orientalis" (Latin) = "eastern".

Holotype: PSS, n° 21-15, an incomplete lower jaw with I_2 (right) and P_1-M_3.

Material: Apart from the holotype, PSS, n° 27-11, a right ramus of the lower jaw with P_4-M_3.

Locality and age: Mongolia, eastern Gobi Desert: Ergilin Dzo (holotype, n° 21-15), Bayan Tsav ravine and Khoer Dzan (n° 27-11); Lower Oligocene, Ergilin Dzo suite, Ergilin Member.

Diagnosis: Smallest species of *Ronzotherium*; length of P_1-M_3 192 mm. P_{3-4} strongly molariform, the hypolophid incomplete and the entoconid isolated. The symphysis shortened; its index of length against length of the dental series is 30%, I_1 reduced, I_2 developed. The cingulum is well developed on all the lower teeth.

Description

The symphyseal region is elevated, its elevation being gradual and starting at the middle of P_3. The symphysis is shortened and rapidly tapers anteriorly, while posteriorly it

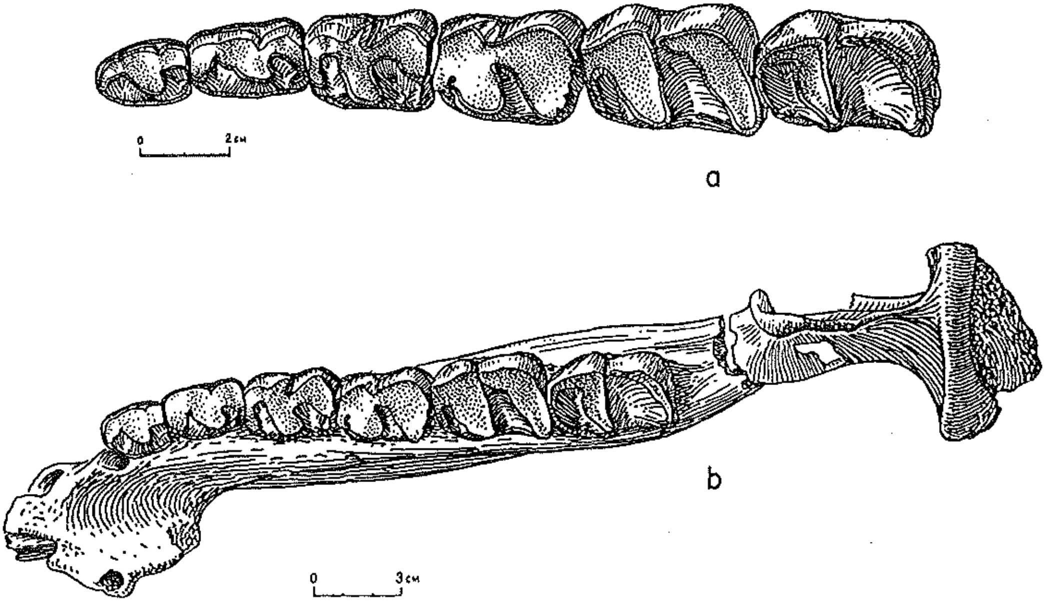

Fig. 31.—*Ronzotherium orientale* sp. nov., PSS n° 21-15, holotype, an incomplete lower jaw with I_2 (right), P_2-M_3; a: occlusal view of P_2-M_3; b: occlusal view of mandible.

reaches the front edge of P$_3$. The anterior end of the symphyseal region is oval in shape. The symphysis is widest at the back between the posterior edges of the two P$_2$'s: 51 mm (tab. 19), which is 89.6% of the symphyseal length. The symphyseal region is narrowest at the I$_2$ alveolus, 34 mm.

The diastema between I$_2$ and P$_1$ is 18 mm, which is almost 1/3rd of the symphyseal length. Of the incisors, only an incomplete left I$_2$ is preserved in the jaw. Its crown is oval in cross section.

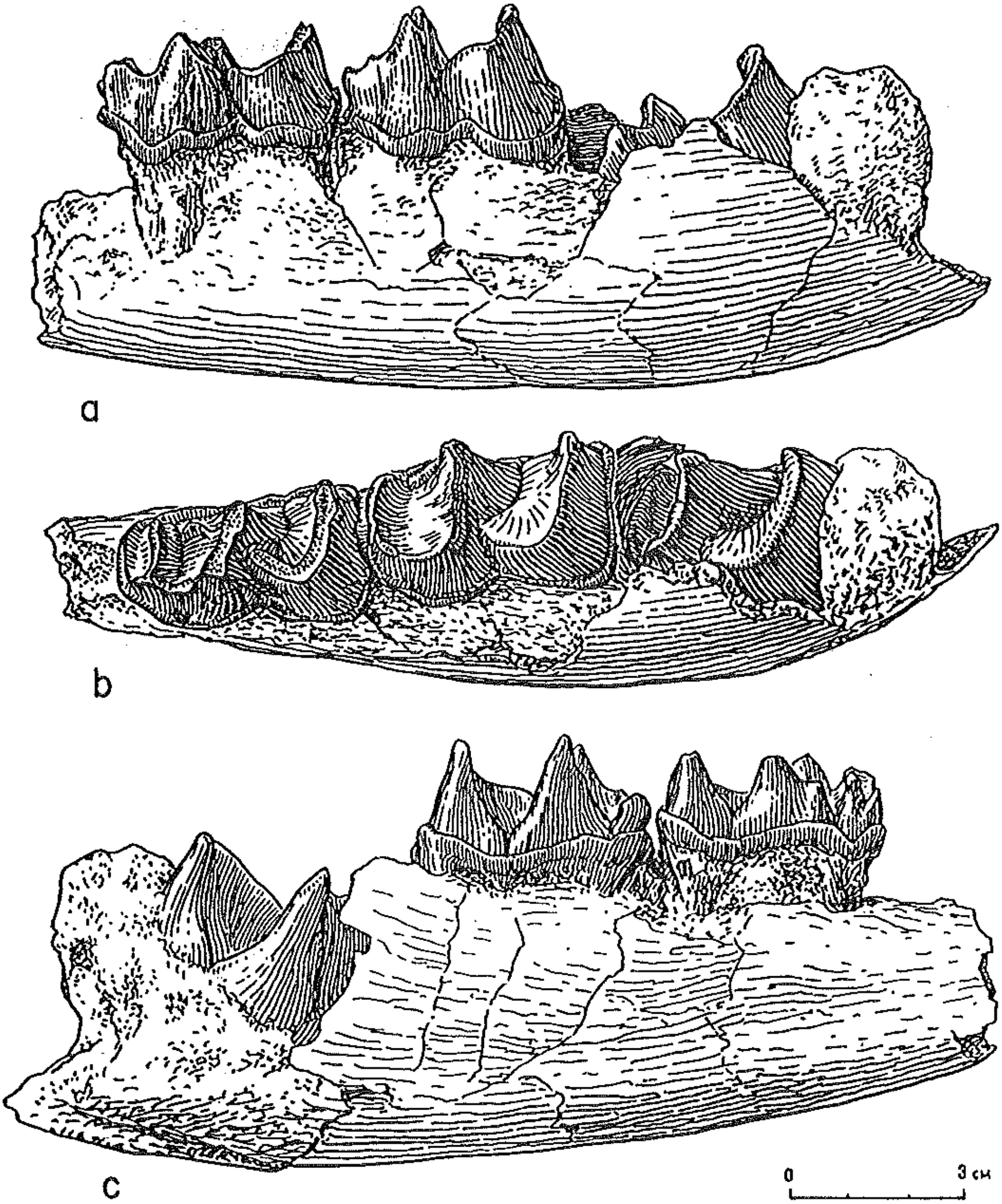

Fig. 32.—*Ronzotherium orientale* sp. nov., PSS n° 21-60, a fragment of the lower left jaw with DP$_3$, DP$_4$ and M$_2$; a: labial view; b: occlusal view; c: lingual view.

The small distance between the alveoli of the incisors suggests that these teeth were closely spaced. As for the first incisors they must have been lost. The I_2 root is relatively short; its tip does not reach as far as the back edge of P_2.

The teeth gradually increase in size from P_1 to M_3. P_1 is not preserved, but judging from its alveolus it was single rooted.

P_2 is double rooted, elongated and tends to be molariform. The hypolophid is poorly developed and the entoconid is not developed at all. P_3 differs from P_2 by being larger and more molariform. The trigonid basin is developed. The entoconid is low but distinct. The hypolophid is distinct although it weakens lingually at the contact with the entoconid. P_4 is strongly molariform but in contrast to the molars has a less well developed hypolophid and an isolated entoconid. The outer branch of the hypolophid is robust. The paralophid is prominent, the trigonid basin is narrow antero-posteriorly. M_1 is rectangular in outline, the trigonid is shorter than the talonid. The entoconid is the highest point of the crown and is

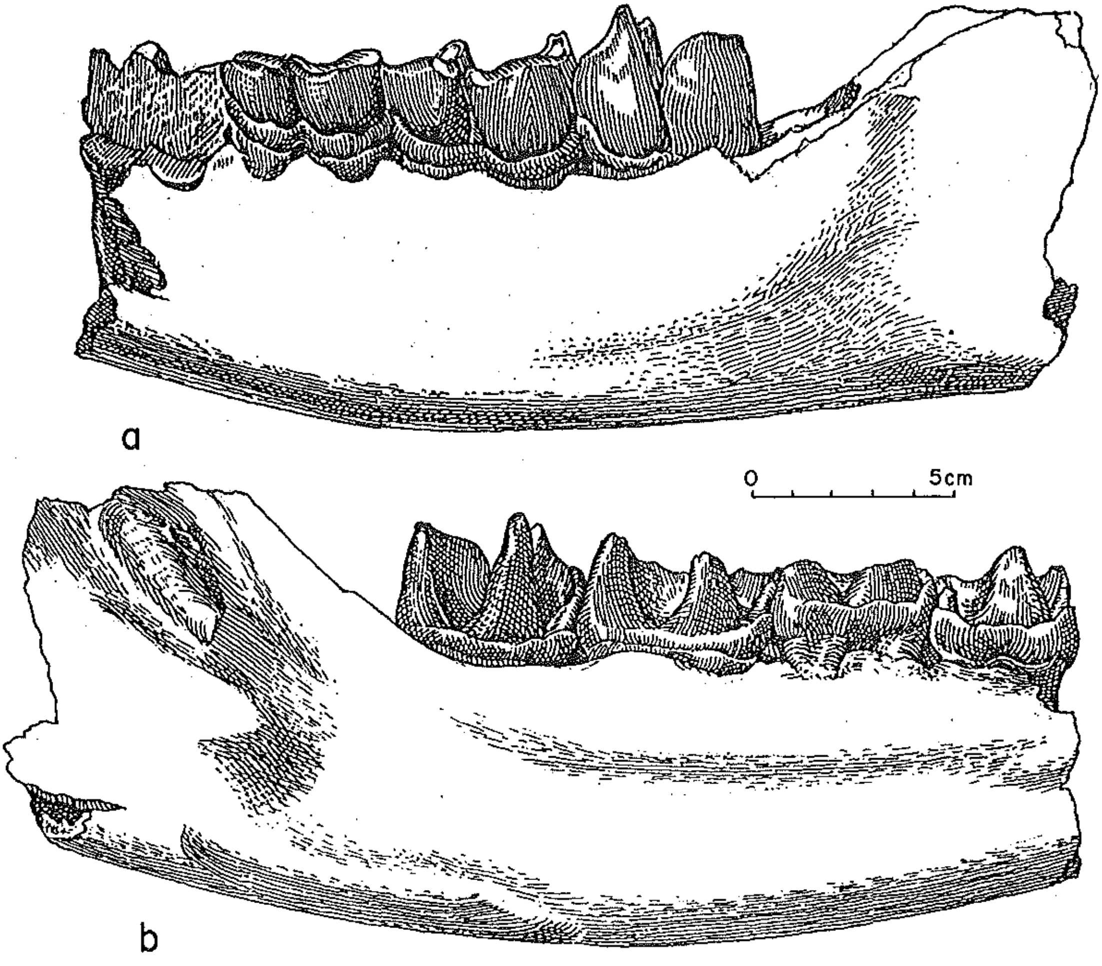

Fig. 33.—*Ronzotherium orientale* sp. nov., PSS n° 27-11, a fragment of the left lower jaw with P_4-M_3; a: labial view; b: lingual view.

Measurements	Holotype n° 21-15
Length of symphysis	58
The greatest symphyseal width at the posterior edge of P_2	51
The smallest symphyseal width at the I_2 alveolus	34
Diastema between I_2 and P_1	18
Height of the horizontal ramus under P_2	35
Height of the horizontal ramus under P_3	44
Height of the horizontal ramus under M_1	61
Height of the horizontal ramus under M_2	64
P_1-M_3	19.2
P_1-P_4	81
M_1-M_3	10.6

Table 19.— Measurements of the mandible of *Ronzotherium orientale* sp. nov.

well developed. M_2 differs from M_1 by being relatively larger and less worn. The paralophid is well marked, its lingual end not reaching the inner edge of the crown. The trigonid basin is short, while the talonid basin is relatively deep. The entoconid is higher than the metaconid. The hypolophid is well developed, and its antero-labial branch closely adjoins the back wall of the metalophid. M_3 is the largest tooth; its paralophid is parallel to the metalophid.

The structure of DP_4 and M_1 is quite distinct on specimen PSS n° 21-60 from the Oligocene of Ergilin Dzo. The DP_4 crown is rectangular, and the tooth is fully molariform. The hypolophid and metalophid are oblique, while the paralophid is almost transverse to the long axis of the tooth. The paralophid is much shorter than the preceding transverse ridges. The entoconid forms the highest part of the crown. The cingulum is well developed and surrounds the whole crown. M_1 is more massive than DP_4. The metalophid and hypolophid are parallel. The lingual end of the paralophid reaches the inner edge of the crown. The cingulum is developed like that of DP_4. M_2 is not erupted. The metalophid is almost at a right angle to the horizontal axis of the tooth. The talonid basin is U-shaped. The

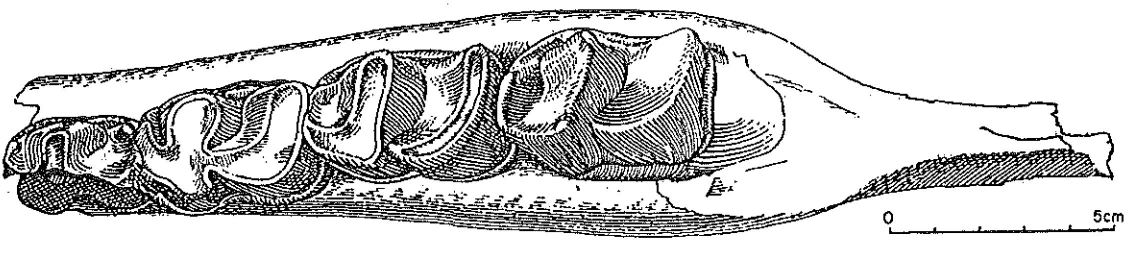

Fig. 34.— *Ronzotherium orientale* sp. nov., PSS n° 27-11, a fragment of the left lower jaw with P_4-M_3; occlusal view.

		Holotype n° 21-15	n° 27-11	n° 27-77
P_1	Length	7.0		
	Width	6.5		
P_2	Length	14.5		
	Trigonid width	15.0		
	Talonid width	15.5		
P_3	Length	22.5		
	Trigonid width	17.5		
	Talonid width	19.5		
P_4	Length	27.0	30.0	22.5
	Trigonid width	21.0	21.0	16
	Talonid width	23.5	21.0	17.5
M_1	Length	29.0	35.0	29
	Trigonid width	23.0	28.0	19
	Talonid width	25.0	30.0	21.5
M_2	Length	35.0	44.0	33
	Trigonid width	26.0	31	22.2
	Talonid width	28.0	31	24
M_3	Length	37.0	45	36
	Trigonid width	27.0	31.5	
	Talonid width	25.0	29.0	

Table 20.— Measurements of the lower cheek teeth of *Ronzotherium orientale* sp. nov.

hypolophid is complete. The heel is not developed. The cingulum is weakly developed and is recorded on the outer side of the crown.

Comparison

It differs from all known species from the Oligocene of Western Europe by its smaller size, an incomplete hypolophid on $P_{3\text{-}4}$ on which the entoconid is practically isolated from the neighbouring cuspules, and a shorter symphysis.

Ronzotherium sp.

(Fig. 35)

Material: PSS, n° 27-98, a fragment of the right ramus of the lower jaw with P_4-M_3.

Locality and age: Mongolia, eastern Gobi Desert, Khoer Dzan; Lower Oligocene, Ergilin Dzo suite, Ergilin Member.

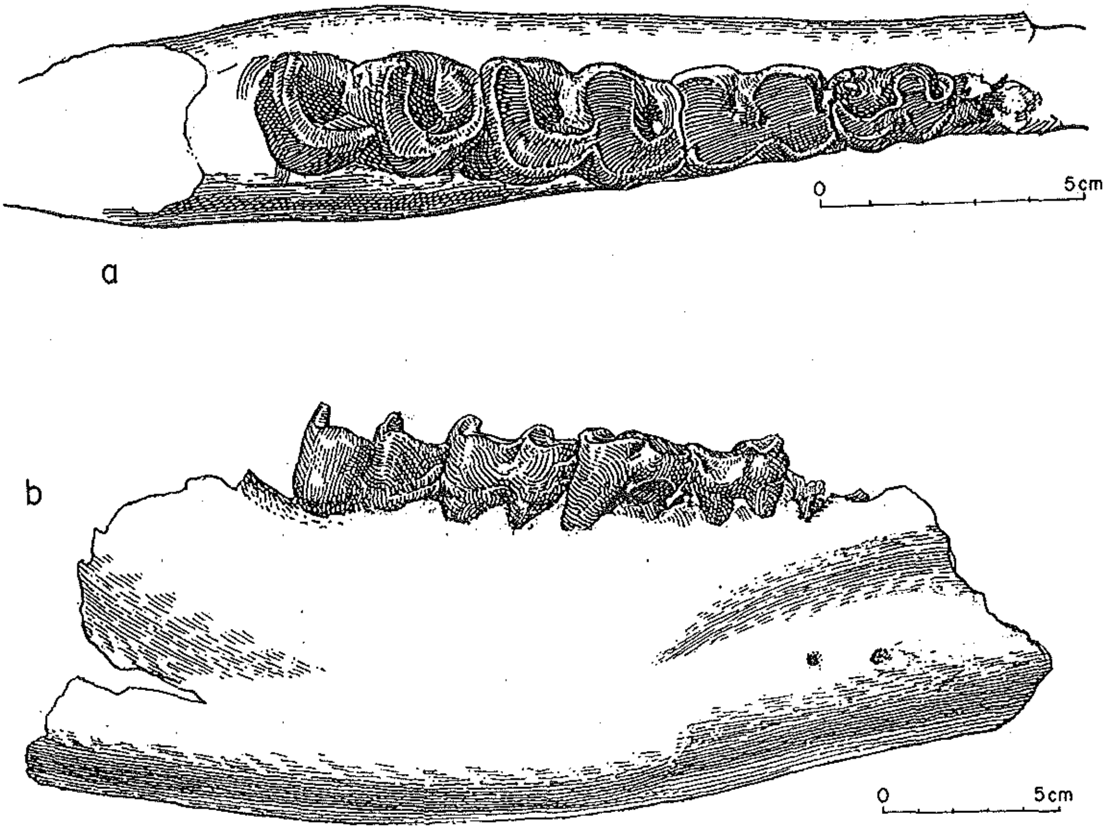

Fig. 35.—*Ronzotherium* sp., PSS n° 27-98, a fragment of the lower right jaw with P_4-M_3; a: occlusal view; b: labial view.

Description

The lower jaw is relatively large; length of M_1-M_3, 128 mm. The teeth gradually increase in size from P_4 to M_3. The lower edge of the horizontal ramus is slightly bent opposite M_3 and gradually deepens posteriorly: 74 mm under P_3, 82 mm below M_1 and 87 mm below M_2. It is deepest below the middle of M_3, being 91 mm, or 2.6 times more than P_3-M_3 (= 34.5). The paralophid on P_4 is distinct, being exposed to wear later than the metalophid. The front end of the hypolophid closely adjoins the back wall of the metalophid. The outer hypolophid wall is quite prominent. The hypolophid weakens and dies away lingually. There are two cuspules (entoconid 1 and 2) at the entrance to the talonid. Entoconid 1 is attached to the lingual end of the hypolophid. Entoconid 2 is near the first one and isolated from other cuspules. Most structures on M_1 have been removed by strong wear. M_2 and M_3 appear similar to M_1.

Comparison and notes

It differs from *R. orientale* by a more distinct hypolophid and by a secondary entoconid on P_4. In addition, the cingulum is less developed and the horizontal ramus of the

	Measurements	n° 27-98
P_3	Length (from alveolus)	21.0
	Trigonid width	13.5
	Talonid width	15.0
P_4	Length	22.0
	Trigonid width	15.0
	Talonid width	17.0
M_1	Length	26.0
	Trigonid width	20.0
	Talonid width	23.0
M_2	Length	34.0
	Trigonid width	23.0
	Talonid width	24.0
M_3	Length	37.0
	Trigonid width	23.0
	Talonid width	25.0

Table 21.— Measurements of the lower cheek teeth of *Ronzotherium* sp.

lower jaw is deeper. P_4 is both absolutely and relatively smaller. Thus, certain features of the lower jaw suggest that *Ronzotherium* from the Oligocene of Khoer Dzan is specifically distinct. However, insufficient material precludes naming it formally.

Genus *SYMPHYSORRACHIS* BELIAYEVA, 1954

Symphysorrachis: Beliayeva, 1954, p. 192.
Ronzotherium: Heissig, 1969, p. 37; Brunet, 1979, p. 104.

Type species: *S. brevirostris* BELIAYEVA, 1954.

Diagnosis: Large sized caenopine rhinocerotids. Length of M_1-M_3, 127 mm. The lower jaw is robust. The horizontal ramus is high; its height is 40% of the P_1-M_3 length. The symphyseal region of medium length, around 60% of that of the dental series. It is angled at 25°, slightly broader and a little constricted in front of the first premolar. Its greatest width is 80% of the symphyseal length, the smallest, around 65% of the latter, and a little more than 80% of the maximum width of the whole region. The lateral walls of the symphysis converge ventrally at an obtuse angle, forming a keel on the lower surface. The diastema between I_2 and P_1 is of medium length comprising nearly 50% of the symphyseal length and 30% of the P_1-M_3 length. Dental formula: I?/2, C1/0, P?/4, M?/3. Incisors large, I_2 robust.

Included species: Type species only.

Notes

Substantiating the systematic independence of the genus *Symphysorrachis*, E.I. Beliayeva (1954) pointed out the following characteristic features: (1) incisors reduced to two pairs and lower canines disappearing, with I_2 bigger than I_1; (2) molariform P_{3-4}: the author believed that the complete set of premolars and brachyodont crowns of these teeth, as well as of the molars, are features suggesting the primitiveness of this genus; (3) presence of the median keel on the lower surface of the symphysis of the lower jaw and the robust and relatively deep horizontal ramus with straight lower edge.

Note that these features clearly distinguish this genus from the known rhinocerotid genera. However, the paper by Beliayeva lacks any comparison with the genus *Ronzotherium* since at that time the latter was known only from an incomplete lower jaw with P_1-M_2 and some carpal and tarsal bones.

Later, the works by Heissig (1969) and Brunet (1979) greatly expanded our knowledge of the morphological characters of the genus *Ronzotherium* on the basis of new collections from various stratigraphic horizons in the Oligocene of Western Europe. Heissig believed that the structure and number of incisors, as well as the molariform P_{3-4} of *Symphysorrachis* was sufficient to relegate the genus to a synonym of *Ronzotheruim*. Brunet shared this view also.

The genus *Symphysorrachis* is distinctly different from primitive specimens of *Ronzotherium* (*R. orientale*) by having a robust median keel on the lower jaw, a reduced I_1 and an expanded anterior region of the symphysis. These characters allow *Symphysorrachis* to be reinstated as a distinct genus.

Subfamily **ALLACEROPINAE** WOOD, 1932

Diagnosis: Medium-sized allaceropine rhinocerotids. The symphyseal region of the lower jaw is relatively short and narrow. The angular process region of the jaw is very prominent posteriorly. Dental formula: I ?/2, C 1/1, P 4/4, M 3/3. Canines strongly

Measurements		n° 27-15	n° 27-16
DP_2	Length	6.0	
	Width	5.0	
DP_3	Length	10.0	
	Width	6.0	
DP_4	Length	18.0	22.0
	Width	10.0	10.0
M_1	Length	16.5	19.0
	Width	12.0	12.5

Table 22.— Measurements of the milk teeth and M_1 of *Allacerops* sp.

developed and larger than the incisors. The diastema between C and P_1 is nearly 25 mm long. Molars are low crowned. The parastylar shelf on the molars is deep. The antecrochet is distinct.

Included genera: Only the genus *Allacerops* WOOD, 1932 from the Oligocene of Europe and Asia.

Genus *ALLACEROPS* WOOD, 1932

Epiaceratherium: Wood, 1932, p. 418.
Allacerops: Wood, 1932, p. 170; Beliayeva, 1954, p. 198; Borsuk-Bialyncka, 1968, p. 155.

Type species: *Epiaceratherium turgaicum* BORISSIAK, 1915.

Diagnosis: As for the subfamily.

Included species: In Asia, two species: *A. turgaica* (BORISSIAK, 1915), and *A. minor* BELIAYEVA, 1954.

Allacerops minor BELIAYEVA, 1954

Allacerops turgaica minor: Beliayeva, 1954, p. 200, pl. 2, fig. 2-7; fig. 6-8.
Allacerops minor BELIAYEVA: Borsuk-Bialyncka, 1968, p. 155, pl. 19, 20.

Holotype: PIN, n° 475-8, the third upper premolar of the left side (P sin.).

Locality and age: Mongolia; (1) The Valley of Lakes; Tatal Gol; Oligocene, Hsanda Gol

Measurements		n° 27-74
P_1	Length	5.0
	Width	4.0
P_2	Length	9.0
	Width	5.0
P_3	Length	11.0
	Width	7.0
P_4	Length	11.0
	Width	7.0
M_1	Length	12.0
	Width	9.0
M_2	Length	16.0
	Width	13.0

Table 23.— Measurements of the lower permanent teeth of *Allacerops* sp.

suite; (2) Trans-Altay Gobi, Ulan Ganga, the uppermost Lower and lowermost Middle Oligocene, Hsanda Gol suite.

Allacerops sp.

(Fig. 36)

Material: PSS, n° 27-15, a fragment of the right ramus of the lower jaw with DP_2, DP_3, DP_4 and M_1; PSS, n° 27-76, a fragment of the left lower jaw with DP_4 and M_1; PSS, n° 27-74, an incomplete lower jaw with DP_4 and M_1; PSS, n° 27-71, an incomplete lower jaw with alveoli for I_1, C, alveoli for P_{1-3} and P_4-M_3 with broken crowns.

Localities and age: Mongolia, eastern Gobi Desert, Khoer Dzan; Upper Eocene-Lower Oligocene, Ergilin Dzo suite.

Description

Specimen PSS n° 27-15 clearly shows some features of the lower jaw and the structure of the milk teeth. The jaw was small and the horizontal ramus straight. Nothing can be said about the structure of the symphysis because of bad preservation. The symphyseal region is angled at 25° (with respect to the jaw's horizontal edge). The elevation begins opposite the middle of P_2. There are two mental foramina, the posterior one is 19 mm below P_3, while the anterior one is 22 mm in front of the posterior one. Judging from the alveolus, the canine was the best developed tooth. The diastema between C and DP_2 is 16 mm, DP_1 is missing, DP_2 is small, chisel-like and single rooted. DP_3 is double rooted and non molariform. DP_4 has a complex structure: the paraconid and paralophid are distinct. The paralophid is parallel to the metalophid. The hypolophid is complete corresponding to the broadest part of the crown. The cingulum is developed only on the anterior and posterior sides of the tooth. M_1 has a typically hyracodontid structure.

Specimen PSS n° 27-16 from Khoer Dzan shows well the structure of DP_4 and M_1. DP_4 is oblong-rectangular, constricted at the front. Its structure shows the features of rhinocerotoids. The paraconid is distinct and much lower than the protoconid. The paraconid/paralophid is distinct and relatively narrow. The lingual end of the paralophid shows a well developed (unnamed) cuspule which is slightly lower than the adjacent paraconid. The front slope of the paraconid is quite prominent, its base fused with the anterior cingulum. The trigonid basin is wide and the metalophid is slightly bent in the middle. M_1 is more robust than DP_4. The paralophid descends steeply from the front slope of the protoconid, reaching the inner side of the crown. The hypolophid, in contrast to the metalophid, is more oblique with respect to the long axis of the tooth. The cingulum is rather indistinct.

Specimen PSS n° 27-14 allows us to judge the general structure and character of the symphysis of the lower jaw of a peculiar rhinoceros from the Oligocene of Khoer Dzan. It has no incisors, canines or P_{1-3} preserved. The alveoli suggest the dental formula I ?/1, C ?/1, P ?/4, M ?/3. Judging from the alveolus, C was comparatively large. There is one pair of small incisors.

The back end of the symphysis reaches the front end of P_2. The diastema between C and P_1 is 18 mm. The narrowest part of the symphysis between I_2 and P_1 measures 31.0 mm.

The lower surface of the symphysis is partly broken thus preventing us from knowing if it had a median keel. P_1 was single rooted, and P_2, double rooted, judging by the alveoli. The hypolophid on P_4 is complete and fused with the entoconid. Hence, P_4 might have been molariform.

Discussion

The affinity of the three described specimens is supported tentatively by the molariform P_4, the character of the posterior end of the symphysis and some other features. Certain ones, like the relatively short symphysis, the presence of C and I_3 and reduction of the molariform P_4, suggest that the remains of this peculiar rhinoceros from Khoer Dzan

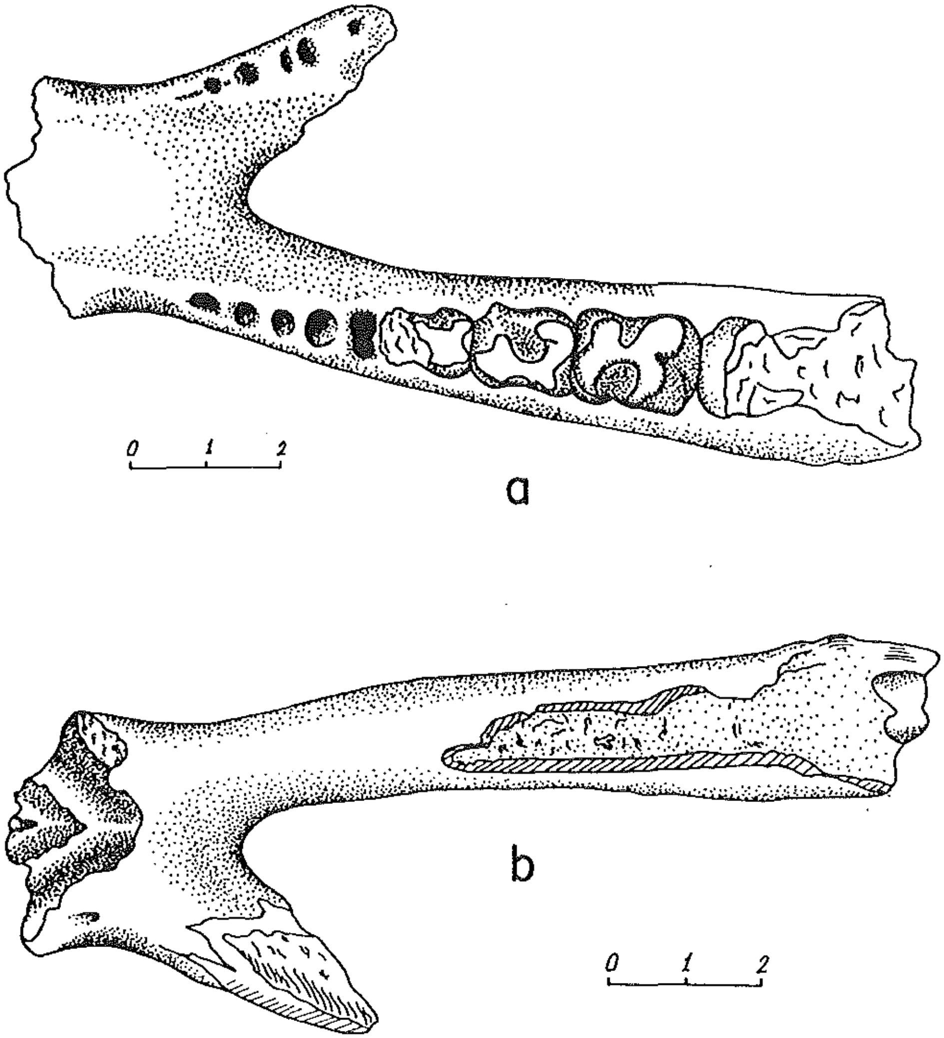

Fig. 36.—*Allacerops* sp., PSS n° 27-71, an incomplete lower jaw with alveolus of I_1, C, P_1-P_3 and broken P_4-M_3; a: occlusal view; b: ventral view.

belong to the genus *Allacerops*, which is already known from the Oligocene of Mongolia. Despite its close resemblance to the species *Allacerops minor*, this form is distinctly smaller (almost two thirds the size), has much less developed incisors and a less distinct cingulum on the lower molars.

Because of insufficient material, the specific affinity of the form remains unclear.

PHYLOGENY OF THE PALEOGENE HYRACODONTIDAE AND RHINOCEROTIDAE

Adaptive radiation of early Tertiary rhinocerotoids of the family Hyracodontidae occurred largely in Asia and North America. It was at its maximum during the Eocene and Early Oligocene in Inner Asia. Radinsky (1967) reviewed all the data available on the systematics and phylogeny of the family up to that date. New collections of recent years allow us to be considerably more precise about not only the stratigraphic distribution but also the phylogenetic links of the group.

The genus *Triplopus* from the Middle Eocene of North America and Asia is considered to be the initial one for the Hyracodontids (fig. 37). This genus is characterized by a comparatively primitive dental system: non-differentiated incisors, canines, the presence of a distinct metacone, etc. *Rhodopagus* and *Pataecops* from the Eocene of Mongolia and China are definitely divergent genera with respect to *Triplopus*. These small hyracodontids show a distinct specialization in the form of an elongated ectoloph and a much reduced (shortened) metaloph on the upper molars. These genera have close phyletic links with each other but their origin still remains unclear (Radinsky, 1967).

The subfamily Indricotheriinae underwent major divergent evolution over the vast territory of Central Asia in the Late Eocene and Oligocene. The well established genus *Forstercooperia* is at the stem of this group. It is known mainly from the Eocene and Early Oligocene of Mongolia and China. This genus must be related to *Triplopus* but is characterized by larger size and specialized molars with strongly developed paracone and metastyle, and distinct transverse ridges. Despite the progressive specializations, it shows well such plesiomorphous features as the metacone on M^3.

Major directions in the evolution of the Indricotheriinae were specialization of incisors, reduction of canines, molarization of premolars, etc. (Radinsky, 1966). Study of the data suggests at least four phyletic lines among the Indricotheriinae, starting with the genus *Forstercooperia*.

In the line *Forstercooperia* → *Juxia* there was a progressive growth in the size of I^1 while I^{2-3} became much smaller than the former. Along with the increasing body size, premolars P^{2-4} became progressively molariform and the area of the molars increased considerably. The terminal form of the lineage, *Juxia sharamurunensis* from the Late Eocene of North China, is characterized by the "indricotheriid type" of P^4 and M^{1-2} structures.

A clearly divergent evolution of the Indricotheriinae may be seen in the lineage *Forstercooperia* → *Urtinotherium* → *Indricotherium*. Specialization within the lineage involved enlargement of I^2 and gradual reduction of I^1, I^3/I_2, I_3, C and intense molarization

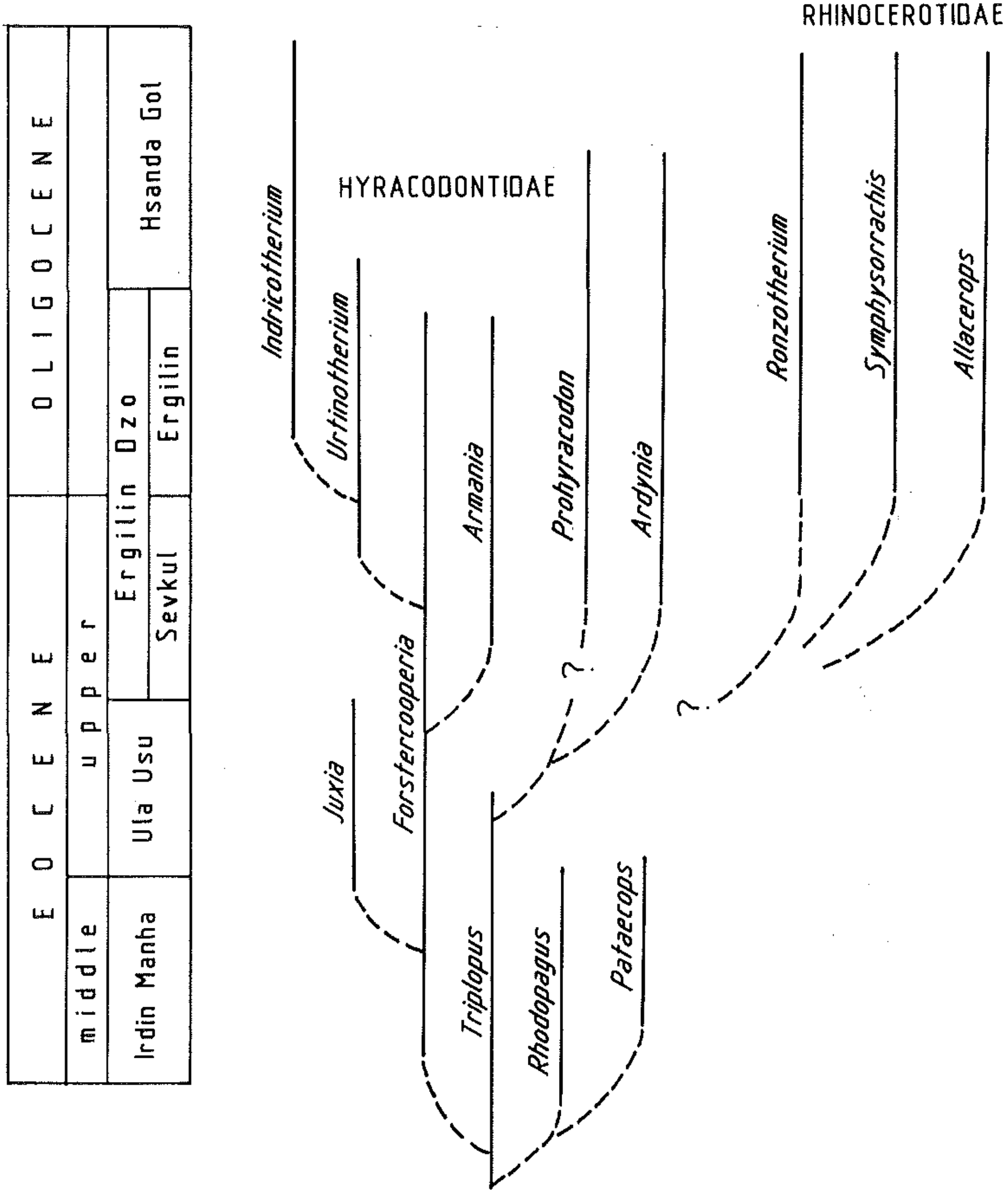

Fig. 37.— The hypothetical phylogenetic lineage of the families Hyracodontidae and Rhinocerotidae.

of P^{2-4}/P_{2-4}. The primitive genus *Forstercooperia* has a complete set of incisors and canines although there is some differentiation in their size, while premolars are less molariform. I_{2-3} of *Urtinotherium* are much reduced in size. I_3 became predominant simultaneously with reduction of the canines. Further development of this lineage reduced the front teeth of *Indricotherium* as well. Finally, I^2/I_2 remained the only functioning incisors in *Indricotherium*. The phyletic line *Urtinotherium* → *Indricotherium*, in contrast to other evolutionary lines in the family, is characterized by procumbency of the front end of the lower jaw and increased molarization of P^{2-4}/P_{2-4}, features exclusive of *Indricotherium*. It should be noted that the genus *Forstercooperia* already showed enlargement of the median toe and the reduced width of the side toes (Radinsky, 1967). With increasing size of the body in *Indricotherium*, reduction of the side toes continued: the first and the fifth disappeared altogether, while the second and fourth became much thinner (Gromova, 1959).

In addition, this lineage shows a general increase in the size of the body leading to gigantism. Apparently, gigantism in mammals had adaptive value. A progressively enlarging body provided the animals with a biological advantage in the struggle for survival by passive (to a certain degree) adaptation to external conditions. These animals were adapted to movement on solid ground and in open spaces. A long neck and a tall body must have been directly related to the way *Indricotherium* fed on the leaves of tall trees (Gromova, 1952).

The lineage *Forstercooperia* → *Armania* shows gradual reduction of I^1, the loss of P^1 and increased molarization of P^4. This branch also shows shortening of the facial region of the skull, bringing the orbit closer to the nasal incision. A major event in the lineage was, unlike in the other evolutionary branches of the family, the increase in height of the tooth crowns (as far as full hypsodonty). Apart from these progressive evolutionary features in the lineage, there are some exceptionally primitive features: the metaloph always remained underdeveloped, in comparison with the protoloph, on the upper molars.

Armania lived among shrubs feeding on the leaves and shoots of low trees. It could be suggested that hypsodonty, despite the imperfect metaloph on the upper molars, points to the adaptation of these animals to eating rather fibrous shrub plants.

The origin and phyletic links of the genus *Prohyracodon* are unknown. Although its geological age is rather late, *Prohyracodon* has some very primitive features in the structure of the front teeth. In particular, the entoconid on P_{3-4} is a separate cuspule, neither completely fusing with the hypolophid nor forming a transverse ridge on the talonid. This genus may be related to still more primitive and as yet unknown Eocene hyracodontids.

The position of the genus *Ardynia* on the phyletic tree of the Hyracodontidae remains unclear. It might be connected with *Triplopus* or a closely related form. The hypothetical line *Triplopus* → *Ardynia* is characterized by the increased diastema between the canines and premolars, the reduced P^1 and molariform P^{3-4}/P_{3-4}. The canines became smaller and incisor-like. *Ardynia* inhabited open spaces; the animals were well adapted to running swiftly and living in the open grassland where they evaded their enemies by running away (Gromova, 1952).

Until recently, the connection between the Hyracodontidae and Rhinocerotidae has been unclear. New collections from the Oligocene of Mongolia suggest that early rhinocerotids of the subfamily Caenopinae originated within the Hyracodontidae. The evolution of the Caenopinae is characterized by reduced canines and specialized incisors I^1/I_{2-3}. The Allaceropinae, in contrast to other rhinocerotids, had canines in both jaws that were bigger than the incisors.

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