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邱占祥　王伴月　著
（中国科学院古脊椎动物与古人类研究所）

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Paracerathere Fossils of China

by

Qiu Zhanxiang Wang Banyue
(Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences)

With 46 Plates

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仅以此书纪念先师
周明镇先生
逝世十周年

In memory of our mentor,
late Professor Zhou Mingzhen,
on the 10th anniversary of his passing

内 容 简 介

本书是对我国所发现的巨犀亚科化石的系统总结。书中对巨犀化石发现和研究历史作了回顾，探讨了巨犀的分类地位、命名、演化趋势及其与环境变化之间的关系等问题。作者将巨犀提升为犀超科中的一个科（Paraceratheriidae）。该科包括两个亚科：柯氏犀亚科（Forstercooperiinae）和巨犀亚科（Paraceratheriinae）。根据现有的材料，特别是保存较好的吻部特征，中国的巨犀亚科化石可分为6属，其中包括一个新属（*Juxia*, *Urtinotherium*, *Paraceratherium*, *Dzungariotherium*, *Aralotherium* 和 *Turpanotherium* gen. nov.）。除未定种外，书中共记述了这6个属中的12个种，着重描述了其中的沙拉木伦始巨犀（*Juxia sharamurenensis*）骨架和美丽巨犀（*Paraceratherium lepidum*）及吐鲁番准噶尔巨犀（*Dzungariotherium turfanense*）的部分骨架，尝试对前两种做了肌肉复原和功能分析，并对它们的外形、体重及年龄做了估算。始巨犀的体重可能在750－890 kg之间，而美丽巨犀则约为15 t重。巨犀在亚洲大陆东部的发展和当时干热气候带的出现有关，而晚始新世晚期则是巨犀身材急剧变大的关键时期。

本书是国内外古近纪地层古生物研究人员的重要参考书，亦可供地质科研人员、大专院校地质系师生和自然博物馆科研人员参考使用。

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Paracerathere Fossils of China

Qiu Zhanxiang　　Wang Banyue
(*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences*)

(Summary)

Contents

PREFACE

The paraceratheres (formerly often called indricotheres) are a group of rhinoceroses autochtonous and endemic almost exclusively to Asia, with only sparse findings in Europe. Their giant size and some features so distinctive from the living rhinoceroses have attracted much attention not only of specialists, but also of laymen. They constitute one of the most heatedly debated fossil groups in mammalian taxonomy. Opinions differ not only at generic and specific levels, but also at family level. Ultimately such a discrepancy has its root in the inadequacy of their fossils. In laymen's eyes, paracerathere fossils seem rather abundant. Here we may feel the effect of the "size." People might be more impressed by a few huge bones of paraceratheres rather than by a small box full of micromammal fossils. In fact, there are only five incomplete skulls in association with their mandibles in all known paracerathere materials. The only two paracerathere skeletons often referred to in scientific papers are in fact composite. Given the above limitations, China has indisputable superiority in this respect. In China, in addition to large quantity of isolated jaws, teeth and postcranial bones, three complete skulls with mandibles have been found (*Juxia sharamurenensis*, *Paraceratherium lepidum*, and *Dzungariotherium orgosense*), of which the first is an almost complete skeleton, and the second possesses an almost complete vertebral column. Most of these materials have only been briefly reported. A detailed, systematic study of them is thus paramount in enhancing our knowledge of the evolution and taxonomy of this group of magnificent rhinoceroses.

Strictly speaking, the present volume is born out of an interrupted program initiated more than 40 years ago. In 1959, the Sino-Soviet Paleontologic Expedition (SSPE) discovered a rhinoceros skeleton from the Shara Murun beds near the Ula-Usu rivulet. The skeleton was preliminarily identified as of the long-sought-after ancestor of paraceratheres, and was listed as the most valuable find of the year (Chow and Rozhdestvensky, 1960). After the unexpected ending of the SSPE in 1960, the skeleton was entrusted to Zhou Mingzhen (= Chow Mingchen) and Qiu Zhanxiang (= Chiu Chanxiang) for a detailed study in 1963. A preliminary report was soon published, where *Juxia sharamurenense* gen. et sp. nov. was established (Chow and Chiu, 1964). In the same year, a field team of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP), discovered rich paracerathere materials from Xinjiang Uygur Autonomous Region. Having these additional materials in hand, Zhou and Qiu decided to enlarge the scope of their study to include all the then known paracerathere materials. The title of the volume was then changed to the present one. By May 1966, the first draft of the volume was completed. Unfortunately, the "Great Cultural Revolution" broke out in June 1966, interrupted the whole plan, and the draft was lost during the turmoil. Thanks to Mr. Zhang Zhenhong, one of the authors' most intimate friends, some parts of the draft, tables, figures and pictures were rescued from the discarded material in wastebaskets. Resumption of the study had not been possible until recent years when the senior author of the present volume was finally freed from various administrative responsibilities, but meanwhile Prof. Zhou regrettably passed away in 1996.

When the senior author of the present volume sat down to resume the writing, the situation was radically changed! Firstly, the number of paracerathere fossils discovered in China since then has greatly augmented. Of particular importance are two partly preserved skeletons unearthed from Xinjiang in 1993 – 1994 and from Nei Mongol in 1995. Secondly, not only new taxa of paraceratheres were established, but also new ideas as to the classification of the whole group were put forward during this time span. Ideas have evolved for the senior author himself as well in his understanding of the evolution and classification of the group. Thirdly, with the amelioration of the Sino-US relationships, it became then possible to observe, at least partly, the paracerathere fossils collected by the Third Central Asiatic Expedition (3CAE) from Mongolia and Nei Mongol during the 1920s, now housed in the American Museum of Natural History (AMNH). The over-simplified description of the skeletal parts presented by Granger and Gregory (1936) rendered it utterly necessary to make a thorough revision of the group as a whole. Fourthly, great advancement had been made with regard to the geology of the deposits yielding rich paracerathere fossils in many places, especially in Dera Bugti area, Pakistan (Welcomme *et al.*, 1997, 2001). Finally, the fundamentals of vertebrate paleontology and geology had made great strides forward in the last 40 years.

As a result of these changes, there is no other choice but to rewrite the volume anew, especially for the parts other than the description of the *Juxia* skeleton. Two particular measures have been taken to remedy the above shortcomings. The first is to add an Oligocene specialist as co-author of the volume. The second is to personally examine the newly found paracerathere fossils and to visit their localities whenever possible. The junior author of the present volume (Wang) was thus chosen for the first purpose. The paracerathere materials housed in Erenhot Dinosaur Museum (for *Aralotherium* sp.), the Nei Mongol Museum (for the skeleton of *Dzungariotherium turfanense*), the Beijing Museum of Natural History and the Turpan Museum (for the skeleton of *Paraceratherium lepidum*) were examined. Geological surveys of some of the paraceratheres-yielding localities, i. e., the Eren region and Wulanmannai Valley (Saint-Jacques), Nei Mongol, the localities near the Feiyue Railway Station, Xinjiang, were conducted. During a visit to the AMNH in 2001, we succeeded in studying some of the 3CAE specimens personally and checked their provenances through Granger's unpublished field notes of the 3CAE activities (1922–1930).

In retrospect, we owe a great debt of gratitude to the late Prof. Zhou Mingzhen. Prof. Zhou deliberately gave the senior author (Qiu), then a freshly graduated young man, a free hand on studying the skeleton of *Juxia*. Under Prof. Zhou's supervision the junior author (Wang) accomplished her doctorate thesis on the skeleton of *Rhinotitan*, which was found together with the *Juxia* skeleton in the same beds of the same locality. It was Prof. Zhou's earnest exhortation, mentoring, and tolerance that permitted us to proceed continuously in the field of vertebrate paleontology. The present volume is thus dedicated to our common teacher, late Prof. Zhou (Nov. 1918–Jan. 1996), at the 10th anniversary of his passing. It is the authors' hope that the publication of the present volume would not fall far short of our mentor's expectation.

I. INTRODUCTION

1. Concept, Discovery and Investigation of Paraceratheres

(1) Concept of Paraceratheres

Up to the mid-1960s, the concept of paraceratheres had been restricted to the Oligocene forms of gigantic size, with their shoulder height allegedly up to 5 m and weight up to about 30 t (but 4.5 m and 15 – 20 t respectively, according to Fortelius and Kappelman, 1993), the largest land mammals ever appeared in history. They are hornless, with long neck and limbs. Their metapodials are exteremely long, with the middle metapodials (McIII and MtIII) the longest and heaviest, the lateral ones strongly reduced and posteromesially positioned (tendency of monodactylism). They were often regarded as a special group of rhinoceroses mixed with some horse-like features.

In the mid-1960s, the concept of paraceratheres changed markedly. First of all, a skeleton of *Juxia sharamurenensis*, a medium-sized (1.9 m high at shoulder), ancestral form of paraceratheres from Late (now Middle) Eocene of Nei Mongol was reported (Chow and Chiu, 1964). Soon after, two other Middle Eocene forms of similar size, *Forstercooperia* and *Pappaceras*, were proposed to be early forms of paraceratheres as well (Radinsky, 1967). If the latter proposal is accepted, the paraceratheres would encompass not only the large-sized Oligocene forms and their direct ancestral form of small size (*Juxia*), but also the early side branches (*Forstercooperia* and *Pappaceras*).

(2) Five Classical Areas Yielding Rich Paracerathere Fossils

There are five major areas particularly rich of paracerathere fossils, all from Asia: Dera Bugti in Baluchistan, Pakistan (from 1907); Aral-Turgai area, Kazakhstan (from 1912); Shand Gol area in Tsagan Nor, Mongolia (from 1922); Eren (formerly as Erlian) region in Nei Mongol, China (from 1922) and Turpan Basin in Xinjiang, China (from 1958). The history of finding and investigation of the paraceratheres in the first three areas has been well known through papers of Forster-Cooper, Borissiak, Osborn, Granger and Gregory, Gromova, Radinsky, MacKenna and others. The following brief account is intentionally restricted to recent advancement in finding and study of paracerathere fossils in Eren region and Turpan Basin in China.

After the founding of the People's Republic of China in 1949, a number of new and important paracerathere fossils were found from the Eren region. They are the *Juxia* skeleton from Shara Murun (Chow and Chiu, 1964), and three specimens discovered by the SSPE in 1959 – 1960 from the Ulan Gochu Formation at Urtyn Obo: a mandible of *Urtinotherium incisium* (Chow and Chiu, 1963) and a maxilla of *Dzungariotherium ardenensis* (Qi, 1989), both of which are now referred to *U. intermedium* in the present volume; and a fragmentary anterior part of skull of *Juxia shoui* described by Qi and Zhou in 1989.

From 1975 to the mid-1990s, a field team of IVPP headed by Qi Tao intermittently surveyed the Eren region and discovered additional material of paraceratheres (Qi, 1987). However, this material has never been studied and published. In May 1985, the Erenhot Dinosaur Museum obtained a large number of broken huge fossil bones from some pits in the suburb of Erenhot, where construction sands were excavated. As the construction continued, the sample has been augmented considerably. All these fossils are tentatively referred to a single form, *Aralotherium* sp. in the present volume.

The first paracerathere fossils of Xinjiang Uygur Autonomous Region were found near the Feiyue Railway Station in east part of the Turpan Basin in 1958 during the construction of the railway from Lanzhou to Ürümqi, the capital of Xinjiang. The finding included several teeth of enormous size, first identified as belonging to *Indricotherium grangeri* (Chow and Xu, 1959). Based on their size and morphology, Qiu transferred these teeth to *Paraceratherium* and erected a new species: *P. tienshanense* (Chiu, 1962). In 1964 and 1966, an IVPP field team made extensive excavations near the Feiyue Railway Station and in the southern border area of Junggar Basin. The fossils found from the Junggar Basin include a huge skull with its mandible and some limb bones. They were later described as a new form, *Dzungariotherium orgosense* (Chiu, 1973). The fossils found from Feiyue in 1966, including fragmentary skulls, mandibles and limb bones, were studied by Xu and Wang in 1978. Two new species were created by them: *Paraceratherium lipidus* (corrected as *P. lepidum* in the present volume) and *Dzungariotherium turfanense*.

In January 1993, a message came to the Institute of Cultural Relics and Archaeology of Xinjiang that huge fossil bones were encountered during the construction of railway about 1 km west of the Feiyue Railway Station (about the same area as the IVPP field no. 64081, excavated by IVPP in 1964 and 1966). The site was excavated twice: in the second half of October 1993, and from June to August in 1994. An almost complete skull in association with mandible, vertebral column from atlas to the 17th thoracic vertebra, all the ribs of right side, and a right tibia, were collected. Later this skeleton was handed over to the Turpan Museum. The skeleton was complemented and mounted under the guidance and assistance of the Beijing Museum of Natural History (BMNH). A replica of the mounted skeleton is now on exhibit at the BMNH. The specimen was preliminarily identified as *Paraceratherium tienshanense* (Zhang *et al.*, 1997), but transferred to *P. lepidum* in the present volume.

Finally, in 2000, Ye *et al.* found a lower jaw with strongly down-turned symphysis in northern part of the Junggar Basin, identified as a new species, *Paraceratherium sui* (changed to *Aralotherium sui* in the present volume).

(3) Localities Yielding Sparse Paracerathere Fossils in China

1) Wulanmannai and Qianlishan District, Nei Mongol (Fig. 2 3)

The first paracerathere fossils were discovered by Teilhard de Chardin and Licent in 1923. The locality was reported on the east bank of the Huanghe River opposite to the church called Saint-Jacques in Dengkou (formerly Bayan Gol). An upper molar and some limb bones of paraceratheres were obtained in 1923 – 1924. The material was identified by Teilhard de Chardin (1926) as belonging to two forms: large and small varieties of *Baluchitherium grangeri*.

After 1949, some other paracerathere fossils were collected from this area. In 1965, the Brigade 109 of the Yinchuan Oil Prospecting Department found some isolated teeth, which have not been studied yet. In 1977, an IVPP field team found some paracerathere fossils as well. The most important finding is that of 1995 made by the Nei Mongol Museum. A partially preserved skeleton was unearthed, consisting of skull, mandible, some six posterior thoracic and five lumbar, some sacral and caudal vertebrae, and a pelvis. Unfortunately, the skull and mandible were heavily damaged during the excavation. The fossiliferous deposits are exposed widely in the Wulanmannai Valley, about 2 km east of the small township Balagon, Hangjin Banner, Ordos City.

Another paracerathere fossil-bearing area lies at the western foothills of the Qianlishan Mountain in Otog Banner, 30 – 40 km south of Dengkou and east of the railway station of Jiangui. In 1978 – 1979 a joint team of IVPP and the Fourth Geologic Mapping Brigade explored this area and found some paracerathere fossils, which were preliminarily identified as an unnamed new species: *Paraceratherium* sp. nov. (Wang *et al.*, 1981).

2) Lingwu-Taole, Ningxia (Fig. 2 4)

It was also Teilhard de Chardin who found the first paracerathere remains from Lingwu, i. e., from Shoei-tong-koeu, in 1923 – 1924. Later, in 1955 a geologic team of the Northwest Geologic Bureau found some skull parts and limb bones of paracerathercs from Lingwu, but from another site, namely Qingshuiying. The material was assigned to *Baluchitherium grangeri* by Young and Chow (1956). The Brigade 110 of the Yinchuan Oil Prospecting Department also obtained some paracerathere fossils from the nearby Taole County in 1965.

3) Danghe area in western part of Gansu (Fig. 2 7)

Bohlin (1946) reported very fragmentary fossils of paraceratheres from that area.

4) East part of Yunnan (Fig. 2 14-15)

In 1958 Hu Chengzhi of the Geological Museum of the Ministry of Geology and Mineral Resources (now Ministry of Land and Resources) collected some isolated teeth from Lunan County (Fig. 2 15), which were studied by Chow (1958), and a new species was established, *Indricotherium parvum* (changed to *Urtinotherium parvum* in this volume). Later, in 1970, the Yunnan Group of the South China Red-beds Expedition of the IVPP made additional collection there. The material was identified as belonging to two forms: a new species of *Forstercooperia*, *F. shiwopuensis* sp. nov., and *Forstercooperia* sp. (Chow *et al.*, 1974).

Probably in the late 1950s, a paracerathere astragalus was found from Shizong (Fig. 2 14) by a local geologist. Further exploration of the site resulted in finding more specimens. All the material was referred to a new species *Indricotherium intermedium* by Chiu in 1962 (changed to *Urtinotherium intermedium* in this volume).

Passing by the Caijiachong locality (Fig. 2 14) in 1972, the Lijiang Team of the IVPP found some paracerathere teeth, which were identified by Tang (1978) as belonging to a new species, *Indricotherium qujingensis* (changed to *Urtinotherium parvum* in this volume). Zhang (1980) reported a tooth of *Indricotherium parvum* (changed to *Urtinotherium parvum* in this volume) from Xuanwei.

5) Lanzhou Basin, Gansu (Fig. 2 5)

The first paracerathere fossils were collected near the Huangyangtou village (Gaolan County), some 5 km north of the Huanghe River by the Fourth Brigade of the Bureau of Geology and Mineral Resources of Gansu in 1964. The best specimen was a mandible, which has not been studied yet. Later, during the field works of the IVPP teams in the 1980s and the early 1990s, additional material was collected from this area near the Zhanjiaping Village (Gaolan County). These specimens have not yet been studied.

6) Bose Basin, Guangxi (Fig. 2 13)

Isolated teeth possibly belonging to *Forstercooperia* were gathered from the Nadu and Gongkang formations in the Bose Basin by a field team jointly organized by the IVPP, Guangxi Oil Prospecting Team and the Provincial Natural History Museum in 1973 (Tang *et al.*, 1974, Ding *et al.*, 1977).

7) Wucheng Basin, Henan (Fig. 2 11)

Also in 1973, the IVPP Henan Team succeeded in obtaining a good sample including partly occluded upper and lower jaws and partly articulated limb bones from the Eocene deposits in the Wucheng Basin (Tongbai County). They were studied and published by Wang in 1976, and four forms, including a new genus and two new species, were described: *Imequincisoria mazhuangensis* sp. nov. (changed to

Forstercooperia mazhuangensis in the present volume), *I. micracis* sp. nov. (changed to *Juxia micracis* in the present volume), *Imequincisoria* sp. (probably belonging to *Forstercooperia*) and *Pappaceras* sp.

8) Changxindian of Beijing (Fig. 2 1)

In 1977, a few isolated teeth were found from Changxindian gravels. They were identified as belonging to *Imequincisoria* sp. by Zhai (1977).

9) Linxia Basin, Gansu (Fig. 2 6)

The first paracerathere fossils of the Linxia Basin were found from the Jiaozigou Formation in 1986 by a joint field team of the IVPP and the Gansu Provincial Museum. These fossils were first described as *Dzungariotherium* cf. *D. orgosense* by Qiu *et al*. in 1990. Recently in 2002, better specimens including a juvenile fragmentary skull were collected from the Yagou gully of the same area. The collection was studied and published as belonging to two forms, *Dzungariotherium orgosense* and *Paraceratherium yagouense* sp. nov. (possibly a species of *Turpanotherium* as suggested in the present volume) by Qiu *et al*. in 2004.

10) Yuanqu Basin, Sahnxi (Fig. 2 12)

A few specimens were reported by Huang *et al*. (1998) as belonging to *Juxia sharamurenensis*.

Paracerathere fossils have also been sparsely found in Europe: in Georgia (Gabunia, 1964), Yugoslavia (Petronijevic and Thenius, 1957), Rumania (Gabunia and Iliesku, 1960) and Bulgaria (Spassov, 1989).

The first recognition of the paraceratheres as a peculiar group of rhinoceroses occurred relatively late. The whole history lasts less than a century, counting from 1907 when the first paracerathere fossils were encountered. They are the latest established group of subfamily or family rank among the perissodactyls.

In the history of investigation of the paraceratheres, three eminent scholars must be mentioned in particular. They are A. A. Borissiak, V. I. Gromova, and L. B. Radinsky. It is their works that had led to the three great strides forward in our understanding of the nature of the paraceratheres.

Borissiak is the pioneer paleontologist in studying *Paraceratherium* osteology. His thorough study of the first paracerathere skeleton provided us with the first comprehensive knowledge of the group (Borissiak, 1923b). He first arranged the group at a subfamily rank (1923) within the Family Rhinocerotidae, but later raised it to an independent family, Indricotheriidae (1939). Gromova made an extremely careful study of all the materials belonging to paraceratheres collected prior to the publication of her monograph (Gromova, 1959). Based on meticulous comparison of all the features she could observe and distinguish, she reduced the contents of the Family Indricotheriidae from three genera and six species to two genera and three species: namely, *Indricotherium transouralicum* (= *I. asiaticum*, *I. minus*, and *Baluchitherium grangeri*), *Paraceratherium prohorovi* (= *Aralotherium prohorovi*) and *P. bugtiense* (= *Baluchitherium osborni*). Her carefully composed diagnoses for the genera *Indricotherium* (*Paraceratherium* in this volume) and *Paraceratherium* (*Aralotherium* in this volume) remain classic even today for all who study the paraceratheres. Radinsky put forward (1966 – 1967) a completely new idea as to the taxonomic position of the paraceratheres in the Superfamily Rhinocerotoidea. He argued strongly that the paraceratheres had nothing to do with the lineage of the true rhinoceroses (Family Rhinocerotidae), but may only be a subfamily of the Family Hyracodontidae. Most of the American rhinoceros scholars represented chiefly by Prothero and Lucas follow this way of thinking, culminating in recognizing only one single Oligocene genus *Paraceratherium*. Although unable to accept Radinsky's arguments (*vide infra*), we fully admit that his idea was a real breakthrough in our understanding of the phylogeny and taxonomy of the rhinocerotoids.

2. Material and Methodology

(1) Material

The material studied in the present volume comprises the following: 1) the accessible part of the specimens collected by the 3CAE from Loh area, Mongolia, and Eren region of Nei Mongol, China, during 1922 – 1930; 2) the skeleton and other odd fossils of *Juxia sharamurenensis*, collected in Shara Murun area, Nei Mongol, by SSPE during the field seasons in 1959 – 1960; 3) the material collected near the Feiyue Railway Station, eastern part of Turpan Basin by the IVPP field team headed by Prof. Zhai Renjie in 1964; 4) the paracerathere material collected by the Erenhot Dinosaur Museum from the Ulan Gochu Formation at Urtyn Obo and Houldjin gravels in Erenhot suburb since 1985; 5) the partial paracerathere skeleton excavated by the Institute of Cultural Relics and Archaeology of Xinjiang from a site 1 km west of the Feiyue Railway Station in 1993 – 1994; 6) isolated teeth and bones found from the Qianlishan district and the partial skeleton from Wulanmannai Valley, Nei Mongol, by the IVPP and Nei Mongol Museum in 1977 – 1979 and 1995; and 7) miscellaneous specimens from Nei Mongol, Gansu, Ningxia, etc. accumulated during the past years, either collected by the authors themselves, or handed over to them by the local geologists.

(2) Comparison

In order to determine the systematic position of *Juxia sharamurenensis* more precisely and to restore its possible way of life, we made much efforts to compare it with as many skeletons of primitive rhinocerotoids as possible. However, such skeletons are rare. Of the European forms only a skeleton of *Allacerops turgaica* was systematically described by Borissiak (1918) in great details. A number of skeletons of primitive rhinocerotoids were found in North America. However, most of their descriptions are sketchy, seldom accompanied by adequate figures and plates. Five North American primitive rhinocerotoids can be compared with *Juxia* osteologically. They are *Hyrachyus eximius* and *Triplopus cubitalis*, described by Cope (1884) and *Hyracodon nebraskensis*, *Trigonia osborni* and *Subhyracodon occidentalis*, described by Scott (1896, 1941).

For comparison with the advanced rhinoceroses of later period the skeletal parts of *Coelodonta antiquitatis* from Sjara-Osso-Gol kept in IVPP and the detailed description of this form by Borsuk-Bialynicka (1973) are extensively used. A skeleton of the living Indian rhinoceros (*Rhinoceros unicornis*) kept in IVPP (O 1383) is also used.

The monographs of Borissiak (1923b), Gromova (1959), and Granger and Gregory (1936) serve as the main sources of osteological information for the Oligocene paraceratheres.

We follow the "Principle of homology" in musculature restoration. A restoration is considered reliable when insertions of certain muscles restored in *Juxia* are identical with, or very close to, those found in all living perissodactyls (horses, tapirs, and rhinoceroses). When not identical with all the living forms, the first to be compared is rhinoceros, the closest related group with *Juxia*, then the tapir, and the last is the horse. In practice, since the horse is the best studied anatomically, the Malayan tapir the next, and the rhinoceros the least, the comparison proceeds from horse to rhinoceros. The major references used in the present volume are Session's "Anatomy of the Domestic Animals" (fourth edition in 1956, its Chinese translation in 1962, mainly for the horse), Stjernman's monograph on the myology of the Malayan tapir extremities in 1932 (also the papers of Murie, 1871, and Bressou, 1950, 1961), and the Beddard and Treves' article on the anatomy of the Sumatran rhinoceros in 1889.

(3) Orientation

The orientation and the directional terms conventionally applied to animal's body in anatomy text books, such as that of Sission's (1956), are taken as a basis throughout the present volume. However, for convenience's sake, the directional terms for the limb bones distal to carpus and tarsus are taken from those generally used by vertebrate paleontologists (Fig. 3).

(4) Terminology

1) Crown elements of cheek teeth

The terms used for the upper cheek teeth are given in Fig. 4. The degrees of the premolar molarization, especially the uppers, can be highly variable in rhinocerotoids. Radinsky (1967) separated them into three: non-molariform, submolariform and molariform. Heissig (1969) made a little improvement based on Radinsky's scheme, resulting in four: praemolariform (= Radinsky's non-molariform), submolariform, semimolariform (new), and molariform, which are adopted here (Fig. 5).

The terminology applied to the lower cheek teeth for the rhinocerotids in particular, and for the perissodactyls as a whole, was inadequate and inconsistent from its very beginning. In Osborn's original scheme (Osborn, 1907, p. 73) only metalophid and hypolophid were named for the crested lower cheek teeth of perissodactyls (Fig. 6 A). At the same time, Osborn used an additional term parastylid in the lower cheek teeth of horses (loc. cit., Fig. 160). In his monograph on titanotheres, Osborn (1929b) substituted protolophid for metalophid and metalophid for hypolophid without further explanation (Fig. 6 B). This caused much confusion in later years. While studying the horses, Stirton (1941) made a finer subdivision of the lophids for the horse (Fig. 6 C). Stirton's system was well adapted to W-shaped lower cheek teeth of perissodactyls (titanotheres, chalicotheres and horses), but some terms of this system were inconsistent with the customary usage applied to the simpler crested lower cheek teeth of tapir and rhinoceros. Most of the later rhinoceros scholars, like Gromova, Heissig, Guérin, *et al.*, used the simple system originally invented by Osborn, using mainly metalophid and hypolophid with some minor amendments (Fig. 6 D). However, this simplified system has been felt more and more inadequate for detailed description of the tooth morphology.

Stirton's terminology (1941) is taken as the basis of the system proposed in the present volume. With a few amendments, this system can easily be applied to all the groups of perissodactyls, not only to the W-shaped teeth in horse, titanotheres and chalicotheres, but also to the di-lophodont and L+U shaped lower cheek teeth in tapirs and rhinoceroses. In this new system a lophid is principally named in accordance with the cuspid sending this lophid buccally and forward. Thus, the lophid extending from paraconid buccally is called paralophid; the lophid extending from protoconid forward, the protolophid; the lophid extending from metaconid buccally, the metalophid; the lophid extending from hypoconid forward, the hypolophid; and the lophid extending from entoconid buccally, the entolophid (Fig. 7). Principally, this system is in good accordance with the ontogenetic development of the lophids.

2) Anatomical terms of skull and postcranial skeleton

The classic anatomical terms proposed by Flower (1885) are widely used throughout the present volume, with only a few adopted elsewhere, which are explained in due places.

(5) Measurements and Abbreviations

1) Measurements

Length (L) is the longest measurable length of the studied specimen. It may not be on the crown surface when the upper tooth is unworn or little worn, but always on the crown surface in the lower tooth. Width

(W) in the upper tooth is measured immediately above the roots where the width is the greatest; while in the lower tooth it is measured at the widest visible part. The lengths of the M3 are measured twice: the largest length of ecto-metaloph (measured obliquely), and the lingual length. The crown height index is taken from Radinsky (1967): paracone height/width of unworn M3. In order to make the comparison of the *Juxia* skeleton with the later paraceratheres as more as possible, the measurements of the postcranial bones are taken mostly as Gromova suggested in 1959. All measurements are in millimeters, except otherwise stated.

2) Abbreviations

L (length); W (width); H (height); D (distance); APD (antero-posterior distance); Lt (left); R (right); PE (proximal end); PAF (proximal articular facet); DE (distal end); DAF (distal articular facet); Ant (anterior); Post (posterior); Mid (middle); Med (medial); Lat (lateral); Lab (labial); Buc (buccal); Ling (lingual); Mes (mesial); Dist (distal); Max (maximum); Min (minimum); Aver (average).

C (cervical vertebrae), T (thoracic vertebrae), Lm (lumbar vertebrae), Mc (metacarpal), Mt (metatarsal), Ph (phalanx).

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences); V (prefix to vertebrate fossils of IVPP); O (prefix to living vertebrates of IVPP); AMNH (American Museum of Natural History); AM (prefix to AMNH fossils, numbers in [ ] are field numbers); 3CAE (Third Central Asiatic Expedition); AMP (Austrian-Mongolian Project); MAE (Mongolian-American Expeditions); SSPE (Sino-Soviet Paleontologic Expedition); SS (prefix to SSPE specimens); TP (prefix to specimens of Turpan Museum); EMM (prefix to mammal fossils of Erenhot Dinosaus Museum); IMM (prefix to specimens of Nei Mongol Museum).

II. SYSTEMATIC DESCRIPTION OF CHINESE PARACERATHERES

Family Paraceratheriidae Osborn, 1923

Subfamily Paraceratheriinae Osborn, 1923

Type genus: *Paraceratherium* Forster-Cooper, 1911

Other included genera: *Aralotherium* Borissiak, 1939; *Benaratherium* Gabunia, 1955; *Urtinotherium* Chow et Chiu, 1963; *Juxia* Chow et Chiu, 1964; *Dzungariotherium* Chiu, 1973; *Turpanotherium* gen. nov.; *Pristinotherium*? Biriukov, 1953.

Geographic and stratigraphic distribution: The area covering the Tropic of Cancer to ~50° N of the Asian Continent, including Baluchistan (Pakistan), Yunnan, Henan, Shanxi, Nei Mongol, Gansu, Ningxia, Xinjiang (China), mid-eastern part of Mongolia, Kazakhstan, and a few places in southern Europe (Georgia, Romania, Bulgaria, and Herzegovina); late Middle Eocene to earliest Miocene (40 – 22 Ma).

Emended diagnosis: Large- to giant-sized rhinoceroses compared with contemporary rhinocerotoids with the only exception of some amynodonts. Shoulder height ~2 to 4.5 m, body length (without tail) ~3 to 7.5 m, estimated body mass ~0.8 to ~15 t.

Skull dolichocephalic, without horns in both sexes. Cranium elongated, especially the part behind postglenoid process, which exceeds 1/4 L of P2 – postglenoid process; paroccipital and posttympanic processes tightly coalesced, forming a robust and thick plate, widely separated from postglenoid process. Nasal long, with its free part slender, but thickened sagittally; nasal notch high and deep, with its posterior border lying above P3 – M2. Rostral part (premaxilla and anterior part of maxilla) strongly elongated or reduced. Dental formula from complete to 1·0·3·3 / 1·0·2·3. The first upper and lower incisors either the largest of the incisors, or the only ones. Canines either slightly larger than third incisors or completely lost. Cheek teeth of rhinoceros pattern: parastyle and paracone small and connate, of about equal size. M1 – M2 Π-shaped, with metacone becoming elongated loph; M3 triangular, with vestigial posterior end of metaloph. m1 – m3 U + L-shaped, with third lophid completely lost in m3. P2 more molarized than P3 – P4, with its hypocone well separated from protocone, but closely connected with metaconule; P3 – P4 sub-molariform, with hypocone widely confluent with protoloph, forming a long hook; metaconule crescent, lying anterior to the posterior end of hypocone, linking with ectoloph and hypocone only when moderately worn. p3 – p4 with long talonids, entoconid either isolated cone-shaped or being cone-shaped in lingual end of entolophid.

Neck (C1 – C7) longer than total skull length. Wings of atlas laterally shortened. C3 – C7 bodies solid to strongly hollowed by enlarged transverse canals with large transverse processes; capita and vertebral fossae rounded or dumbbell-shaped. No true diaphragmatic vertebra in thoracic and lumbar regions. Spinous processes of last 3 T's and all Lm's slightly backward slanting or vertical; posterior surfaces of spinous processes of anterior T's deeply excavated; zygapophyses of Lm's either simply convex-concave, or saddle-shaped forming embracing articulation.

Limb bones slender to graviportal. Scapula and humerus about equally long, but much shorter than radius-ulna. Scapula proportionally wider, Max W about 3/5 – 3/4 of its Max L (H), with about equally large supra- and infra-spinous fossae and rudimentary acromion. Caput of humerus wider than long (APD); deltoid tuberosity weakly developed or vestigial; lateral epicondyle either undeveloped, or situated high, extending upward and laterally, with its lateral border straight. Radial tuberosity of radius represented by rough area, never developed into deep depression; radius articulating with three proximal carpal bones. Ulna not strongly curved, with olecranon short and primarily extended backward. All carpal bones with little developed posterior processes, with progressively flattened proximal and distal articular surfaces and "hindering facets" on anterior parts in later forms. Magnum becoming wider than high in later forms, while trapezoid and unciform narrowed. Third trochanter of femur weakly developed or vestigial. Astragalus from about equally H and W to much wider than high, with its trochlea changing from strongly concave-convex to little relieved. Manus from tetradactyl to tridactyl. Both manus and pes strongly monodactylized, with lateral metapodials considerably reduced and turning backward and mesially. PhI-II of middle digit from pillar-formed to oval dish-formed.

Remarks: Four subfamily names were proposed for the paraceratheres: Indricotheriinae (Borissiak, 1923b; Lucas *et al.*, 1981; Lucas and Sobus, 1989; Dashzeveg, 1991 etc.), Baluchitheriinae (Osborn, 1923), Paraceratheriinae (Osborn, 1923; Simpson, 1945; McKenna and Bell, 1997) and Forstercooperiinae (Kretzoi, 1940). The first three names were created in the same year, 1923. *Paraceratherium* is the earliest established and valid genus of the paraceratheres. *Baluchitherium* soon turned out to be preoccupied by *Paraceratherium*. Thus the name Baluchitheriinae is no longer based on valid generic name. Based on new material described in the present volume, especially the skull and mandible found from Xinjiang (TP 9401, *vide infra*), we came to the conclusion that *Indricotherium* is synonymous with *Paraceratherium*. This strongly supports the view that Paraceratheriinae are to be chosen as the only legitimate subfamily name based on the type genus *Paraceratherium*. This happens to be just what Simpson proposed more than 60 years ago in his famous "Classification of Mammals" (Simpson, 1945, p. 257). On the other hand, we suggest to exclude *Forstercooperia* and *Pappaceras* from the Subfamily Paraceratheriinae, admitting that they may take their origin from the same ancestral group giving rise to the first true paraceratheres (*Juxia*), but evolved in directions different from that of the true paraceratheres. It is recommended here to creat a higher, family rank, Paraceratheriidae, to encompass these two lineages.

Juxia Chow et Chiu (= Zhou et Qiu), 1964

Forstercooperia (partim), Radinsky, 1967: 18–24, Figs. 8 D, 9 C
Forstercooperia (*ergiliinensis*) (?), Gabunia and Dashzeveg, 1974: 497, Fig. 1; Dashzeveg, 1991: 49–51, Fig. 22
Imequincisoria (*mazhuangensis*, partim), Wang, 1976: 104–106, Pl. I
Imequincisoria (*micracis*), Wang, 1976: 106–107, Pl. III 1–2
Imequincisoria (?) sp. (partim), Wang, 1976: 107–109, V 5074. 4–5, 8
[non] *Juxia* (*sharamurenense*), Tiwari, 2003: 103–113, Fig. 4, Pl. I 1–4

Type species: *Juxia sharamurenensis* (corrected from original *sharamurenense*, which is in error in gender, based on article 32 of "International Code of Zoological Nomenclature", third ed., 1985).

Other included species: *J. micracis* (Wang, 1976), *J. shoui* Qi et Zhou, 1989 and *J.? ergiliinensis* (Gabunia et Dashzeveg, 1974).

Geographic and stratigraphic distribution: China: Shara Murun and Urtyn Obo areas of Siziwang Banner, Nei Mongol, from Shara Murun and Ulan Gochu (?) formations, late Middle to early Late Eocene; Wucheng Basin, Henan, from Wulidun formation, late Middle Eocene. Mongolia: Ergilin Dzo, from Ergilin Member, Late Eocene.

Emended diagnosis (mainly based on type species): Smallest and most primitive paracerathere. Body size about 1/2 as that of *Paraceratherium grangeri*. Skull dolichocephalic, with long cranium. Sagittal crest long and high, with its length exceeding 1/4 of total skull length; grooves between paroccipital and posttympanic processes on lateral surface still observable. Nasal wide, with its dorsal profile almost straight, and anterior tip reaching the level of anterior end of muzzle; posterior border of nasal notch above P3, distant from anterior margin of orbit, with irregularly lobate projection at its posterosuperior corner. Dental formula complete. Incisors longer (mesiodistally) than wide (labiolingually), with mesial and distal ridges; first pairs being the largest. Canines incisiformed, only slightly larger than third incisors. P1 present, triangular, P2 with metaconule clearly separated from hypocone, P2 – P4 with prominent para-and metacone ribs; M1 – M2 with metacone rib and antecrochet, though feeble. Crown height index < 0. 6. p1 present, p3 – p4 with rudimentary entoconid; p2 – m3 with trigonid markedly higher than talonid, protolophid and hypolophid sharply descending anteriorly.

Neck (C1 – C7) slightly longer than skull. C without greatly hollowed transverse canal; planes of capita and vertebral fossae form acute angles with bodies; transverse processes plate-formed; capita and vertebral fossae about equally wide and high in C4 – C7. T probably 18, spinous processes excavated posteriorly. Lm six, with long, laterally extended transverse processes and imbricating zygapophyses. Rib curved column in shape, with its cross section being roughly rectangular, concave on anterior and posterior sides.

Limb bones long and slender. Deltoid tuberosity of humerus and third trochanter of femur feeble. Radius-ulna longer than humerus by 1/4, ulna markedly more slender than radius. Magnum higher than wide, narrower than unciform. Lunar rested mainly on unciform, hardly contacted with magnum. Astragalus slightly higher than wide, ridges of trochlea markedly oblique, and medial groove deep, sustentacular facet higher than wide, obliquely positioned. Cuboid articulated with MtIII. Manus tetradactyl, with McV suspending above the ground. McIII and MtIII about 40% as long as radius and tibia respectively. Distal parts of lateral metapodials deviating from the middle ones. All Ph's long, PhI-PhII not disk-like, PhI longer than wide, PhIII with deep central cleft on distal margin.

Remarks: The status of *Juxia* as a valid genus had been doubted in 1960s and 1970s. Radinsky (1967) transferred *Juxia* and *Pappaceras*, together with *Eotrigonis borissiaki* from Asia, and *Hyrachyus grandis* from North America, to the genus *Forstercooperia*, thus making the latter a transpacific genus in distribution. Chow *et al*. (1974) maintained the validity of the genus *Juxia*. Accepting Chow *et al*.'s view in general, Lucas *et al*. (1981) enlarged the contents of *Juxia* to include the genus *Imequincisoria* erected by Wang in 1976.

As Chow *et al*. (1974) pointed out, the differences between *Juxia sharamurenensis* and *Forstercooperia totadentata* were so obvious that their generic status should be regarded fully warranted. In addition to the differences pointed out by Chow *et al*., the following can be added. 1) In *Forstercooperia* the nasals are wide and short, with their lateral borders converging rapidly only near the anterior end, thus the anterior tip suddenly becoming acute; whereas in *Juxia* the nasals are long and narrow, with their lateral borders evenly converging anteriorly, thus the anterior tip being slender and pointed. 2) In the former the I2 – I3 (I1 is unknown) and C are all conic in form, wider (labiolingually) than long (mesiodistally), without ridges, and closely arranged. They are thus markedly different from those in the latter (*vide supra*). 3) In the former the P2 – P4 are wider, with weak lingual cingulum, attenuated or lost at middle; whereas in the latter these teeth are proportionally longer, with continuous lingual cingulum. 4) The former form is larger, although it is earlier in appearance (Irdin Manha). We note here that most of the distinctive features of *Juxia* are reminiscent of those of later Oligocene paraceratheres. *Forstercooperia totadentata*, on the other hand, might belong to a sideline, probably split from the same ancestral stem forms giving rise to *Juxia*. They should not be grouped in the same subfamily, let alone the same genus.

The nature of *Forstercooperia ergiliinensis* (Gabunia and Dashzeveg 1974) is still not fully certain. Lucas and Sobus (1989) transferred it to the genus *Juxia*. In tooth morphology and size (Tab. 4), it is closer to *J. sharamurenensis* rather than to *Forstercooperia* or *Pappaceras*. The single specimen of this form was reportedly found in the Ergilin Member (Late Eocene) of the Ergilin Dzo Formation, seemingly too late for such a primitive form.

Pappaceras confluens differs from *Juxia sharamurenensis* slightly less than *Forstrcooperia* does. Nevertheless, its distinction from *Juxia* is evident. 1) Its nasals and nasal notch are more similar to those in *Forstrcooperia* than those in *Juxia*. 2) Its I1 is not the largest of the incisors, and the lower incisors are more vertically implanted, while the lower incisors are obliquely implanted and the i1 is horizontal in *Juxia*. 3) There is no indication of the grooves on the lingual side between the protocone and hypocone in P2 – P4 in *Pappaceras*. 4) No entoconid can be seen in p3 – p4 in *Pappaceras*. 5) It is smaller in size. On the whole, it is inadvisable to merge *Pappaceras* and *Juxia* into one genus.

As regards *Imequincisoria*, the problem seems more complicated. A closer comparison of the concerned fossils led us to think that *I. micracis* may be a form closer to *J. sharamurenensis* than to *I. mazhuangensis*. The distinction of *I. mazhuangensis* from *Juxia* may be summarized as follows. 1) Its general size is larger (Tabs. 4 – 5). 2) In P2 – P4 the hypocone is not separated from the protocone clearly; in P2 – P3 the metaconule is straight and pointed anterolingually to join the protocone. 3) Molars are higher crowned. The paracone H of a slightly worn M2 is 33 mm, and that of M3 is 26 mm. The same measurements taken from similarly worn M2 and M3 in *Juxia* are 24.5 mm and 21 mm respectively. 4) The protolophid and hypolophid in m1 – m3 are higher, less steeply sloping anteriorly, resulting in increasing the height of the ectoflexid. The height of ectoflexid in an m3 of *I. mazhuangensis* measures 16 mm, while that of *Juxia* is only 12.5 mm. It might be more than probable that *I. mazhuangensis* is a member of the genus *Forstercooperia*, while *I. micracis* is not, but a member of the genus *Juxia*. If this eventually proves to be correct, the assembled incisors referred by Wang (1976) to *I. mazhuangensis* might in reality belong to *Juxia*, judging by their close morphologic similarity with those of *Juxia* (*vide infra*). Another important fact supporting the above idea is the presence of two types of carpal bones associated with these two forms. The small-sized bones are almost identical to those of *Juxia sharamurenensis*. A small-sized unciform shows clearly that its manus should be tetradactylous as in *Juxia* (Pl. XIX 7). The large-sized bones are not only bulkier than those of *Juxia*, but the unciform shows clearly that the manus is tridactylous as is shown in Pl. XIX 8 of the present volume (*vide infra*). As a result of the above comparison, we are inclined to transfer *I. micracis* to the genus *Juxia*, thus *Juxia micracis*, and *I. mazhuangensis* to *Forstercooperia*, thus *Forstercooperia mazhuangensis*.

Just recently, a skull found from the Eocene molasse deposits of Liyan Formation at Lodakh in the part of Kashmir under India's jurisdiction was described as belonging to *Juxia sharamurenensis* (Tiwari, 2003). Judged from the tooth morphology of the skull, which is characterized by clearly separated protocones in premolars and large antecrochets in molars, it is almost certain that the skull should belong to *Aprotodon*.

Juxia sharamurenensis Chow et Chiu (= Zhou et Qiu), 1964

(Pls. I – XVIII, XLIV – XLVI; Figs. 8 – 28; Tabs. 1 – 34, 40, 52 – 57)

Holotype: V 2891, nearly complete articulated skeleton of an adult indivudial (about 22 – 25 years old, *vide infra*), consisting of skull, mandible, atlas, C3, C5 – C7, T1 – T5, 4 middle and the last 3 T's, Lm1 – Lm2, Lm4 and the last Lm; first right rib, middle ribs of both sides, some posterior right ribs and rib fragments; scapulae, humeri of both sides, right radius and ulna, proximal ends of left radius and ulna; scaphoid, lunar, unciform (without posterior process) and McIV of right side; innominate bones, femuri, patellae, tibiae and fibulae of both sides (without distal end of right fibula); left navicular, right ento- and mesocuneiforms, left MtII, right MtII (without distal end) and MtIII; 2 PhI's, 1 PhII and 1 PhIII of middle digits, 2 PhII's, 3 PhII's and 2 PhIII's of lateral digits. Most of the bones are violet or brown in color. Preservation of the fossils is generally good, but most of the long bones are compressed and vertebrae crushed and damaged.

Other referred specimens: Specimens found from the same beds of the same locality: 1) SS 4103.1 – 2, incomplete skull and mandible of an adolescent individual (12 – 15 years old, *vide infra*), kept in Paleontologic Institute of Russia, casts and photos in IVPP. 2) V 2891.1, left scaphoid, lunar, cuneiform and unciform of the same individual. 3) V 2891.2, left McIII – IV (without distal ends). 4) V 2891.3, astragalus. 5) V 2891.4, a broken calcaneus. 6) V 2891.5, MtII – IV. 7) V 2891.7, isolated limb-bones, including distal end of scapula, scaphoid, unciform, distal end of femur, patella, 3 fragments of tibiae, 4 astragali, cuboid, and ectocuneiform. It is almost certain that part of above listed specimens could belong to the skeleton, but it is impossible to know which really do so.

A fragmentary cranial part of skull of young age (V 2892) and maxillae with M1 – M3 of both sides (V2893) were previously referred to the present species by Chow and Chiu in their preliminary report on the species (1964). A closer examination of them revealed that they probably do not belong to this species.

On the other hand, Radinsky (1967) referred six 3CAE speciemns (AM 20286 – 20288, 81806, 26750 and 26753) to *Juxia sharamurenensis*. All these specimens are smaller than the holotype (vide Radinsky, 1967, p. 24). The right pes (Radinsky, 1967, Fig. 10) would be only about half the size of the holotype (V 2891), were the scale in Radinsky's Fig. 10 correct. It seems unlikely that the above listed 3CAE specimens all belong to *Juxia sharamurenensis*.

Locality and horizon: Near the well of Ula Usu, in lower part of Shara Murun Formation, consisting mainly of light brown clays, late Middle Eocene.

Diagnosis: Compared with *J. micracis*, *J. sharamurenensis* is primitive in having about equal-sized incisors, with the first pairs being only slightly larger than the others; having weak cingulum and mesial and distal crests. Crista and accessary cristae in postfosette scarecely developed in P2 – P4. It differs from *J. shoui* in nasal notch being particularly deep, posterior end of which lying above posterior half of P3, instead of above P2, having longer C – P1 diastema, relatively large P1, and well separated hypocone from protocone in P2.

Description and Comparison

(1) Skull and Mandible

The skull of the holotype is comparatively well preserved, but had been subjest to lateral compression, with ventral side being badly damaged. The bone sutures are mostly obscure or completely lost, except those between premaxilla and maxilla, on zygomatic arch, and between the two nasals.

1) Description

Occipital view (Pl. III 1b, Fig. 8, Tab. 1): The occipital view of the skull is bell-shaped, higher than wide, broader at base, with strong constriction at the level of the lower end of the upper 1/3. The occipital crest is well developed, forming a curved, wide band of rough surface, projected above the temporal and beyond the nuchal surface, with its middle being the most prominent and thickest part (17 mm). At the point of the constriction on lateral side, the occipital crest divides into two fine crests: one turns downward and forward, changing into the temporal crest; the other is feebler, stretching downward onto the lateral surface of the coalesced paroccipital-posttympanic process. The exoccipital sagittal crest, where nuchal ligament attaches, is fine but still prominent, bordered bilaterally by a pair of deep fossae (Fig. 8 s). The lateral ridges of the fossae converge ventrally and change into a large protuberance above the foramen magnum (Fig. 8 p).

The lateroventral border of the condyle is more or less ridge-like (linea divisa condyli, *vide* Flerow, 1957, p. 14 – 15), separating the condyle into a posterior and a ventral surface.

Lateral view (Pls. I 2, II 1; Fig. 9; Tab. 1): The skull, especially its cranium, is proportionally low and long. If the postorbital process is taken as the dividing point, the cranial and the facial parts are about equally long. The distance between the posterior borders of the condyle and the postglenoid process is slightly more than 1/5 as long as that between the posterior border of the condyle and the P1 (Tab. 1, ratio 4). The occipital condyle is large, hemispherical in form. The linea divisa condyli forms an angle of about 45° with the cranial axis. This angle is important in deciding the angle between the skull and the neck (*vide* Flerow, 1957). The lower border of the condyle constitutes the lowest point of the cranium. The upper 1/3 of the occiput slants backward, but not beyond the condyle. There are as many as 10 postparietal foramina (for the term see Scott, 1896, p. 358) on the temporal surface. The paroccipital and posttympanic processes are completely coalesced into one process, with a vertical furrow on the lateral side of the process and a foramen at the furrow's upper end (Pl. I 2 f). The posttympanic process is large, about twice thicker (APD) than the paroccipital one. The coalesced process is widely separated from the postglenoid process.

The upper profile, with the exception of the free part of the nasals, which slopes slightly downward, forms almost a straight line. The postorbital process on the frontal bone is blunt, lying above the posterior border of M3, whereas the postorbital process on zygomatic arch is scarcely noticeable (Pl. I 2). The zygomatic arch is generally weak and long, ascending posteriorly. Its posterior end is enlarged into a lobe-shaped blade protruded upward, with its anterior rim ascending particularly steeply. The lateral surface of this blade is roughly vermiculated. Otherwise the zygomatic arch is rather slender. The zygomatic arch ends above the anterior half of M2 anteriorly, slightly posterior to the anterior rim of the orbit.

The posterolateral portion of the nasal expands onto the facial surface, occupying its dorsal 1/3. The free part of the nasal is very long and slender, with its tip approximating the anterior end of the premaxilla. The cross section of this free part of nasal is roughly equilateral triangular (Fig. 9). The nasal notch is very long, with its posterior border being irregular in form, having two nodules (Pl. I 2). The nasal notch ends above the posterior half of the P3 posteriorly. The nasal bone posterior to the nasal notch is thin. The infraorbital foremen is situated below, or slightly behind the posterior end of the nasal notch, above P3. The premaxilla is long and thin, beginning at the middle of the nasal notch posteriorly (Fig. 9). The maxillo-premaxilla suture extends anteriorly beyond C.

Dorsal view (Pl. I 1): The sagittal crest is strongly compressed laterally, forming a high plate in its middle portion. It is ~170 mm long, splits posteriorly into two diverging ridges, thus forming a triangular area of about 50 mm long. Anteriorly, at the level slightly anterior to the glenoid cavity, the sagittal crest bifurcates into two frontal ridges leading to the frontal postorbital processes. The zygomatic arches are only moderately expanded, with their maximum points of swelling at the anterior end of the glenoid cavity. A sagittal groove is formed along the suture between the nasals. The premaxilla becomes thin anteriorly, and a deep groove is present between the two premaxillae (covered by nasals in dorsal view).

Ventral view (Pls. II 2, III 1a; Fig. 11 A): The ventral side is poorly preserved. The condyloid fossa lying between the condyle and the paroccipital process is large and deeply concave. The hypoglossal foramen is also large, farther away from the condyle. The basioccipital and basisphenoid bones are broad, with a wide sagittal ridge. The basilar tubercles are very prominent. The cross section of the paroccipital procees is irregular in shape, but wider than long; whereas that of the posttympanic process is about equally long and wide. The postglenoid process is situated in the medial half of the glenoid cavity. The posterior border of the palate is located at the posterior border of M2. The premaxillae are thin and straight, slightly converging anteriorly. The anterior border of the muzzle has a sagittal notch. The incisive foramen is very long, extending to the posterior side of the I1 anteriorly. Other structures on the ventral side are mostly obliterated.

Mandible (Pls. III 2, IV 2; Fig. 10; Tab. 2): The mandible of V 2891 is well preserved, with its right ramus being almost complete, except i3 and c, which are lost. The mandible is low and long. Its lower border is basically straight, with a feeble convexity under m3, and the symphysis weakly ascending anteirorly. A single mental foramen is situated under p3 – p4. The ascending ramus is very low, but rather broad (APD). The condyle is situated low, only 55 mm higher than the alveolar border in V 2891. It forms a transverse bar, with a small round surface at its posteromedial corner, articulating with the postglenoid process of the skull. In posterior view, on medial side, below the bar is a rugose concavity, and external to it is a prominent process (Fig. 10 1), which is called postcotyloid process by Osborn (1898, p. 117). Below the postcotyloid process the posterior border of the ascending ramus is smooth, then becoming a plate-like projection turning inward. This projection may serve as the attachment for the m. sterno-mandibularis (Fig. 10). The coronoid process is broad at base, tapering rapidly upward, with its posterior border slanting stronger than its anterior border. Its tip turns scarcely backward. The masseteric fossa is confined to the upper half of the ascending ramus, very deep (20 mm) above its shelf-like lower border. The remaining parts of the ascending ramus are smooth, and the area for muscular attachment at the mandibular angle is not distinct. The mandibular foramen on the medial side of the ramus is located slightly lower than the alveolar border.

SS 4103.2 (Pl. IV 2) is about the same as V 2891, with the only distinction that the ascending of the lower border of symphysis being steeper, a character possibly caused partly by deformation.

2) Comparison

Though basically similar to all of the most primitive rhinocerotoids (Hyrachyinae and Hyracodontinae), *Juxia* differs from them in a number of features in skull and mandible. The plesiomorphic features shared commonly by all of them are as follows. The skull is dolichocephalic, with postorbital process lying at about the middle of the skull. Dorsal profile of skull is rather straight, with the top of the nuchal surface lying not posterior to condyle. Sagittal crest is high and long. Irregular nodules are present at the dorsoposterior corner of the nasal notch. Pseudo-meatus acusticus externus is widely open. However, *Juxia* possesses a series of apomorphic feature of its own as follows: 1) The paroccipital and posttympanic processes are completely coalesced to form a large, wide and thick single prossess. 2) The basicranium is proportionally lengthened. 3) The condyles are larger and higher relative to the low nuchal surface. 4) The free part of the nasal is slender and long, thickened sagittally (triangular in cross section) instead of being plate-like. 5) The nasal notch is particularly deep, reaching the level of P3 posteriorly, and close to the orbit. 6) The ascending branch of the premaxilla is shortened, without direct connection with nasal. 7) Incisors are arranged in two more or less straight lines weakly converging anteriorly, instead of forming a curve. 8) Ascending ramus of mandible is particularly low, height of the coronoid process being less than 1/2 of the mandible length (Tab. 2 ratio 3). 9) Posterior border of mandible is nearly vertical with weakly expressed mandibular angle.

The skull and mandible of *Hyracodon* are highly specialized among the most primitive rhinocerotoids. The muzzle part of the skull (including the nasals) is strongly shortened, nasal notch is very shallow, but the nuchal surface slants strongly backward, beyong the condyle. The posterior border of the mandible slants strongly, forming a very pronounced mandibular angle, and the tip of coronoid process is strongly turned backward. Other primitive rhinocerotids (*Teletaceras*, *Trigonias*, *Subhyracodon*, *Amphicaenops* etc.) differ from *Juxia* in majority of the above listed features, except the 6) and 7).

Forstercooperia totadentata is so far known only by an anterior part of skull. Its muzzle is very short; the nasals are wide and plate-like, with the tip forming a stubby triangle; the nasal notch is very shallow, posterior end lying above the canine; and the ascending branches of premaxilla is long and broad, widely connecting with nasal. In all these features *Pappaceras confluens* is rather close to *Forstercooperia totadentata*. The mandible *of Pappaceras confluens* is further different from *Juxia* in having a much pronounced mandibular angle and upturned symphysis with almost vertically implanted incisors.

Although enormously larger than *Juxia*, the large-sized paraceratheres remain close to *Juxia* in a number of apomorphic features in skull morphology. The common features shared by them are, for instance, the propotionally larger condylc, the extremely large and completely coalesced paroccipital and posttympanic processes, the long cranium and the nasal notch, the long and pointed nasals, etc. However, a number of features seen in *Juxia* have changed or become lost in large-sized paraceratheres during their further evolution. These are: 1) The long and high sagittal crest turned into a flat surface bordered by diverging parieto-frontal ridges. 2) The premaxilla became either strongly elongated with a single, much enlarged I1 (in *Paraceratherium*), or strongly reduced with atrophied incisors (*Dzungariotherium* and *Aralotherium*). 3) The ascending ramus of mandible became much higher relative to the mandible length. 4) The symphysis became highly divergent in morphology, either became much robust, with its posterior border shifted backward to p4 (*Paraceratherium*), or turned downward together with the single enlarged i1 (*Aralotherium*), or strongly reduced (*Dzungariotherium*), or stretches directly forward with divergent i1 (*Turpanotherium*). All these patterns of symphysis can clearly be seen in Fig. 31 in Part IV.

(2) Dentition

Dental formula is complete (3·1·4·3).

1) Description

Incisors (Pls. II 2, III 2, IV; Fig. 11; Tab. 3): In the holotype (V2891), all the six preserved incisors are heavily worn, whereas all the incisors in SS 4103. 1 – 2 (casts) are only slightly worn. The incisors are progressively smaller from front to rear, about equally and sparsely spaced. I1 has its crown rounded in cross section, about equally stout as its root. The mesial and distal ridges divide the crown into a larger and convex labial surface and a smaller vertically concave lingual surface bordered by clear cingulum at the base. I2 is similar to I1, but smaller and lower. I3 is still smaller, with its lingual cingulum indistinct.

On the holotype wear facets can be clearly seen. There is only one distal facet in I1, whereas I2 – I3 have both mesial and distal facets respectively, though smaller than in I1.

Lower incisors in SS 4103.2 are better preserved (Pl. IV 2). They are slightly larger and narrower labiolingually than the uppers. In morphology and disposition they are about the same as the uppers. The crown of i1 is stouter than the root because of its broadened base. The i1 is almost horizontally directed, while the i2 is procumbent. The crown of the i3 is nearly vertical.

In holotype the wear facet in i1 is almost perpendicular to the crown axis, while in i2 wear facets are present on both mesial and distal sides, as in I2.

Canines (Pls. III 2, IV; Fig. 11; Tab. 3): In holotype only the left upper canine is preserved, but the alveoli of the others are distinctly shown. In SS 4103. 1 – 2 all four canines are preserved. The canines are incisiformed, but larger than incisors. The crown shape of the upper canine is roughly similar to that of I3, with anterior and posterior ridges, weak lingual cingulum and an anterior wear facet, but its root is more robust than its crown. Its distance to I3 is slightly larger than the diastemata between the incisors. The lower canine is more laterally compressed than the upper one, situated closer to i3 than C to I3. Its root is about equally stout as the crown.

It can be concluded that the upper and lower incisors and cainines are alternately arranged, with the uppers being 1/2 tooth in front of the corresponding lower ones. Therefore, with the exception of the first pair of incisors and the canines, each incisor has two wear facets.

Cheek Teeth (Pls. I 2, II, III 2, IV; Fig. 12; Tabs. 4 – 5): Two complete sets of upper and lower cheek teeth (V 2891, SS 4103.1 – 2) are preserved in the collection.

P1: In holotype, the tooth is heavily worn, leaving a small anterior pit and fully exposed dentine in the posterior half. It is roughly triangular in outline, slightly longer than wide, and two-rooted. The paracone is prominent and swollen in the middle of the buccal wall. The parastyle is large only at the base; while the metacone is only about 1/3 the size of the paracone, weakly swollen labially. The connection between the protoloph and ectoloph is very narrow, lying far anterior to the paracone. The lingual half of the P1 in SS 4103.1 is broken away.

P2: The P2 is perfectly preserved in SS 4103.1. It is roughly square in outline, with its anterolingual corner rounded. The paracone and metacone are distinctly shown on both the lingual and buccal walls of the ectoloph. The protocone is slightly larger than hypocone, but both are lower than para- and metacone. They are scarcely coalesced with each other, with deep separating groove expressed on lingual side except at the base. The protoloph is connected to the ectoloph by a thin ridge in front of the paracone. The metaconule is distinct and crescent in form, weakly connected with hypocone and ectoloph. Continuous cingulum is developed around the anterior, lingual and posterior sides of the tooth, while the buccal cingulum is weak. In holotype, the separation of hypocone from protocone is considerably weak, leaving the lingual groove almost obliterated.

P3: The P3 is similar to P2 in basic structure, but wider than long, with paracone and metacone of about equal size. The protoloph is thick and high; the protocone is confluent with the hypocone, but still with a groove on the lingual side.

P4: It is similar to P3 in general structure, but the protocone is even less separated from the hypocone, which extends slightly lingually, with less clearly expressed lingual groove. The parastyle and parastyle fold are better developed.

As described above, the P2 – P4 are basically submolariform, while the P2 being slightly more molarized.

M1 – M2: They are quadrate, with more distinct parastyles and parastyle folds on buccal walls. The metacone forms a complete loph with scarcely expressed metacone rib. Both protoloph and metaloph are fully formed, but the latter is shorter than the former. The lophs are simple, without clear indication of secondary structures (crochet, antecrochet, crista etc.). The lingual cingulum is weak, or interrupted at the protocone and hypocone.

M3: The tooth is triangular in outline. The ectoloph merges with metaloph almost completely, with a rudiment of metacone expressed as a fine ridge starting from the middle of the crown and culminating at the base in a form of tubercle bordered lingually by a depression. Otherwise the tooth is similar to M1 – M2.

p1: The p1 is single-rooted, and its crown takes the form of a laterally compressed cone. The protoconid is situated in the center, sending three crests form its top: anterior, posterior and posterolingual one which is the weakest. Buccal and lingual cingula are distinct at the anterior and posterior ends, but lost at the middle on the lingual side.

p2: Its crown is like that of p1 in general form, but larger and supported by two roots. The protoconid is robust, sending a ridge anteriorly to form the protolophid. The anterior end of the protolophid turns lingually, forming a tubercle. The hypolophid is short and low, occupying only the posterior 1/4 of the tooth. A narrow ectoflexid can be seen. The surface posterolingual to the hypolophid is shallowly depressed, forming a rudimentary talonid. The cingulum is like that in p1, but the buccal one is stronger and U-shaped.

p3 – p4: They are alike in form and structure. The trigonid is U-shaped, formed by the low and short paralophid, the anteriorly sloping protolophid and the highest metalophid. The posterolabial corner of the protoconid is not ridge-like, nor covered by tubercles. The talonid is semi-L-shaped, with a low, but fully formed hypolophid, but an incomplete entolophid consisting of a small entoconid weakly linked with the entolophid. The buccal cingulum is prominent at the anterior and posterior ends and well developed at the posterior half of the tooth. The lingual cingulum is only absent at the lingual side of the metaconid. The p4 is more square in form than p3, with fully developed trigonid and higher entoconid, more clearly separated from the entolophid.

m1 – m3: The three molars are nearly of the same typical U + L pattern of rhinoceros. The paralophid is low and cingulum-like, and the hypolophid descends sharply forward, connecting the metalophid almost at its base.

2) Comparison

The incisors and canines of *Juxia* are markedly different from those of the other primitive rhinocerotoids. In Hyrachyinae and Hyracodontinae the incisors form an arc and usually closely implanted; the first pairs are never so enlarged as in *Juxia*, and the i1 is more or less vertically positioned instead of being horizontal. Their incisors and canines are mostly conical and pointed (*Hyracodon*), or roughly chisel- or scraper-like (*Triplopus*, *Ardynia*).

Allacerops turgaica differs from *Juxia* in having much enlarged canines, which is rather unique in primitive rhinocerotoids.

The earliest representative of the Rhinocerotidae, *Teletaceras*, has already greatly enlarged, button-shaped I1 and tusk-shaped i2, which are unanimously accepted as highly diagnostic for the true rhinoceroses.

In *Forstercooperia totadentata* and *Pappaceras confluens* the left and right rows of anterior teeth are more or less straight and anteriorly converging, like in *Juxia*. However, the upper incisors and canines of *Forstercooperia totadentata* are all stubby, conical in form, wider than long, and closely arranged. *Pappaceras confluens* is closer to *Juxia* in general morphology of the front teeth than *Forstercooperia* is. However, its second pairs of incisors are the largest among the incisors, and all the lowers, including the i1, are nearly upright in position. The incisors attributed by Wang (1976) to *Imequincisoria mazhuangensis* (transferred to *Juxia micracis* in this volume) conform closely with those of *Juxia* in morphology.

Of the large-sized paraceratheres, *Urtinothrium* is the only form with the full number of incisors and canines as *Juxia*. Nevertheless, in *Urtinotherium* the first incisor (known only for the lower) is proportionally much more enlarged than in *Juxia*. All the other Oligocene paraceratheres possess, at the most, only the first pairs of incisors, with highly reduced upper canines in rare cases.

The upper cheek teeth of Hyrachyinae differ from those of *Juxia* sharply. 1) They are much smaller, with their P1 – M3 length never exceeding 130 mm (vide Wood, 1934). 2) The para- and metacone remain more conical in shape, shown especially on the buccal wall. 3) The upper premolars are basically praemolariformed, with the degree of molarization increasing backward. 4) The lingual cingulum is generally poorly developed, often lost at the middle. 5) The parastyle in upper premolars is particularly prominent, covering the whole anterobuccal corner of the protoloph, which is highly characteristic of the tapirs. 6) The hypolophid and entoconid in lower premolars are only weakly developed.

The upper cheek teeth of the early members of Hyracodontinae, like *Triplopus*, are still very close to those of Hyrachyinae. However, those of the later forms, such as *Hyracodon* etc., are already specialized. The degree of molarization is more advanced, with P2 – P4 being semimolariform or molariform. Their crowns are more hypsodont, with the height index as high as 0.78 – 1.1, and the talonids in p2 – p4 are almost fully developed.

The upper premolars of *Allacerops turgaica*, although not fully molarized, are much more advanced, characterized by the flattening of the buccal wall and the existence of particularly high posterolingual cingulum. The p2 – p4 of this form have already fully developed talonids, forming complete entolophids.

The earliest rhinocerotid, *Teletaceras radinskyi*, is still small-sized, with its P1 – M3 length not surpassing those of Hyrachyinae (Tabs. 4 – 5). Morphologically, it differs from *Juxia* in the following ways. 1) In P2 – P4 the groove separating the hypocone from protocone on lingual side is hardly present or absent, whereas the metaconule is well separated from the protoloph-hypocone loop at the upper half of the crown. 2) The rudiment of the metacone in M3 is relatively large. 3) The p1 is highly reduced, very small and simple in structure.

In *Forstercooperia totadentata* only the upper premolars are available for comparison. They are quite close to those of *Juxia* in general morphology indeed. Their features differing from those of *Juxia* are the crown being much wider than long, the lesser degree of separation of the hypocone from the protocone, the long, narrow and crested metaconule linking ectoloph in early stage of wearing, and the attenuation of the lingual cingulum at the middle.

It is interesting to note that the cheek teeth of *Forstercooperia ergiliinensis* (Gabunia and Dashzeveg, 1974) are very close to those of *Juxia*. We tentatively transferred this form to the genus *Juxia*.

The affinity of *Forstercooperia shiwopuensis* (Chow *et al.*, 1974) and *Eotrigonias borissiaki* (Beliayeva, 1959) is difficult to recognize because of the paucity of their fossils.

The morphology of the cheek teeth of *Pappaceras confluens* are closer to *Juxia* than that of *Forstercooperia totadentata* is. *Pappaceras* differs from *Juxia* in having weaker groove separating the hypocone from protocone, hypocone extending posterobuccally instead of posterolingually, and the absence of entoconid in p3 – p4.

The similarity between *Juxia* and the large-sized paraceratheres is striking (Fig. 12). However, the latter are much more advanced in the following features. 1) The P1 becomes more reduced, or lost, and the p1 is completely lost. 2) The P2 is almost molariform. 3) The antecrochets and constriction folds in the upper molars are developed. 4) The p2 is strongly reduced, becoming single-rooted, and the entoconids in p3 – p4 are larger.

(3) Cervical Vertebrae (C's)

1) Description

Atlas (Pl. V 1, Fig. 13, Tab. 6): The atlas is well preserved, only slightly compressed in dorsoventral direction. It is butterfly-shaped, about twice wider than long. The anterior border of the dorsal arch has a broad and deep V-shaped median notch. The anterior median notch on the ventral side extends backward longer, forming a narrow cleft. The paired posterior articular surfaces (Fig. 13D 8) are broad, with their upper and lower borders being subparallel and lateral borders rounded. The surfaces face mesiocaudally, forming a wide curve, when seen from above. The dorsal tubercle is situated in the posterior half of the dorsal arch, forming a rugose triangular surface (Fig. 13A 1). The intervertebral foramen (Fig. 13A 2) is situated at the level of the anterior border of the wing, linking with the acute alar notch (Fig. 13A 3) by a groove. The ventral side of the ventral arch is smooth, with a pointed posterior tubercle (Fig. 13D 5), which is bordered bilaterally by a pair of small depressions. The wings are nearly horizontal, extending laterally and slightly backward. The borders of the wings are thick and rough. The anterior border is short, far away from the strongly projected anterior part with the anterior articular cavities, while the lateral borders extend posterolaterally. At the posterior end of the wing, close to the lateral border of the posterior articular surface, is the small posterior orifice of the vertebrarterial canal (Fig. 13D 9). The dorsal surface of the wing is broad and slightly concave, while the ventral surface is perforated by the foramen alare inferior (Fig. 13B 6). A wide depression is developed mesial to this foramen (Fig. 13B 4).

C3 (Pl. V 2, Fig. 14, Tab. 7): As the atlas, it is slightly compressed and the transverse processes are damaged and incomplete. The body is long, and oblique to the caput and vertebral fossa. The angle between ventral surface of the body and the surface of the caput is about 40° (Fig. 14A$_{\alpha}$), and between the former and the vertebral fossa is about 60° (Fig. 14A$_{\beta}$). The ventral spine is present in the anterior half of the body. The convexity of the caput and the concavity of the vertebral fossa are slightly weaker than in posterior C's. Both the caput and the vertebral fossa are oval in outline, slightly wider than high, the latter being larger. The upper border of the caput is weakly concave in the middle. The arch, zygapophyses, and transverse processes appear very large relative to the body, but the zygapophyses are smaller compared with those in other posterior C's. The articular facets on pre- and postzygapophyses are nearly horizontal in position, but at different levels: those on the prezygopophyses being higher than those on the postzygapophyses. The prezygapophysis facet faces upward and projects anteriorly scarcely beyond the caput, while the postzygapophysis facet faces downward. Seen from above, the four zygapophyses form a trapezoid plate, longer than wide, with the anterior part slightly narrower than the posterior part. The spinous process is weak and ridge-like. The transverse processes are broad, plate-like. The transverse canal (canalis transversarius) is short, about 1/2 the length of the base of the transverse process, and not particularly expanded to hollow the body.

C5 (Pl. V 3, Fig. 15 A, Tab. 7): The caput and the vertebral fossa are more rounded in outline, nearly parallel with each other, and more convex and concave than in C3. The zygapophyses are comparatively larger and the prezygapophysis projects beyond the caput. The four zygapophyses form a trapezoid plate, wider than long, with the anterior part markedly wider than the posterior part. Otherwise C5 and C3 are basically alike.

C6 (Pl. VI 1, Fig. 15 B, Tab. 7): The postzygapophysis is more reduced, with its articular facet more inclined, facing downward and externally. The trapezoid plate formed by the four zygapophyses are even wider. The transverse process is rather complexly structured, with the cross section of its base irregular in form (Fig. 15 B d). The anterior and the third branch of the transverse process unite to form a broad thin plate, with a notch separating them.

The salient features of C3 – C6 can be summarized as follows: 1) The bodies are rather long, with their ventral spines developed only in the anterior halves. 2) The capita are positioned higher than the vertebral fossae, but both are oval in outline, strongly convex and concave respectively, forming an angle around 40° – 60° with the axes of the bodies. 3) The zygapophyses are relatively large, forming large trapezoid plates, with the prezygapophyses projecting anteriorly and slightly beyond the capita. The articular facets of the pre- and postzygapophyses are roughly parallel with each other, facing upward and downward respectively. 4) The transverse processes are well developed, mostly plate-like, without distinct branching.

C7 (Pl. VI 2, Fig. 15 C, Tab. 7): Body is distinctly shortened, and the caput is not so strongly elevated relative to the vertebral fossa as in other C's. The ventral spine is short, developed in anterior half of the body and bordered bilaterally by depressions. The ventral spine is replaced in the posterior border of the body by two small tubercles. The caput is about hemispherical in form, with its upper border nearly straight. The posterior end of the body is considerably widened by the addition of the paired foveae articulating with the heads of the first ribs. The prezygapophyses remain very large, facing upward and mesially, extending far beyond the caput, while the postzygapophyses are much smaller. The spinous process becomes suddenly very high in comparison with those of the preceding C's. A pair of small concave facets can be seen at the base of the posterior side of the spinous process, apparently for the articulation with the corresponding facets of T1. The trnasverse process is undivided, rod-like, with its posterior side at the middle of the body.

The lengths of the axis (epistropheus) and the C4 are estimated based on the relative proportion between the C's. The total length of C1 – C7 is estimated as about 640 mm, slightly longer than that of skull

(595 mm).

2) Comparison

The atlas of *Hyrachyus eximius* is much smaller than that of *Juxia*, about 1/3 as large as that of the latter, but proportionally they are alike (Tab. 6). Both have alar notches instead of foramina. However, in *Hyrachyus eximius*, the intervertebral foramen is situated within the notch, and the dorsal arch is extremely high. The atlas of *Triplopus cubitalis* is even smaller than that of *Hyrachyus eximius* (Tab. 6). It differs from that of *Juxia* in being proportionally longer, with extremely narrow (in transverse direction) wings, the alar notch taking the form of a deep cleft, and the ventral tubercle being situated in the middle of the ventral side. According to Matthew (1915, Pl. CII 6), the lateral border of the atlas in *Hyracodon* extends posteromesially, instead of posterolaterally as in *Juxia*. There is neither the large depression situated mesial to the foramen alare inferior, nor the ventral tubercle in *Hyracodon*.

The atlas of the primitive rhinocerotids, as exemplified by *Trigonias*, *Subhyracodon* etc., is very similar to that of *Juxia* in general. However, the anterior part of the atlas containing the anterior articular cavities does not so strongly protruded forward as in *Juxia*, and the alar notch is usually deeply incised. The atlas in later rhinocerotids is readily distinguishable from that of *Juxia* by its extreme broadening (in transverse direction) of the wings.

In large-sized paraceratheres the atlas has been known only for three forms: *Paraceratherium bugtiense*, *P. lepidum* and *Aralotherium prohorovi*. They are very similar to that of *Juxia* in general form and structure, but all are enormous in size and hollowed in the central part of the bone. The atlas of *P. bugtiense* differs from that of *Juxia* in a number of features (Fig. 16): 1) It is proportionally longer (Tab. 6). 2) The dorsal tubercle is particularly developed and shifted toward the anterior end, forming a pair of large prominences. 3) The wings tilt strongly downward in their posterior parts. 4) The posterior opening of the canal is shifted upward, situated at the posterior border of the dorsal surface of the wing. The atlas of *P. lepidum* is probably the most similar to that of *Juxia*, only much more enlarged. The wings of the atlas of *A. prohorovi* extend more posteriorly than in *Juxia*, clearly expressed in the direction of its anterior border, which is posterolateral.

According to Cope, the capita and vertebral fossae in C3 – C7 are roughly perpendicular to the axes of their bodies in *Hyrachyus eximius*. Their spinous and transverse processes are very long, the latter being clearly separated into branches. Although rather contradictory in description (Cope, 1884; Wood, 1934), the length of C1 – C7 would not be longer than that of skull.

Based on the figures in Matthew (1915) and Scott (1896), the C3 – C7 of *Hyracodon nebraskensis* are similar to those of *Juxia* in the lengthening of the bodies in general, and C1 – C5 in particular, and the very low spinous processes in C3 – C5. However, the distinction between the two is obvious. 1) In *Hyracodon nebraskensis*, C3 – C5 are generally very elongated, longer than wide (seen from dorsal side); while in *Juxia* C5 – C7 are all wider than long. 2) In the former the capita and vertebral fossae in C3 – C7 are perpendicular to the axes of the bodies, while in the latter the capita and fossae are markedly oblique relative to the bodies. 3) In the former the ventral spine is very well developed, extending across the whole body, while in the latter it is weak and restricted to the anterior half of the body. 4) In the former the upper branch of the transverse process is simply rod-like, while in the latter it is more plate-like and complicated in structure.

In primitive rhinocerotids, like *Trigonias*, *Subhyracodon* etc., the general morphology of C3 – C7 is rather similar to that of *Juxia*. However, they are much shorter, with the capita and vertebral fossae being less strongly oblique relative to the bodies, the facets on the zygapophyses being smaller, and the transverse processes of the C6 being simpler. In later and living rhinoceroses the C's are readily distinguishable from those in *Juxia*. Their capita and vertebral fossae are all higher than wide, and less obliquely positioned relative to bodies. The vertebral (neural) canals are very large compared to the bodies, and the facets on zygapophyses are all clearly tilted, the anterior ones facing mesiodorsally, and the posterior ones lateroventrally.

The C3 – C7 of large-sized paraceratheres are very close to those of *Juxia* in general morphology. The features commonly shared by them are: 1) All the C's, especially C3 – C5, are very much elongated. 2) The facets on zygapophyses are flat, and nearly horizontally positioned, without tilting. 3) The spinous processes are very low, except in C7. 4) There are only lower branches of transverse processes in C3 – C6, and the upper branch of the transverse process in C6 is very complexly constructed. The large-sized paraceratheres, as exemplified especially by *Paraceratherium lepidum*, differ from *Juxia* in the following features: 1) The C1 – C7 are not only absolutely larger and longer than those of *Juxia*, but much more lengthened relative to the skull. The length of C1 – C7 has been estimated as almost twice as long as the skull length in *P. lepidum*. 2) The capita and vertebral fossae are much more transversely widened, with clearly concave upper borders, making them dumb-bell in outline. 3) The capita and vertebral fossae are more or less perpendicular to the axes of the bodies. 4) The branching of the transverse processes in C3 – C5 is clearer, with the well separated posterior branch stretching markedly ventrally and caudally. 5) The transverse canals are greatly inflated to make the bodies largely hollowed.

(4) Thoracic Vertebrae (T's)

1) Description

Altogether there are 12 thoracic vertebrae preserved.

T1 (Pl. VI 3, Tab. 8): The T1 is damaged, with parts of its right transverse process and upper half of the spinous process missing. The body is relatively small, with its width being less than 1/3 of the entire width of the T1. The caput is roughly pentagonal in outline, slightly wider than high, strongly convex, especially in its lower part, where the caput faces ventrally. The vertebral fossa, slightly wider than high and deeply concave, is more oblique to the axis of the body than the caput. The ventral spine is well developed in the anterior part, rather sharp-crested, becoming indistinct on posterior side. Costal facets is situated relatively low, with their upper borders lying at the mid-height of the body. The vertebral foramen is roughly triangular in shape with a wide base, which is still narrower than the width of the body. The facet on the prezygapophysis is large and elliptical in outline, facing anterodorsally. No metapophysis is formed on zygapophysis. Postzygapophysis is distinctly smaller than prezygapophysis. The vertebral notch lying at the base of the pedicle of the arch is deep and rather wide. The transverse process stretches posterolaterally, with a facet articulating with the tubercle of rib on the lower side. The spinous process is high, slating backward, laterally flattened, with rather sharp anterior border, but widened on posterior side, which is deeply excavated sagittally in the lower part. The lateral surface carries a groove on each side and the top of the spinous process is thickened.

T2: It is poorly preserved.

T3 (Pl. VII 1): The T3 is similar to T1, but slightly higher. The costal facets, especially the posterior ones, are situated higher, with their lower borders lying near the mid-height of the vertebral fossa. The facet on prezygapophysis is present, but much smaller than in T1. The spinous process is slightly longer than that of T1, slightly narrower in the part between the middle and lower 1/3. The posterior side of the spinous process is excavated also in the upper part forming grooves extending along the whole spine. A weak sagittal crest is developed in the groove.

T4 – T5 (Pl. VII 2, Tab. 8): These two vertebrae are similar in form. Their bodies are similar to that of the preceding one, but with weaker ventral spine, and the curvature of the caput and vertebral fossa being weaker. The costal facets for the heads of the ribs are placed higher, the anterior ones lying at the upper half of the body, connecting laterally with the facets for the tubercles of ribs to become an elongate articular surface. The prezygapophysis facet is shifted to the anterodorsal part of the neural arch, and the prezygapophysis itself is practically wanting. The paired prezygapophysis facets are still large, elliptical in shape, facing anterodorsally, and connected with each other by the thin dorsal arch. The transverse process is located at anterior part of the body, with a metapophysis (mammillary) process on its dorsal side directing anterodorsally. The spinous process is broader and thicker than that of T3, and probably the longest in T's.

Four poorly preserved intermediate T's and three posterior T's, including the last two (Pl. VII 3 – 4) are available for study. The last two T's are nearly of the same shape. For the last two T's, the body is large, with flat caput and vertebral fossa, both triangular in form, the caput being slightly higher and narrower than the vertebral fossa. The ventral spine is prominent and occupies the entire length of the body, which is deeply concave bilateral to the spine. The anterior costal facets articulating with the head and tubercle of ribs are united to form a single large one. No posterior costal facet is present in the last T. Zygapophysis facets are of concave-convex embracing type, with the anterior facet embracing the posterior one of the preceding vertebra. A prominent ridge-like metapophysis is developed at the upper part of the prezygapophysis. The transverse process is small, and concave upward. The spinous process is upright in position, laterally thin, but broad anteroposteriorly, especially near the base, without posterior groove.

The main features of the T's of *Juxia* may be summarized as follows.

It is not fully certain how many T's are there in *Juxia*. Among the twelve T's, the anterior five and the posterior three are continuous, but the rest of them are unassociated and their position in the series can not be determined. In general, the number of T's in perissodactyls varies from 18 to 20 (Flower, 1885). *Juxia* may have a similar number of thoracic vertebrae.

The bodies of the T's are large in anterior and posterior regions of the vertebral column, but smaller in the middle part, those of the posterior region having the largest bodies. In general, the body is wider than high. The caput is roughly pentagonal in shape in the anterior T's, while the vertebral fossa is oval in outline, becoming progressively rounded triangle in posterior T's. The convexity of the caput and the concavity of the vertebral fossa are progressively weakened toward the rear. The ventral spine is prominent in the anterior and posterior ones, but indistinct in the intermediate ones. A pair of ventral depressions are developed on each side of the ventral spine in anterior T's, but in posterior T's the depressions are so enlarged that the whole surfaces bilateral to the ventral spine face ventrolaterally, making the cross section of the body triangular in shape. The costal facet articulating with the head of rib is large in the anterior T's and is lowly positioned, progressively becoming smaller and finally lost, and higher placed in the rear. The large and flat prezygapophysis facet remains on the prezygapophysis itself in T1 – T4, beconming smaller and shifted on the anterodorsal plate of the neural arch in the intermediate T's, transforming into large and concave-convex embracing pattern in the posterior T's. The metapophysis becomes increasingly large backward. The transverse process is placed lower and separated from the caput in the anterior T's, becoming smaller and higher in position in the rear T's. The spinous processes is large even in T1, reaching to maximum height in T4, and then diminishes toward the rear. T16 may be the diaphragmatic vertebra, with the first vertical spinous process. The spinous process is broad and thick, with acute anterior border, but broader posterior side carrying deep grooves in anterior T's. In the posterior T's, the spinous process becomes thin and plate-like, without groove on the posterior side, and the top is thickened and roughened.

2) Comparison

Our knowledge of the T's in primitive rhinocerotoids are very meager either due to a paucity of material or a lack of adequate description. But from some brief descriptions so far available, we can see that they can readily be distinguished from those of *Juxia* in general. In *Hyrachyus eximius* the upper ends of the spinous processes of the T's, especially those of the anterior ones, were slanting forward in their upper parts, and the metapophysis, well developed. Both of these features have not been seen in *Juxia*. According to Scott (1896) and Matthew (1915), the body of the T's in *Hyracodon nebraskensis* was longer than high, with long ventral spine extending across the whole body, and the metapophysis being well developed. The lower parts of the spinous processes in all T's are deflected dorsocaudally, without any indication of median grooves on posterior sides. Thus, there is no diaphragmatic vertebra.

Some T's of *Allacerops turgaica* were described by Borissiak (1918) in detail. The anterior T's are similar to those of *Juxia* in having their bodies wider than high, with costal facets positioned low, and the zygapophyses relatively large, etc. However, in *Allacerops* neither median grooves on the posterior sides of the spinous processes in T's, nor the zygapophyses of embracing type in the posterior T's were reported.

The differences of the T's between *Juxia* and the later rhinocerotids, exemplified by *Coelodonta antiquitatis* and *Rhinoceros unicornis*, are obvious. In the latter group, the facets on the zygapophyses are generally much smaller, the transverse processes and the costal facets are positioned high, the costal facets are relatively larger, and the spinous processes of all the T's are deflected dorsocaudally, thus no diaphragmatic vertebra is present. Furthermore, in the anterior and middle T's, the grooves on the posterior sides of the spinous processes are narrow and shallow, but filled by very prominent sagittal crests; the zygapophysis facets in the last several T's remain simply structured, without embracing each other.

Based on the descriptions by Borissiak, Granger and Gregory, and Gromova, especially on the newly discovered material of *Paraceratherium lepidum* (*vide infra*), the similarities and differences between *Juxia* and the large-sized paraceratheres can be summarized as follows. The features commonly shared by them are mainly in having wider bodies in all the T's, and large median grooves on the posterior sides of the spinous processes and the large, strongly laterally extended transverse processes in anterior and middle T's. However, even in these features the degree of specialization is much more advanced in the large-sized paraceratheres. In addition to the enormous size difference, the distinction between *Juxia* and the large-sized paraceratheres can be summarized as follows: 1) In the latter group, all the spinous processes deflected dorsocaudally, without forming a diaphragmatic vertebra, while in *Juxia* the spinous processes of the T's posterior to the T16 are all upright in position. 2) All the zygapophysis facets of the T's are more or less equally developed in the latter group, while in *Juxia* those in the anterior T's are much enlarged, diminishing gradually backward. 3) In *Juxia*, the zygapophysis facets of the last 2 T's are embracing in pattern, becoming more similar to those of Lm's, while in the latter group these facets are roughly about the same as in other T's. 4) In the latter group the ventral spines is almost completely absent in all the T's, while in *Juxia* the ventral spines are developed in anterior and posterior T's.

(5) Lumbar Vertebrae (Lm's)

1) Description

Four Lm's are preserved (Pls. VII 5－6, VIII 1－3; Tab. 9).

Lm1: It is only partly preserved. Its body is close to those of the last two T's. The caput is roughly heart-shaped, slightly higher than wide, with upper border being concave. The caput is nearly flat, slightly concave in the center. The vertebral fossa is of about the same form, but slightly wider. The ventral spine is prominent, extending across the whole body. The surfaces bilateral to the ventral spine are concave and large. The prezygapophysis facets are deeply concave and saddle-shaped, facing anteromedially, with their anterior borders projecting beyond the caput. The postzygapophysis facets are convex and saddle-shaped, facing lateroventrally, with their posterior borders extending beyond the vertebral fossa. Metapophysis is located high, higher than prezygapophysis, forming a sharp crest descending abruptly caudally. The transverse process is plate-like, extending outward horizontally. The spinous process is high, twice as high as the body, broad anteroposteriorly and thin transversely. Both its anterior and posterior borders are sharp and crested, but the latter has a median groove near the base. The apex of the spinous process is thickened and roughened on top.

Lm2 (Pls. VII 5, VIII 1; Tab. 9): It is better preserved, in general very similar to Lm1, but differs slightly from the latter in having higher metapophysis and larger and wider postzygapophysis.

Lm4 (Pls. VII 6, VIII 2; Tab. 9): The body is broader, with width of caput 1.5 times greater than height. The ventral spine is indistinct, so that the surfaces bilateral to the spine face mainly downward. The transverse process is narrow at base, and its posterior border is about 18 mm in front of the vertebral fossa. The spinous process is still higher and inclines forward.

The last lumbar vertebra (Pl. VIII 3): Of the vertebra only the body and parts of transverse processes are preserved. The caput takes the form of a flattened ellipse, with the height of the caput half as its breadth, while the vertebral fossa takes the form of a rounded trapezoid with very broad base. The ventral spine is indistinct. The transverse process extends laterally and forward, with sharp anterior border, and the posterior border enlarged at the basal part to become an oval and concave articular surface for the sacrum.

Since the last lumbar vertebra can not be properly articulated with the Lm4, it is possible that an intermediate lumbar vetebra may have existed. In this case, *Juxia* might have 6 lumbar vertebrae. If the incongruence between the Lm4 and the last lumbar vertebra is caused purely by compression, then *Juxia* may have only 5 lumbar vertebrae.

2) Comparison

According to Cope, *Hyrachyus eximius* has seven lumbar vertebrae. The bodies are very long, twice longer than body height, all with ventral spines. The transverse processes are all very broad (in anteroposterior direction), extending anterolaterally, and the spinous processes are short, with their height about equal to the body length. *Hyracodon nebraskensis*, as Scott mentioned, may have only five lumbar vertebrae, with short bodies and weak transverse processes. *Trigonias osborni*, according to Scott's description, may also have five lumbar vertebrae, with shorter transverse and spinous processes. Otherwise the lumbar vertebrae of this form are close to those of *Juxia*. According to Borissiak, *Allacerops turgaica* has only three lumbar vertebrae, as in later rhinocerotids and living rhinos. The lumbar vertebrae of the living rhinos are readily distinguished from those of *Juxia*. The body is high, the zygapophysis facet is flat, similar to those in T's, with small and low metapophysis, and short and backward inclined spinous process. The transverse process tapers rapidly toward its lateral extremity, taking the form of a triangle.

Although different opinions exist as to the number of the Lm's (three by Borissiak and Granger and Gregory), the large-sized paraceratheres may have four Lm's as evidenced in the recently discovered material of *Dzungariotherium turfanense* (*vide infra*). The Lm's in *Juxia* and large-sized paraceratheres are alike in general morphology, in having low and broad bodies, ventral spines developed on the anterior ones, large zygapophysis facets, and thin, plate-like transverse process extending directly outward. However, the zygapophysis facets in the large-sized paraceratheres are all flat, without changing into embracing apparatus. Furthermore, the spinous processes in the latter group are comparatively low and thick (in transverse direction), and all incline backward.

(6) Ribs

Altogether 13 ribs are preserved, only two of them are complete.

First rib (Pl. VIII 4): The rib is well preserved. In proximal end the head and the tubercle are separated by a deep longitudinal groove. The head bears two about equally large facets. The tubercle is slightly larger than the head. It forms a slightly elliptical surface extending in longitudinal direction, being aligned with the shaft in a straight line. The shaft of the rib is flat and long and progressively broadened toward the lower end. The distal end is rough, apparently caused by a costal cartilage. Its total length is 353 mm.

Intermediate left rib (Fig. 18): The head bears two facets of equal size, separated by a longitudinal groove, the anterior one being convex and the posterior flat. Posterolateral to it is the tubercle, facing dorsomedially. External to it is a deep groove for ligament attachment. The neck of the rib is not clearly marked off, with a deep groove in front for the attachment of ligament. The shaft is stout. The muscular groove in the middle of the anterior border is deep and extends downward for a considerable distance, while the groove in the middle of the posterior side fades out in the lower part (Fig. 18). Its length is 720 mm, measured along the curviture. It is probably the fifth or the sixth rib.

It was reported by Cope that all the ribs in *Hyrachyus eximius* were very slender, the first rib being without particular widening in distal end. According to Scott, the anterior ribs in *Hyracodon nebraskensis* were laterally flattened, and the posterior ribs were slender and rod-like. In primitive rhinocerotids only the first five ribs are flattened laterally, the ribs posterior to the fifth one became rod-like. In later rhinocerotids and living rhinos all the ribs became plate-like. The first rib of *Paraceratherium asiaticum*, according to Borissiak (1923b), differs from that of *Juxia* in having very widened distal end and the tubercle coalesced with the head. Further, in *P. asiaticum* most of the ribs except the most posterior ones have the cross sections of the shaft longer than wide, with sharp anterior and posterior borders. In *Juxia* the cross sections are wider than long, with concave anterior and posterior borders in the intermediate ribs.

(7) Forelimb

1) Scapula (Pl. IX 1, Fig. 19, Tab. 10): It is roughly fan-shaped in outline, with its length slightly larger than that of the humerus. Its anterior, vertebral and upper half of the posterior margins form a rather smooth curve. The scapular spine (Fig. 19 A 4) is well developed, starting from the neck and disappears until close to the dorsal margin, with a very large spinal tuberosity (Fig. 19 A 1) slanting strongly backward and a rudimentary acromion (Fig. 19 A 5). The supraspinous and infraspinous fossae are about equal in size. The glenoid cavity is oval in shape, concave strongly longitudinally, but weaker transversely. The scapular tuber (Fig. 19 A 6) is well developed, semispherical in form, separated from the glenoid cavity by a deep groove; the coracoid process is probably small, but wanting in the holotype skeleton.

The scapula of *Hyrachyus eximius* is very small, only 1/2 as long as that of *Juxia*, and differs from the latter in morphology. It is generally triangular in shape, with very narrow neck, vertebral border being straight, and the postero-vertebral corner forming a right angle. The scapular spine is low, without evident spinal tuberosity and acromion, but the scapular tuber is prominent. In general form the scapula of *Hyracodon nebraskensis* is similar to that of *Juxia* in having curved vertebral margin and large spinal tuberosity, but differs from the latter in being very long, with its length about twice greater than its breadth and the absence of an acromion. The scapulae of the primitive rhinoceroses, such as *Trigonias* and *Subhyracodon*, are about the same as that of *Hyracodon nebraskensis*. However, in later rhinocerotids and living rhinos the scapulae are already quite distinct from that of *Juxia*. They are proportionally longer, usually more than twice longer than wide, with very large spinal tuberosity and the clear separation of the scapular tuber from the glenoid cavity by deep groove, but no acromion.

No complete scapula of the large-sized paraceratheres was ever reported. Two distal parts were described by Gromova (*Aralotherium prohorovi*) and Borissiak (*Paraceratherium asiaticum*) respectively. Therefore, the upper part of the scapula of large-sized paraceratheres is unknown. It is interesting to note here that Gromova noticed the presence of an rudimentary acromion in *Aralotherium prohorovi*, as in *Juxia*. The presence of an acromion here is a quite unique feature among the whole group of perissodactyls. As can be judged by these two specimens, the scapulae of the Oligocene paraceratheres are distinguished from that of *Juxia* by the following. 1) The necks are narrow, widths of which are only about those of the glenoid cavities, while in *Juxia* the former is definitely larger than the latter. 2) The scapular tubers are much larger than in *Juxia*, situated low and not clearly separated from the glenoid cavities by a groove as in *Juxia*. 3) The spinal tuberosities are considerably reduced. The enormous spinal tuberosity restored by Granger and Gregory (1936, Fig. 37) seems to be groundless.

2) Humerus (Pls. IX 2, X 1; Fig. 20; Tab. 11): Both humeri of the holotype skeleton are well preserved, the upper half of the right one being slightly compressed anteroposteriorly.

The caput tilts backward, with its articular surface facing upward and backward. The curvature of the articular surface in anteroposterior direction is strong, but very weak in transverse direction so that the upper margin of the caput becomes almost straight, seen from posterior side. The lateral tuberosity is bifid; the anterior part is low and thin, turning medially to partly cover the bicipital groove; and the posterior part is large and voluminous, with its upper border higher than the caput. The medial tuberosity is smaller and not bifid. The bicipital groove is rather wide, but shallow, with the intermediate ridge not clearly expressed, but shifted laterally.

Seen from the front, the upper half of the shaft is wide, forming roughly a triangle pointing downward, and the distal end is narrower. The deltoid tuberosity is situated slightly above the middle of the shaft on the lateral side of the shaft. The humeral crest leading from the deltoid tuberosity to the posterior border of the lateral tuberosity, accompanied by another fine ridge diverging slightly more backward. Slightly below the middle of the posterior surface of the shaft is a nutrient foramen. On the medial side the teres tuberosity is situated slightly lower than the level of the deltoid one.

The distal trochlea is rather asymmetrical. The medial condyle takes the form of a truncated cone thinning laterally, while the lateral condyle is narrower than the medial one and provided with a blunt ridge running parasagittally, situated nearer to the medial half of the condyle. The intercondylar groove is situated slightly lateral to the middle of the trochlea. The coronoid fossa is slightly bifid, and the olecranon fossa is very deep. The lateral epicondyle is scarcely larger than the medial one.

The humerus of *Hyrachyus eximius* is particularly slender (Tab. 11 ratio 3). Both the proximal and distal ends are not particularly widened. Both proximal tuberosities are small, situated not higher than the caput, and the deltoid and teres tuberosities are scarcely developed. The distal trochlea is very narrow and high, the lateral condyle being very small. The humerus of *Triplopus cubitalis* is similar to later rhinoceroses in having high lateral tuberosity over the caput and the large deltoid tuberosity, but remains rather primitive in distal end. It differs from that of *Juxia* by having small epicondyles, the medial one being even larger than the lateral one, very asymmetrical trochlea with deep intercondylar groove and sharp ridge on the lateral condyle. Furthermore, it differs also by having higher positioned deltoid tuberosity and more or less hemispherical caput. The humerus in *Hyracodon nebraskensis* remains slender, but is shorter than scapula. It is similar to that of *Juxia* in structure of proximal end as a whole, but the caput is longer than wide, just opposite to that of *Juxia*. The distal end is even more specialized. The trochlea is rather close to that in some horses: trochlea very narrow, high, and skew, condyles more symmetrical, both with sharp ridges, and lateral condyle becoming concave lateral to the ridge, etc.

Although the primitive rhinocerotids have already acquired the rhino-type humerus in general morphology, as in *Juxia*, obvious distinctions between them can readily be detected. The humerus in the former group has the proximal end thicker (anteroposteriorly) than wide, the caput of semispherical form, the lateral tuberosity strongly bending medially to cover almost the whole bicipital groove, and the lateral condyle being much smaller than its medial counterpart. The humerus in later rhinocerotids is already strikingly different from that of *Juxia* as follows. 1) The humerus is much more stout absolutely and in proportion. Width of its distal end may reach to about 1/3 of the total length of humerus. 2) The caput is semispherical in form. 3) The bicipital groove is shifted laterally, situated anterolateral to the caput. 4) The medial, lateral and deltoid tuberosities are all very well developed, with the latter becoming hook-like. 5) The lateral epicondyle becomes enormously enlarged. Both lateral condyle and epicondyle stretch slightly downward. 6) The olecranon fossa is wide and low.

The humeri in large-sized paraceratheres bear clear signs of graviportal adaptation. They are very stout in general (Tab. 11), without marked thinning in the mid-shaft. The caput tilts backward only slightly so that it is close to be in line with the axis of the shaft. The curvature of the caput is correspondingly weak in both directions. The medial tuberosity is larger than the lateral one in contrast to the case as in *Juxia* and in all other rhinoceroses. The deltoid tuberosity is scarcely developed. The relief of the distal trochlea is considerably flattened, with the ridge on the lateral condyle rather indistinct. A stricking similarity between *Juxia* and the large-sized Oligocene paracertheres is the form of the caput, which is much wider than long.

3) **Radius** (Pl. XI 1, Fig. 21, Tab. 12): The right one is perfectly preserved, but the left one is only represented by its proximal end.

The bone is extremely long, longer than humerus, and sigmoid in anterior or posterior view. The proximal articular surface is inversely symmetrical to the trochlea of the humerus, but much shorter in anteroposterior direction. The surface faces upward and anteriorly, not perpendicular to the shaft, but slopes down anteriorly (Pl. XI 1c). The sagittal ridge is high and blunt, and the lateral groove can be seen from the anterior side (Pl. XI 1a). The medial and lateral proximal tuberosities are not well developed, represented mainly by rugosities. The two facets articulating with ulna, situated on the posterior side of the proximal end, connect each other at the middle. The medial one is small and forms a narrow strip, but the lateral one is rather large and semilunar in shape, situated lower than the medial one (Pl. XI 1b, Fig. 21 A).

The radial tuberosity takes the form of an elongated triangle, not strongly swollen, nor deeply excavated, situated in the medial 2/3 of the proximal end of the anterior side. The rough area on the lateral part of the posterior side is very long (Pl. XI 1b i), apparently serving as attachment of the interosseous ligament.

On distal end there are three facets articulating with three proximal carpal bones (Fig. 21 D). Two large ones articulate with scaphoid and lunar respectively. The scaphoid one is roughly rectangular in outline, with its anterolateral part being concave, and its posterior half strongly convex, extending to the posterior side, forming a transverse half-cylinder. The lunar facet is roughly fan-shaped, with its lateral border directing posteromedially. This facet is shallowly concave, and restricted mainly to the distal side. A small facet is annexed to the anterolateral corner of the lunar facet, and is hardly separable from the later. The small facet is undoubtedly articulated with the cuneiform (Fig. 21 D 3). This can also be verified in the structure of the cuneiform. A small facet is present also at the distal part of the lateral side of the radius, which should be articulated with the distal end of the ulna. Above the distal end of the dorsal side of the shaft a middle groove bordered bilaterally by prominent ridges can be seen, which may extend upward for quite a long distance. This groove is evidently the place lodging the m. extensor carpi radialis.

The radius in *Hyrachyus eximius* is similar to that of *Juxia* in its distal end articulating with three proximal carpal bones, but differs in being shorter relative to humerus. Just opposite to *Hyrachyus eximius*, the radius of *Triplopus cubitalis* is longer than humerus as in *Juxia* (even proportionally longer), but its distal end articulates with only scaphoid and lunar, and the line separating the two facets for the carpal bones is not directly anteroposterior, but oblique in direction. Furthermore, the proximal articular surface is roughly rectangular in outline, while that in *Juxia* is clearly trapezoid. In *Hyracodon nebraskensis*, the radius is about equally long as the humerus. In general morphology it is rather close to that of *Triplopus cubitalis*, with the relief of the proximal articular surface even more pronounced.

In primitive rhinocerotids the radius becomes stouter, always shorter than humerus, with its maximum width being about 1/4 of its length (1/6 in *Juxia*). In most cases the radius articulates only with scaphoid and lunar. In later rhinocerotids and living rhinos the radius becomes more clearly medi- or graviportal in character, and differs from that of *Juxia* more markedly in the following ways: 1) The radius is shorter and stouter, with its extremities particularly broadened. Maximum width is equal to, or more than, 1/4 of its length. 2) The proximal articular surface is shallowly concave, in low relief, with its lateral half being considerably smaller than the medial half. 3) In distal end the facet articulating with lunar is smaller than that articulating with scaphoid. 4) The posterior end of the facet articulating with scaphoid is narrow and pointed. 5) The anteromedial corner of the distal end is always more downward stretched, taking the form of a process. 6) The longitudinal groove on the dorsal side of the distal end is very weakly expressed.

The radius in large-sized paraceratheres differs from that of *Juxia* considerably. 1) It becomes stouter (Tab. 12). 2) The proximal articular surface is shallowly concave, in low relief, as in later true rhinoceroses. 3) In distal end the facet articulating with cuneiform is large, running through the whole length of the distal end. 4) In some advanced forms (*Aralotherium*, *Turpanotherium*) special "hindering facets" are developed in anterior parts of the facets articulating with scaphoid and lunar.

4) **Ulna** (Pls. X 2, XI 2; Fig. 22; Tab. 13): As the radii, the right ulna is perfectly preserved, whereas of the left ulna only proximal part is preserved.

The ulna is extremely long, curved and torqued. The proximal end is the most robust part of the bone, plate-like, lateral side being convex, and medial side concave. The upper border of the olecanon extends mainly backward, only slightly upward, and its lower border starts 10 cm lower than the lower margin of the semilunar notch and extends upward and posteriorly, forming an angle with the posterior border of the shaft. The olecranon process is rather high vertically, with its posterior border convex. The semilunar notch is of common rhino-type.

The upper part of the shaft is curved anteriorly. The inward torsion of the distal end relative to the upper part of the shaft is about 90°. The cross section of the upper part of the shaft forms a triangle with concaved lateral sides, transforming into an anteroposteriorly elongated ellipse in the mid-lower part of the shaft. The distal end bears a confluent facet articulating with cuneiform in front and pisiform behind (Fig. 22 B–C $_c$). On medial side there is a small facet articulating with radius (Fig. 22 B $_r$).

As in the case of radii, the ulna in *Hyrachyus eximius* is shorter than humerus, that of *Triplopus cubitalis* is longer than humerus as in *Juxia*, and that of *Hyracodon nebraskensis* is only very slightly longer than humerus. However, the proximal ends of the ulnae in all the above three forms are proportionally smaller and extend mainly upward. Scott (1896) mentioned that in *Hyracodon nebraskensis* the lateral part of the articular facet of the semilunar notch was limited to the upper half of the notch, a character not seen in *Juxia*.

In later rhinocerotids the ulnae are much stouter, no less stout than radii. The olecranon always extends mainly upward. The distal end in most cases articulates with only cuneiform and pisiform, but may also with lunar.

In large-sized paraceratheres the ulnae are very similar to that of *Juxia* in features diagnostic of the latter, as the slenderness, the curvature and torsion of the shaft, the lowly situated and posteriorly directed olecranon, and the configuration of the articular facets on distal ends. However, the differences between them are obvious. 1) In large-sized paraceratheres the ulnae are proportionally stouter than in *Juxia* (Tab. 13). 2) In the former the olecranon and the semilunar notch are all much broader, with the curvature and relief of the notch being weaker. 3) In the former there are two or three facets articulating with radius, lying in the distal end of the medial side of the ulna (one in *Juxia*). 4) In the former the lower border of the olecranon form a smooth curved line with the posterior border of the shaft, instead of being angled as in *Juxia*.

5) **Carpals**: Of the carpal bones no trapezium, trapezoid, magnum and pisiform are preserved.

Scaphoid (Pl. XI 3, Tab. 14): Altogether five specimens are in the collection. The bone is irregularly cubic in form, with its distolateral angle on dorsal side being the most protruding part of the bone. It is longer (APD) than high, which is greater than width. The proximal articular facet is rectangular in outline, convex in anterior part, but concave posteriorly. The distal end is composed of three facets articulating successively with magnum, trapezoid and trapezium. That for the magnum is the largest, triangular in form, and saddle-shaped; that for the trapezoid is also saddle-shaped; and that for the trapezium is a very small and rounded in form, facing posteriorly. On lateral side of the bone there are two facets articulating with the lunar. The upper one forms a horizontal strip, while the lower one is semilunar in form, shorter than the upper one.

There is little information about the scaphoid in the most primitive rhinocerotoids. It is reported that the scaphoid in *Hyrachyus eximius* is very high and narrow, about twice higher than wide (one and a half in *Juxia*, *vide* Tab. 14), while in *Triplopus cubitalis* it was suggested by Cope to be wider than high, and in *Hyracodon nebraskensis* the distal facet articulating with the magnum is situated very low, that for the trapezoid is strongly concave, and that for the trapezium faces principally downward. In these features the most primitive rhinocerotoids are all different from *Juxia*.

The scaphoids in primitive rhinocerotids are already close to those in later rhinocerotids and living rhinos in morphology, expressed in the following points: 1) The proximal articular facets are pentagonal, or triangular in outline. 2) The distolateral angle of the scaphoid is far more protruding downward and laterally, occupying almost the whole proximal surface of the magnum. 3) The facet articulating with the trapezoid is situated more medially relative to that for the magnum. 4) The facet articulating with the trapezium faces mainly downward.

The scaphoids in later rhinocerotids and living rhinos are more specialized in the above mentioned characters. 1) The lower half of the scaphoid is much broader than the upper part of the bone. 2) The proximal articular facet is pentagonal in outline and strongly concave with a large portion of the anterior part of the facet being convex. 3) There is a distinct torsion between the proximal and distal facets. All the distal facets are strongly saddle-shaped. 4) The upper and lower facets articulating with the lunar on the lateral side of the bone are almost diagonally positioned owing to the torsion between the upper and lower surfaces.

The similarity between the scaphoids of *Paraceratherium asiaticum* and *Juxia* in general morphology is striking (Borissiak, 1923b, Pl. 5－6). However, there are some differences between them as shown in the following. 1) In *P. asiaticum* the scaphoid is about equally high and wide, seen from dorsal side. 2) The upper facet articulating with the lunar is very long, with its posterior end turning downward (Borissiak, 1923b, Pl. VII 6c). 3) The most protruding portion of the posterior border is situated in the lower 2/3 (in upper 2/3 in *Juxia*).

The scaphoid of *Aralotherium prohorovi* as described by Gromova is characterized by the bone being low and broad, with very long distolateral process, the flattened articular facets in general and the presence of a "hindering facet" in the anterior part of the proximal facet. Similar "hindering facet" is also present in *Turpanotherium*.

Lunar (Pls. XII 1, XIII 3; Tab. 15): A complete right lunar and a damaged left one are preserved. The anterior part of the proximal facet is strongly convex anteroposteriorly, forming a stout transverse half-cylinder. A large part of this facet turns onto the anterior side of the bone (Pl. XII 1a). Its posterior half is short and narrow, restricted to the medial half of the proximal side. On each of the medial and lateral sides of the bone two small facets are present, forms of which conform to those in scaphoid and cuneiform respectively. The distal end of the bone bears two facets. The medial facet articulating with the magnum is narrow anteriorly, but much widened posteriorly. Its anterior part is flat, facing more medially than downward; while the posterior part is spherically concave mainly to receive the spherical caput of the magnum. Seen from dorsal side, the insertion of the distal end of the lunar between the magnum and unciform is strongly asymmetrical so that the lunar rests almost totally on unciform (Pl. XIII 3). The volar process is rather voluminous, but is not clearly differentiated and demarcated from the other part of the bone (Pl. XII 1e).

It is difficult to tell the differences of the lunar of *Juxia* from those of the most primitive rhinocerotoids because of the lack of adequate description of the latter. However, the published figures seem to suggest that in *Hyrachyus eximius* the insertion of the lunar between the magnum and unciform is rather symmetrical. The extension of the proximal articular facet onto the dorsal side of the lunar as shown in *Juxia* has never been found in the latter group. Comparison of the lunars between *Juxia* and the primitive rhinocerotids is difficult, partly because of the paucity of information of the latter group. In later rhinocerotids and living rhinos the proximal articular facets are mainly restricted to the anterior halves of the bones, and the hook-like volar process is very well differentiated, very long and robust. By this feature the true rhinoceroses can be easily separated from *Juxia*.

Lunars of the large-sized paraceratheres are generally quite similar to that of *Juxia*, especially in proportion and form of the articular facets. Nevertheless, the lunars in the former group differ from that of the latter in a number of features. 1) The lunars are always lower in proportion (Tab. 15), with clearly differentiated volar process. 2) A narrow strip of flat area develops near the anterior border of the proximal facet. In more advanced forms, like *Aralotherium prohorovi*, this area changes into a "hindering facet". 3) The proximal articular facet is convex in both directions, and in *Aralotherium prohorovi* it changes into a large hemisphere. 4) The upper facet on the medial side articulating with scaphoid is separated into an anterior and a posterior ones, the posterior one of which is situated lower, on the volar process. 5) The insertion of the distal angle between the magnum and unciform is more or less symmetrical.

Cuneiform (Pls. XII 2, XIII 3; Tab. 16): There is only one specimen with its anteromedial corner being damaged.

The bone is about equally high and long (APD), but higher than wide. Seen from above, the medial edge forms an obtuse angle at the middle with almost rectilinear anterior and posterior sides; while the lateral and posterior edges form an arc. The proximal end bears three facets articulating with radius, ulna and pisiform respectively. That for the ulna is the main facet, fan-shpaed, slightly saddle-shaped (concave longitudinally and convex transversely), while those for the radius and pisiform are narrow fan-shaped, of about equal size and connected with each other at the middle of the medial side. The facets articulating with the lunar on medial side conforms to those of lunar. The distal end bears only one facet articulating with unciform. It is roughly triangular in outline, slightly saddle-shaped.

The cuneiform of *Hyrachyus eximius* is unique in being L-formed, seen from the dorsolateral side. It is about equally high and wide, and does not articulate with the radius. In *Triplopus cubitalis* the articulation with the radius is also absent, and the facet articulating with the pisiform is confluent with the main proximal facet articulating with the ulna. Neither *Hyracodon nebraskensis* has a facet articulating with radius. Judging from the short description and figures given by Scott, the cuneiforms of primitive rhinocerotids are already close to those of later rhinocerotids and living rhinos in general structure. Their cuneiforms are shorter (APD) than high and wide, with the articular facets being strongly saddle-shaped. Correspondingly, the two facets articulating with the lunar on medial side of the bone are also short. The facet articulating with the pisiform is shifted laterally, located at the posterolateral corner of the bone.

In large-sized paraceratheres the cuneiforms are close to that of *Juxia* in having three fan-shaped proximal facets, of which the two facets articulating with radius and pisiform being about symmetrically situated, and the facets articulating with ulna and unciform being only weakly saddle-shaped. However, cuneiforms in large-sized paraceratheres differ from that of *Juxia* in being always lower than long (APD) and the proximal facet articulating with the radius is considerably enlarged. Furthermore, in *Paraceratherium asiaticum* the proximal facets articulating with radius and pisiform are separated from each other, and there is a tiny facet articulating with McV posterior to the distal facet articulating with the unciform. In *Aralotherium prohorovi* the cuneiform is even lower and narrower than in *P. asiaticum*, and the anterior portion of the distal articular facet changes into a "hindering facet". However, in *A. rohorovi* the proximal facets articulating with radius and pisiform are connected as in *Juxia*.

Unciform (Pl. XII 3 – 4, Tab. 17): There are three specimens, only one of them are well preserved, but also slightly damaged.

Seen from the front, the bone is rhombic in shape, higher than wide, with its upper two edges being shorter and slightly concave, and its two lower edges being longer and confluent at their lower ends. The proximal end bears two facets articulating with lunar and cuneiform. Both they are fan-shaped and slightly saddle-shaped, the lateral one being slightly larger. The medial and distal sides of the bone from a continuous curved surface occupied by four facets articulating with magnum, McIII – McV respectively (Pl. XII 4). The medial one is that for the magnum, forms an acute angle with the proximal facet articulating with the lunar. The facet next to the magnum one is the narrowest one articulating with the smaller of the two proximal facets of the McIII. The facet articulating with the McIV may be the largest one, and that for the McV is the most lateral one, which may extends postriorly onto the volar process (Pl. XII 4). The volar process is robust, but not very elongated, extending laterally and downward.

The poor information of the unciforms of primitive rhinocerotoids only allows us to make the following points. The unciform in *Hyrachyus eximius* is wider than high (Tab. 17). The unciform in *Triplopus cubitalis* is about equally high and wide, with very narrow and long volar process, turning sharply downward, and bears a very small facet articulating with McV, which must be very much reduced. The unciform in *Hyracodon nebraskensis* is very close to that of *Triplopus cubitalis* in morphology. The unciform in *Allacerops turgaica* is more similar to that of *Juxia*, but differs from the latter in having a very large facet articulating with the magnum and a slender and long volar process.

The unciforms in primitive rhinocerotids, like *Trigonias osborni* and *Subhyracodon occidentalis*, differ from that of *Juxia* in being wider than high, with a higher situated facet articulating with McV. In later rhinocerotids and living rhinos, exemplified by *Coelodonta antiquitatis* and *Rhinoceros unicornis*, the unciforms are always wider than high, with all the articular facets being very wide, the facet for McV being restricted to the anterior half of the lateral side of the bone, and a very large volar process.

The unciforms in large-sized paraceratheres are very specialized and differ from that of *Juxia* markedly. Generally, they are wide and flattened, wider than high, especially when seen from the anterolateral side, and take the form of an irregular rectangle rather than a rhombus. The lower border is nearly horizontal, the medial and lower borders forming an arc bearing three facets articulating with magnum, McIII – IV. The facet articulating with McV is not only much smaller, but also shifted entirely on the volar side of the bone. The volar process is small, weakly stretches posteriorly and downward, but is already well differentiated from the rest part of the bone. The unciform in *Aralotherium prohorovi*, compared with that of *Paraceratherium* *asiaticum*, is even narrower transversely, and the facet articulating with McV is absent in 2 of 7 specimens.

6) Metacarpals: Of the metacarpals no McII and McV are preserved.

McIII (Pl. XIII 2 – 3): The McIII is represented in the collection only by a left one without distal end (V 2891.2).

The proximal end bears two facets: the larger medial one articulating with magnum, with its dorsal border being clearly curved and slanting medially; the smaller one articulating with unciform, still considerably large, with its dorsal border more or less straight and slanting more steeply laterally. The angle formed by the above two facets is about 90°. Seen from above (Pl. XIII 2b), the medial facet is trapezoid in outline, with its posterior border being only slightly shorter and irregularly curved. The surface is saddle-shaped, strongly convex anteroposteriorly, but weakly in transverse direction. The lateral facet is triangular in outline, situated only in the anterior 2/3 of the proximal end, slightly convex anteroposteriorly and flat transversely. The shaft is straight, with a considerably large, roughened bulge on the medial half of the proximal end on dorsal side below the facet articulating with magnum. The cross section of the shaft in the upper end is roughly triangular. Slightly downward, two ridges appear bilaterally on medial and lateral borders of the posterior side. The ridges become wider and wider separated from each other downward, making the posterior side of the shaft broader. All the posterior, medial and lateral surface of the shaft are rather flat. The lateral ridge is stronger than the medial one. In distal half the cross section of the shaft becomes more or less oval in shape. Max W of PE is 49.6 mm, Max APD of PE is 46.1 mm; W of mid-shaft is 40 mm, APD of mid-shaft is 22.6 mm.

No distal end of McIII is known in *Hyrachyus eximius*. The only observed distinguishing character of this form from *Juxia* may be the less degree of widening of the proximal end of McIII relative to its shaft and the less degree of overlapping of the McIII over the McIV. The McIII in *Triplopus cubitalis* is particularly long, its total length being about 8.5 times greater than its proximal width (~5.5 times in *Juxia*). Otherwise, it is close to that of *Hyrachyus eximius*. In proportion the McIII of *Hyracodon nebraskensis* is about the same as in *Juxia*. However, the dorsal and volar surfaces of the shaft in this form are nearly flat, and the medial and lateral surfaces are rounded.

All the rhinocerotids have proportionally shorter McIII, with both proximal and distal ends considerably widened. In *Trigonias osborni* the length of McIII is only 3.7 times greater than its proximal width. In later rhinocerotids and living rhinos the volar process of the proximal end possesses a prominent facet articulating with McIV. This process is absent in *Juxia*.

In large-sized paraceratheres the McIII is close to that of *Juxia* in having a triangular proximal end without laterally stretching volar process, and flat posterior, medial and lateral sides in the upper half of the shaft. However, in the former group the McIII is much more robust, with its length being only about three times greater than widths of its two ends. The proximal facets are flatter, with the lateral facet articulating with unciform is much narrower (seen from the front) and trapezoid in outline followed by a deep notch (seen from above).

McIV (Pl. XIII 1, 2a; Tab. 18): A complete right McIV is preserved in the holotype (Pl. XIII 1), while a left one (V 2891.1) is represented only by its upper half (Pl. XIII 2a).

McIV is much slenderer than McIII, with its distal end diverging laterally and turning slightly clockwise. The proximal end bears a single facet articulating with unciform, the facet being narrow and long, triangular in outline, slightly saddle-shaped, weakly convex anteroposteriorly, and very weakly concave transversely. On proximal end of the medial side there are two small and flat facets articulating with McIII, directly bordered with the proximal facet. The posterior one is larger, pocket-shaped, facing medially, while the anterior one is smaller, facing medially and upward (Pl. XIII 1b). On proximal end of the lateral side there is only one small facet articulating with McV ((Pl. XIII 1a mcV). It is bean-shaped, extending posteriorly and slightly downward. Below this facet is a long deep groove, extending to the middle of the shaft, and bordered by prominent and roughened ridges bilaterally (Pl. XIII 1a x). The cross section of the shaft is triangular in outline, with that of the lower part clockwise turned relative to the upper part of the shaft. The distal articular trochlea is elongated in anteroposterior direction, with its middle ridge occupying the posterior 2/3 of the facet, and the anterior 1/3 of the facet being hemispherical. The ridge is bordered by a pair of grooves deepening posteriorly, especially the lateral groove. A pair of deep fossae are present on both medial and lateral sides of the distal end, and above the fossae are a pair of tuberosities. Both fossae and tuberosities serve as the places for attachment of collateral ligaments of the fetlock joint.

In *Hyrachyus eximius* the proximal end of the McIV is higher at the lateral border than at the medial border, and the facet in general is at the same level as that of the McIII. As the McIII, the McIV of *Triplopus cubitalis* is also proportionally longer than that in *Juxia*, and its distal end presses close to McIII without divergence from it. The middle ridge of the distal trochlea is short, restricted in the posterior half of the facet, thus invisible from front. Although in proportion the McIV of *Hyracodon nebraskensis* is close to that of *Juxia*, the morphology of the distal half of the bone is rather close to that of *Triplopus* than to *Juxia*.

In all the rhinocerotids the McIV is less reduced relative to the McIII than in *Juxia*. It is proportionally shorter and broader, with the proximal facet articulating with the McV becoming reduced, and the middle ridge of the distal trochlea becoming shorter, restricted to the posterior half of the trochlea, bordered by shallow grooves bilaterally. These features can be seen even in the earliest (*Teletaceras radinskyi*) and early forms of rhinocerotids (*Trigonias osborni*, *Subhyracodon occidentalis*).

In large-sized paraceratheres the McIV is more reduced relative to McIII than in *Juxia*, with its Max W being less than 1/2 of that of McIII (>1/2 in *Juxia*). Its proximal articular facet becomes concave in both directions rather than saddle-shaped, its articulation with the McIII is only by an anterior facet, and the facet articulating with the McV becoming shifted on volar side, or completely lost.

7) Reconstruction of carpal and metacarpal parts (Pl. XIII 3, Fig. 23): The Plate XIII 3 is the reconstructed carpal and metacarpal bones of *Juxia sharamurenensis* in their dorsal view (pisiform and trapezoid can not be seen) based on available material. The reconstructed parts are marked by the letter x. Although invisible in reconstruction, the general form of the pisiform and trapezium can partly be deduced based on the neighboring bones. The pisiform must be considerably large judging by the large facets on ulna and cuneiform, while the trapezium should be quite small and shifted on the volar side based on the small facet on the volar side of the scaphoid.

A few words should be said about the McV of *Juxia*. While studying the McIV of *Teletaceras radinskyi*, Hanson (1989) pointed out that the presence or absence of a McV could be deduced from the morphology of the proximal end of the McIV. According to him, if the proximal end of McIV is higher at lateral side than at medial side, no McV should be present, or vice versa. Our comparative study of the McIV and unciforms in tetradactyl *Plesiaceratherium gracile* and tridactyl living form (*Rhinoceros unicornis*) does not substantiate Hanson's hypothesis. In *Plesiaceratherium gracile* the facets articulating with McV on both unciform and McIV are very wide (but restricted in anterior halves of these bones), and on the lateral side of the McIV below the proximal facet for the McV is a long groove bordered by prominent ridges bilaterally. These are the signs of the contact of the McIV with the rather long McV (Fig. 23 A–B). On the other hand, in *Rhinoceros unicornis* both the facets articulating with the McV are highly reduced, and there is no long groove below the proximal facet articulating with the McV on the lateral side of the McIV (Fig. 23 E–F). In both characters, the large size of the facets on McIV and the unciform and the presence of the groove and ridges on McIV, *Juxia* is close to those of the tetradactyl rhinoceros (Fig. 23 C−D). Therefore, *Juxia* should have a fully developed McV, though the smallest among the metacarpals. This tends to show that the orientation of the proximal facet of McIV seems irrelevant to the presence or absence of the McV.

The carpal and metacarpal bones of *Juxia sharamurenensis* can thus be characterized as follows: Both carpus and metacarpus are very high. Taken as a whole, the carpal bones form a rectangle in dorsal view, but almost each bone, with the exception of pisiform and probably trapezium, is higher than wide. The trapezium is shifted backward to the volar side of the carpus. The distolateral process of the scaphoid is not strongly protruded. The distal end of the lunar is asymmetrical, mainly resting on the unciform. The ulnar elements of the carpus, cuneiform and unciform, are narrow and high. The proximal and distal rows of the carpal bones are deeply interlocking between themselves. The metacarpus is tetradactyl. McIII serves as the axis relative to McII and McIV, with a wide facet articulating with unciform, the narrowest part being situated immediately below the proximal end. McII and McIV are slender relative to McIII, with their distal ends diverging from the McIII. The proximal end of McII is situated much higher than that of McIII, which overlaps the McIV considerably. McV is the smallest and shortest among the metacarpals, but still quite long, probably longer than half length of McIV and with phalanges of its own. By theses characters *Juxia* is readily distinguished from any other rhinoceroses.

8) Phalanges

It is difficult to separate the phalanges of the anterior limb (fingers) from those of the posterior limb (toes), except for the first phalanges; neither the phalanges of the second finger or toe from those of fourth finger, except those of the fourth toe, which are the largest among the lateral phalanges. All the phalanges are dealt with here together, irrespective of whether they belong to fingers or toes.

PhI of middle digit (Pl. XIV 1−2, Tabs. 19−20): V 2891.7 is tentatively assigned to PhI of middle finger, while V 2891 to PhI of middle toe. Based on the assumption that the medial half is stouter than the lateral half in the phalanges of the middle digit, V 2891.7 is considered here as a left PhI, while V 2891 is a right one.

The proximal end of the PhI of middle toe (V 2891) is much thicker (APD) than its distal end (Pl. XIV 2a). The proximal articular facet (Pl. XIV 2b) is oval in outline, with a shallow indent at the middle of the volar side. The surface is concave deeply longitudinally, but weakly transversely, with the sagittal groove reaching almost to the dorsal margin. The distal articular facet (Pl. XIV 2c) is not perpendicular to the long axis of the phalanx, but faces downward and posteriorly. Its dorsal border is more or less straight, but its volar border concave. It is weakly separated into two convex parts by a shallow and wide sagittal depression. On dorsal side of the phalanx a V-shaped roughened prominence (Pl. XIV 1b $_v$) is situated slightly above the middle of the phalanx. Below it is a large depression (Pl. XIV 1b $_d$). Immediately above the distal end and below the above depression a smooth band (Pl. XIV 1b $_f$) can be observed, which was termed by Gromova (1959) as a "pseudo-articular facet." An elongated groove is present on each of the medial and lateral sides slightly above the distal end of the phalanx, and above the fossa is a weakly prominent rough area of irregular form, both of which are for the insertion of collateral ligaments of pastern joint. On the volar side of the phalanx, immediately below the middle indent is a shallow concavity bordered below by a V-shaped rugose ridge (Pl. XIV 1a $_c$), where ligamenta sesamoidea cruciata are attached (Camp and Smith, 1942). Bilateral to this V-shaped ridge is a pair of tuberosities called proximal prominences by Camp and Smith in 1942 (Pl. XIV 1a $_t$). However, no V-scar so characteristic in advanced equids is developed. A pair of large depressions is present on both sides slightly above the distal end of the phalanx. This depression is composed of two parts: the upper one is larger and deeper, making the lateral border of the phalanx laterally bulging; and the lower is smaller and shallower, situated immediately above the distal articular facet (Pl. XIV 1a $_{1-2}$).

The PhI of the middle finger as defined by us (V 2891. 7) differs from that of the toe in having a rounded and roughened area instead of a V-shaped ridge on dorsal side, a shallower depression below this roughened area and less clearly expressed "pseudo-articular facet" at the distal end of the anterior side of the phalanx.

Except for that of *Triplopus cubitalis*, the PhI of middle finger of *Juxia sharamurenensis* is the most slender one among all the rhinocerotoids so far known, including *Hyracodon nebraskensis*. In *Hyrachyus eximius* the PhI of middle toe is known. Its H/W ratio is 113.6%, close to that of *Juxia* (118.9%), but smaller than that of *Triplopus cubitalis* (125%). In all other rhinocerotoids so far known the H/W ratios of PhI of middle fingers or toes are less than 100%, i. e., wider than high (Tab. 20). In *Hyracodon nebraskensis* it is 90%. The deep sagittal groove of the proximal articular facet of PhI in *Juxia* is also unique among the rhinocerotoids where this groove remains markedly shallow and short.

The PhI in large-sized paraceratheres is so flattened that it becomes dish-like. The distinction between it and that of *Juxia* is so obvious that further comparison is unnecessary.

PhII of middle digit (Pl. XIV 1, 3; Tabs. 19 – 20): There are altogether four specimens, three of which are complete.

The bone is short and wide. It is about half the height of the PhI. The proximal articular facet (Pl. XIV 3b) is inversely corresponding to the distal articular facet of the PhI, with a middle longitudinal ridge and bilaterally situated depressions. Seen from lateral side, the proximal surface forms an ~70° angle with the axis of the PhII. The distal articular facet (Pl. XIV 3c) is large and trapezoid in outline, with its volar side being wider than its dorsal one. The surface is convex longitudinally, with a sagittal depression. A considerable part of the surface turns onto the volar side of the bone, so that, seen from lateral side, the distal end of the bone forms a semicircle. The dorsal surface of the bone is rather flat, with an upward bulge at the middle of the proximal border. On volar side, immediately below the proximal facet the bone is bulged and roughened (Pl. XIV 1a), being the place for attachment of the ligamentum sesamoideum rectum through the fibrocartilaginous plate (Camp and Smith, 1942). On distal end of the volar side a pair of small facets is formed (Pl. XIV 1a x), joining the back part of the distal articular facet. On proximal part of the lateral side there is a roughenend area for attachment of the ligamenta collateralia of pastern and M. flexor digitalis superficialis (Pl. XIV 3a).

In all the other rhinocerotoids the PhII of middle finger or toe is wider than long as in *Juxia*. The PhII in *Hyrachyus*, *Triplopus* and *Hyracodon* are proportionally higher (Tab. 20). The sagittal bulge on the proximal border of the PhII so clearly expressed in *Juxia* may be a distinctive character differing from the other members of the rhinocerotoids. As the PhI, the dish-like PhII in large-sized paraceratheres is so peculiar that a comparison with it seems superfluous.

PhIII of middle digit (Pl. XIV 1, 4; Fig. 24; Tabs. 19 – 20): There are only two specimens, one of which is complete.

The bone roughly takes the form of a trowel, broader than high, with its dorsal surface being convex, and volar surface roughly flat. The proximal articular facet is bean-shaped in outline, with its relief inversely corresponding to that of the distal end of PhII. The facet is perpendicular to the vertical axis of the bone. On its volar border there is a narrow strip of smooth area (Pl. XIV 4 y), where the distal sesamoid bone is to be placed. Its anterior border is weakly convex, without forming a clear extensor process. On dorsal side, below the proximal end, there is a clear depression (Pl. XIV 1b e), serving apparently as the place for attachment of the m. extensor digitalis communis. The dorsal surface, especially its lower half, is covered by numerous irregular grooves radiating distally. The distal margin is thin, forming an irregularly serrated arcuated ridge with a deep and wide sagittal notch. The angles (anguli soleae) are bifid, separated by an intermediate notch.

The proximal angle is wider longitudinally (Fig. 24 A 3), but shorter than the distal one, which is pointed at the end (Fig. 24 A – B 9). The intermediate notch extends mesially, forming the weakly expressed dorsal sulcus (Fig. 24 A 2). At both ends of the sulcus a foramen can be seen. On volar side, the paired volar foramina are present under the two extremities of the proximal articular facet (Fig. 24 B 6). The semilunar crest is weak (Fig. 24 B 8), but the sagittal prominence of the flexor surface is not clearly shown. Neither the volar sulcus (Fig. 24 B 5) linking the volar foramen nor the intermediate notch is clearly represented.

In most forms of the Hyrachyinae and Hyracodontinae, the PhIII of middle digit is higher than wide, or, at most, equally high and wide (in *Hyrachyus eximius*). In morphology they are also different from that of *Juxia*. In *Hyrachyus eximius* the distal margin of the PhIII is angled in shape, without sagittal notch on distal edge, and the dorsal sulcus and foramina are not developed at all. In *Triplopus cubitalis* the PhIII has a sagittal notch, but the PhIII is the longest among the rhinocerotoids. Its height is 2.5 times greater than width. In primitive rhinocerotids the PhIII is similar to that of *Juxia* in shape and H/W ratio, but with evidently little developed sagittal notch. In later rhinocerotids and living rhinos the PhIII of middle digit is sharply distinguished from that of *Juxia* in size, form and proportion. It is very much broadened and low, with its anguli soleae undivided, turning upward and backward, but without sagittal notch on distal margin.

In large-sized paraceratheres the PhIII is not only very wide and low, but very thick (APD). Its width is twice greater than height, which is about equal to thickness. Furthermore, there is a large and clear proximal prominence, but no distal sagittal notch, or the notch transformed into a wide concave curve. The proximal angle is scarcely developed, while the distal angle (sole angle) is usually very long.

Altogether fifteen phalanges of lateral digits are preserved in the IVPP collection. Since these bones are less diagnostic than those of middle digits, they will be briefly described below, without trying to find out which finger or toe they belong.

PhI of lateral digits (Pl. XIV 5 – 6; Tabs. 21, 23): Altogether there are seven specimens. The bone takes the form of an asymmetrical prism, with its mesial side being slightly shorter. Its proximal facet (Pl. XIV 6a) is perpendicular to the anterior border of the phalanx. The facet is spherically concave, with a middle longitudinal groove reaching scarcely to the dorsal margin and ending at the volar margin by a shallow notch. The distal facet (Pl. XIV 6d) is not perpendicular to the shaft, facing downward and posteriorly. It is irregularly saddle-shaped, slightly concave transversely and convex longitudinally. At the lower end of the dorsal side a smooth "pseudo-articular facet" is formed (Pl. XIV 5a f). At the proximal end of the volar side a pair of prominent tuberosities are developed bilaterally. The fossae on the distal ends of both the mesial and lateral sides are very deep. The scars for the attachment of the tendon of flexor muscles are located immediately above the distal margin of the phalanx.

PhII of lateral digits (Pl. XIV 5, 7, 9; Tabs. 21, 23): Altogether six specimens are found. They are cubic in form. The extensor process is well developed at the proximal end of dorsal side. The distal facet is large, trochlear in shape: strongly convex longitudinally with a deep middle groove. The volar border of the distal facet is considerably higher than its dorsal one. A "pseudo-facet" is developed at the distal end of the dorsal side. The fossae at the distal ends of the mesial and lateral sides are as in PhI, very deep.

PhIII of lateral digits (Pl. XIV 5, 8, 9; Tabs. 22 – 23): Altogether two PhIII's are preserved. The bone is asymmetrical. Its proximal facet inversely corresponds to the distal one of the PhII, but with a rhomboid facet where distal sesamoid is to be placed. The extensor process at the middle of the dorsal border of the proximal facet is prominent. A triangular depression is present below the extensor process. The dorsal surface is covered with longitudinal fine grooves and foramina. The dorsal sulcus is short and ended with foramina. The middle notch at the distal margin is very deep, almost reaching to the depression below the extensor process. The sole angle on the mesial side is highly reduced, but the lateral angle is subdivided. The proximal part is scarcely developed, but the distal one is long and pointed. The volar surface is more convex than in the PhIII of middle digit, with a pair of clearly shown volar foramina.

All the phalanges of lateral digits of rhinocerotoids, including *Juxia*, are quite similar in morphology. They differ from each other mainly in size and proportion (Tab. 23). Generally speaking, the phalanges of lateral digits in Hyrachyinae and Hyracodontinae are smaller and more slender. In rhinocerotids these phalanges are generally lower and more robust.

The differences of these phalanges between *Juxia* and large-sized paraceratheres seem to be more obvious than those between *Juxia* and other rhinocerotoids. The cross section of the PhI of lateral digit in large-sized paraceratheres is triangular instead of rectangular as in *Juxia*. Its distal surface is so strongly slanting that it forms a continuous line with the volar side of the bone, seen laterally. All the articular facets of the phalanges are weakly concave or convex. The sole angle on mesial side is well developed, and the angle on lateral side is particularly long.

(8) Hindlimb

1) Innominate bones (Pl. XV 1, Tab. 24): The pair of the innominate bones are tightly coalesced and well preserved in the holotype. The bones, especially their anterior parts (ilia), were subjected to vertical compression, and therefore appear to be somewhat flattened.

The wing of ilium is roughly fan-shaped and the body is trihedral. The greater sciatic notch (the mesial border of the wing and body) is very deep, with a swelling in the middle, representing the upper end of the auricular surface on the mesial side of the wing. The crest of ilium (anterosuperior border of the wing) is nearly straight, only slightly concave near the sacral tuber. The lateral border of the wing and body is also deeply concave. The sacral tuberosity is broad, thickened, with rough dorsal surface. The coxal tuberosity is very large and long, about half as long as the ilium crest, with its lateral surface being roughened, forming an angle of about 120° with the ilium crest. An additional tubercle is formed on its posteroventral side. The external or gluteal surface is smooth and slightly concave, with the gluteal line (Pl. XV 1 g) being indistinct and situated more laterally. The internal or pelvic surface is convex, with a large and very rough auricular surface on its lower part. The body of ilium is short and broad, with its cross section being wider than thick. The psoas tubercle is located in the middle of the body. The two scars for the tendon of the m. rectus femoris (of the m. quadriceps femoris) are located close to the dorsal side of the acetabulum.

The body of ischium is irregularly quadrangular in shape, longer than wide, and its anterior border being the posterior border of the obturator foramen. The lateral border of the body is thick and slightly concave; the mesial side is thin and connected with its counterpart in their anterior halves. The posterior halves of the two bodies diverge apart, forming a wide and deep ischiadic arch. The pelvic surface slopes strongly toward the symphysis, probably due partly to compression. The anterior part of the ischiadic spine is sharp-edged, followed by a deep notch (Pl. XV 1 x), then becoming blunt.

The transverse part of the pubis is columnar, roughened on its anterior side, but becoming thin on its posterior border to form the obturator foramen. The pectineal eminence (eminentia iliopectinea) is present, but unimportant. The pelvic surface is flat or even slightly concave in posterior part. The ventral surface is convex in sagittal part.

The acetabulum is rather anteriorly situated so that the anterior rim of the pubis is located behind the anterior border of the acetabulum (Pl. XV 1). The acetabulum is a hemispherical cavity. The acetabular notch is narrow, almost closed at the border of the acetabulum. The obturator foramen is elliptical in form, nearly twice as long as wide. The long axis runs nearly in anteroposterior direction.

In general morphology the ilium of *Hyrachyus eximius* is very close to that of *Juxia*. However, it differs from the latter in being longer so that the acetabulum is situated in the posterior part of the innominate bone instead of being at about the middle of this bone as in *Juxia*. The ilium of *Hyrachyus eximius* is rather triradiate. The sacral and coxal tuberosities are supported each by a "handle," and the crest of ilium is concave rather than straight. The innominate bone of *Hyracodon nebraskensis* is poorly known. According to Scott (1986), the body of ilium may be longer and the obturator foramen larger than in *Juxia*.

The innominate bones in some primitive rhinocerotids, such as *Trigonias osborni*, are readily distinguished from that of *Juxia*. The wing of ilium in these forms is much widened, with its crest being convex. Furthermore, as can be judged from the figures (Scott, 1941, Pl. LXXXIII 8), the ischia do not unite with each other in ventral parts at all, and the pubis symphysis forms a ridge on ventral side and a tubercle on anterior border. Some other primitive rhinocerotids, such as *Subhyracodon occidentalis*, may have their innominate bones very similar to that of *Juxia*. However, their ilium bodies are longer and the coxal tuberosities are even larger than in *Juxia*. In later rhinocerotids and living rhinos the innominate bones are quite different from that of *Juxia* in general morphology. They are generally much broadened and shortened. The ilium is short and the crest is always convex so that the ilium takes the form of a very much widened fan. The ischium and pubis are proportionally short, the acetabulum is comparatively large, situated in the posterior part of the innominate bone, and the obturator foramen is almost round.

So far the innominate bones of the large-sized paraceratheres have been little known. Borissiak (1923b) briefly described a right innominate bone, mostly restored with plaster and badly deformed. Even so it shows some features similar to those of *Juxia*, especially in the form of ilium, such as the strongly concave lateral border, the presence of a swelling at the middle of the sciatic notch, the ilium crest with a shallow concavity near the sacral tuber, and the broad and short ilium body. *Paraceratherium asiaticum* differs from *Juxia* in such aspects, as the ilium crest being more or less convex, the ischium and pubis being comparatively short, and the shorter obturator foramen. The ilium of *P. grangeri* reconstructed by Granger and Gregory (1936, Fig. 47) is rather misleading. The restoration of the extremely strong convexity of the ilium crest seems to be groundless.

2) Femur (Pls. XV 2, XVI 1; Tab. 25): The femora of both sides are well preserved in the holotype, though partly compressed, especially at the ends.

The bone is long and slender, but only slightly longer than tibia. The shaft is more or less cylindrical in middle part, broadly convex in front and rather flat on posterior side. The shaft is flattened proximally and becomes thicker toward the distal end. The posterior side is flat on the upper half, with broad and deep trochanteric fossa, which extends downward to the level of the lower border of the lesser trochanter. The supracondyloid fossa (Pl. XVI 1a f) is not very large and deep, situated at the lateral side of the posterior side, above the lateral epicondyle. The surface medial to the fossa is rough, where m. gastrocnemius should attach (Pl. XVI 1a g). The medial side of the shaft bears the lesser trochanter, beginning ~60 mm below the caput, extending downward and ended at the level slightly above the upper border of the 3rd trochanter. The third trochanter is situated slightly above the middle of the shaft. It is prominent, extending laterally and turning anteriorly at its end. The posterior side of the third trochanter is rough.

Both capita of the two femora are slightly compressed. Their original form must be spherical. The caput stretches medially and upward. The fovea of caput (Pls. XV 2b c, XVI 1a c) is large, situated in the middle of the posterior side of the caput. The caput is well demarcated all around, so that the neck is distinctly shown. The greater trochanter is well developed, but not clearly divided. Its anterolateral part (Pl. XV 2a lt) is slightly lower than the caput, with a large triangular rough area at its end, whereas the posterior part (Pl. XVI 1a pt) is slightly higher than the caput.

The trochlea of the distal end for lodging the patella is long (high) and narrow, wider in upper part than in lower part. The lateral ridge is slightly shorter (APD) but stronger, and more obliquely situated than the medial ridge is. The medial ridge is longitudinally more convex than the lateral ridge. Its upper end constitutes the most prominent part of the trochlea and is situated higher than the lateral ridge. The intermediate groove is rather deep. The depression above the trochlea is prominent. The lateral condyle is slightly larger than the medial one. Its linkage with the trochlea is largely interrupted by the triangular fossa extensoria (Pl. XVI 1b $_e$). The intercondyloid fossa is narrow and deep. Both epicondyles are relatively small, the lateral one being even smaller.

The femur of *Hyrachyus eximius* resembles that of *Juxia* in general proportion and morphology. However, it differs from the latter in having a much higher greater trochanter (higher than caput), the more prominent lesser trochanter, and the higher position of the third trochanter (Osborn, 1929b, Fig. 681 A). The femur of *Hyracodon nebraskensis* is even more similar to that of *Juxia* in the upper half of the bone, but differs more markedly in distal end. According to Scott (1941, p. 838), the depression above the trochlea is very deep and greatly expanded upward, but the trochlea itself is wide, rather flattened, with both ridges being almost equally developed.

In primitive rhinocerotids, such as *Trigonias osborni* and *Subhyracodon occidentalis*, the femora became much thicker and shorter. Their lengths are only about three times greater than their widths (Tab. 25). According to Scott (1941, p. 784), the caput of the femur in *T. osborni* is higher than the greater trochanter, and the lateral epicondyle is very large, and laterally widened. The femur of *Allacerops turgaica* resembles that of *Juxia* in general, but the trochlea is much broader and low.

The femora in later rhinocerotids and living rhinos have quite different form compared with that of *Juxia*. They are much shorter, but are the longest among the long bones. The shaft is flat, especially in proximal part. The greater trochanter is lower than the caput, and the caput fovea is small but deep. The third trochanter is very large, curved forward, and situated rather low, at the middle of the shaft. There is no distinct supracondyloid fossa on the distal end of the posterior side. The distal end is about equally wide and thick. The trochlea is low and broad, and the condyles shorter.

The femur in large-sized paraceratheres is widely different from that of *Juxia* in morphology. In the former group the neck of the femur is scarcely demarcated from the caput, which faces almost directly upward. The greater trochanter is lower than the caput, scarcely extending posteriorly. Both the lesser and the third trochanters are highly reduced. The trochlea of the distal end is proportionally lower and wider.

3) **Patella** (Pl. XV 3, Tab. 26): There are three specimens, all well preserved.

The bone is rather irregular in shape, slightly higher than wide. The middle part of the lateral side is rather straight, almost vertical, but the lower part is concave, whereas the medial side is irregular, the middle being a pointed angle, the upper part weakly concave and the lower part convex. The proxiaml side is concave at the middle. The anterior surface is rough and strongly convex. An elongate depressed area is present on the medial part of lower end on the anterior side, apparently for the attachment of the middle patellar ligament. The posterior surface articulating with the trochlea of the femur is narrower than the total width of the patella, leaving a large non-articular area on the medial side. The articular surface is divided by a blunt longitudinal ridge into two areas: a smaller lateral and a larger medial area, the medial one being more concave than the lateral one. The proximal border or basis of the patella is irregular in shape, with a strip-like concave area for the attachment of the m. quadriceps femoris.

The patella is rarely described in detail in literature. Judging from the figures (Cope, 1884, Pl. LIV), the patella of *Hyrachyus eximius* differs from that of *Juxia* sharply. It is very thick (APD) proximally, but thin distally. According to Scott, the patella of *Hyracodon nebraskensis* is small and thin, oval in outline, with low and wide middle ridge on the posterior articular surface. The patella of *Trigonias osborni* may be more or less of the rhino-type. It is wider than high. In later rhinocerotids and living rhinos the patella differs from that of *Juxia* in being rhomboid in shape, wider than high, with an enlarged medial angle where the patellar fibrocartilage is to be attached, and the proximal border (basis) being very thick with large surface for attachment of the m. quadriceps femoris.

In large-sized paraceratheres the patella is quite similar to that of *Juxia* in proportion. The differences between them are mainly expressed in the configuration. In *Paraceratherium asiaticum* the lateral side of the patella is straighter, whereas the medial one is strongly bulged, resulting in greater degree of asymmetry. The patella of *Aralotherium prohorovi* is even more asymmetrical, taking the form of a triangle, with its lateral border being weakly concave.

4) Tibia (Pl. XVI 2–3, Fig. 25, Tab. 27): In addition to the pair of tibiae of the holotype, there are three other fragments (V 2891.7).

The bone is long and slightly twisted, seen from the front or back. The tibial crest occupies the upper third of the shaft on the anterior surface, ending by a low ridge-like tubercle at its lower end, but an enlarged tibial tuberosity at the upper end. The tibial tuberosity is excavated by a long and deep pocket-shaped groove in its middle. Below the tibial tuberosity the crest is sharp, with a rough surface on its medial side for the attachment of the semitendinous muscle. The proximal part of the medial side is broad and rough, smooth in the middle and distal parts. The groove for the deep digital flexor extends obliquely, in the direction from behind downward and anteriorly. The lateral side is smooth and broad in proximal part, forming deep groove lateral to the tibial crest. In the posterosuperior corner of the lateral side, the facet articulating with the fibula is located underneath the proximal surface. A triangular rough area for coalescence with the fibula is located in the distal part of the lateral side. The proximal part of the posterior side is deeply excavated, widened near the proximal end. The popliteal lines are not very marked as usual. The posterior side of the shaft is clearly separated from the lateral one by a ridge leading from proximal end downward and forward, making the shaft twisted.

The proximal extremity of the bone is large, thicker than broad. The medial condyle is flat, oval in outline, with a rough area on its medioposterior side. The lateral condyle is lower in position than the medial one, and its posterior side extending farther backward and downward. The intercondyloid eminences are very high, with the lateral one being higher and longer than the medial one. The intercondyloid fossa is narrow. The extension of the lateral articular surface on the lateral intercondyloid eminence is large and steep, with its anterior surface facing laterally and the posterior surface backward. In front of the intercondyloid eminences, a pair of small pits is present on each side, apparently for the attachment of the tendon of cruciate ligament and meniscus.

The distal end is relatively small. Its cross section is trapezoid in shape, with a shorter posterior side. On distal side the ridge and grooves of the trochlea are prominent and directed obliquely forward and laterally. The medial groove is longer than the lateral one, but the two are of the same breadth and depth. The medial malleolus develops only in the anterior part, with the groove for long digital flexor across its middle of the medial side. There is a small smooth facet on the lateral side to articulate with the fibula. The medioposterior angle is large and projecting.

The tibia of *Hyrachyus eximius* is comparatively thick and short (Tab. 27). The proximal end is wider than thick, with both of medial and lateral condyles being wider. The intercondyloid eminences are low, and the medial malleolus extended stronger medially. The tibia of *Hyracodon nebraskensis* is very similar to that of *Juxia* in general proportion. It differs from the latter more markedly in the distal articular facet. The grooves are very narrow and deep, markedly oblique in direction.

In the early rhinocerotids, such as *Trigonias osborni* and *Subhyracodon occidentalis*, the tibiae became proportionally thicker and shorter. The width of the proximal end reaches to ~1/3 of the total lengths of the tibiae (~1/4 in *Juxia*). Otherwise they are quite similar to that of *Juxia*. In later rhinocerotids and living rhinos the tibiae are even thicker and shorter than those of the primitive rhinocerotids. The widths of the proximal ends reach ~2/5 of the total lengths of the tibiae. Furthermore, the medial condyle of the proximal end is much larger than the lateral one; the medial and lateral intercondyloid eminences are either equally large, or the medial one is larger than the lateral one; the tibial tuberosity is very voluminous; the tibial crest is less elevated, but longer extended downward. The distal articular facet is very broad, with asymmetrical grooves and low middle ridge. The medial malleolus is longer in anteroposterior direction, pushing the groove for the long digital flexor backward.

In large-sized paraceratheres the tibiae also became short and thick, but the extremities are not much widened than the shaft, and the whole tibia is pillar-like. The articular facets of the proximal end are dish-shaped, with low intercondyloid eminences and shallow intercondyloid groove. The tibial crest is thin, but extends to the distal end of the bone. The distal articular facet is very wide. The grooves are very shallow and the middle ridge is very broad and low.

5) Fibula (Pl. XVI 4, Fig. 25 B, Tab. 28): Both fibulae are preserved in the holotype. The left one is complete, but the right one is broken distally.

The shaft is slender and twisted. Its middle part is rod-like, but flattened both proximally and distally. The proximal end is thin and plate-like, with its lateral side being rough and convex, and the medial side vermiculated, where coalescence between tibia and fibula occurred. The medial side of the shaft narrows downward and turns backward to the posterior side. The distal end is narrower in anteroposterior direction than the proximal one, but thicker transversely. On its medial side, above the malleolus is a rough surface coalescing with tibia. The lateral side is rough and convex, without clear indication of the groove for m. extensor digitalis lateralis. The lower part of the distal end forms the lateral malleolus, which bears three small articular facets. The anterosuperior facet articulating with tibia is small and strip-like, facing medially and upward; the facet articulating with the astragalus is situated inferoposterior to the former facet; and the facet articulating with the calcaneus faces downward, and not clearly marked off from the other facets (Fig. 25 B 3-4).

The fibula of *Hyrachyus eximius* was very briefly described by Cope. Judging from his figures (Cope, 1884, Pls. LIV, LV 6), the fibula of that species is very close to that of *Juxia* in morphology. Its shaft is slender, with its proximal end anteroposteriorly expanded and its distal malleolus large. According to Scott (1896), the degree of reduction of the fibula in *Hyracodon nebraskensis* is about the same as in *Juxia*. The only possible difference between them may be the presence of a groove for the m. extensor digitalis lateralis on the posterior end of the lateral malleolus in *H. nebraskensis* (indistinct in *Juxia*). The lateral malleoli in *Trigonias osborni* and *Subhyracodon occidentalis*, according to Scott (1941), are very large, with clear grooves for the m. extensor digitalis lateralis at the middle. In later rhinocerotids and living rhinos the fibulae are decidedly stouter, with enlarged extremities.

The fibulae in large-sized paraceratheres are little known. In *Paraceratherium asiaticum* the fibula is probably as slender as that of *Juxia*, but its proximal end may be more reduced and the broadened part of the distal end may extend more upward (Borissiak, 1923b, Pl. VII 1). In *Aralotherium prohorovi* the proximal end is markedly smaller than the distal one (Tab. 28). Gromova also mentioned that there is a distal facet articulating with calcaneus, a character found in *Juxia*, but not in other rhinocerotids.

6) Tarsals

Astragalus (Pls. XVII 1-2, XVIII 5; Fig. 26; Tab. 29): No astragalus is preserved in the holotype, but two complete and three broken ones are available (V2891.3, V2891.7).

The astragalus is high and narrow, with its trochlea occupying most of the proximal and dorsal surfaces. The trochlea is high and oblique, higher than wide. The obliquity angle of the trochlea relative to the base of the astragalus (α) is 115°, while the torsion angle (β) is about 20° (Fig. 26). The medial and lateral ridges of the trochlea are elevated high relative to the deep intermediate groove. Both ridges are transversely asymmetrical, with their mesial slopes less steep than their lateral ones, but the lateral ridge is more asymmetrical than the medial one. Longitudinally, the curvature of the two ridges is about the same, forming a semicircle. The boundary between the trochlea and the neck of the astragalus is not clearly defined. On plantar side there are three facets articulating with the calcaneus. The one articulating with the cochlear processes (Pl. XVII 1b 1) is the largest and situated on the superolateral corner of the plantar side. It is vertically concave, higher than broad, with a small extension at its distolateral side. The medial one articulating with the sustentacular process is elongated, kidney-shaped, nearly flat, or slightly convex, with its convex medial border nearing the medial border of the astragalus. The third one is a small, elongated arc at the inferolateral corner of the plantar side. The interspace between these facets is rough, unarticulated area. On the superomedial corner of the plantar side a well developed tuberosity is developed for the ligament attachment.

The distal side is composed of two articular facets. The medial one articulating with the navicular is very large, trapezoid in outline, saddle in form, convex in anteroposterior direction, weakly concave transversely. Lateral to it is the small narrow facet articulating the cuboid.

The astragali in Hyrachyinae and Hyracodontinae are generally very high and narrow (Tab. 29). The differences between the astragali of *Hyrachyus eximius* and *Juxia* are as follows. 1) In the former the neck of the astragalus is clearly shown and higher than in the latter. 2) The ridges of the trochlea are sharper, and the medial ridge is higher than the lateral one. 3) The tuberosity situated at the distal end of the medial side is very prominent. The astragalus of *Hyracodon nebraskensis* is very similar to that of *Hyrachyus eximius*. However, in the former species, the sustentacular facet and the distolateral one form a united L-shaped facet. Furthermore, the distal facet articulating with the cuboid may be particularly small and posteriorly shifted so that the calcaneus seems to be connected only with the navicular, seen from the front.

The astragali in primitive rhinocerotids are close to that of *Juxia* in morphology. However, they differ from that of *Juxia* in having sharper ridges and the wider distal facet articulating with the cuboid, clearly seen from the front. The astragali in later rhinocerotids and living rhinos are much wider than high; the trochleae are not so obviously oblique relative to the bases of astragali; the trochleae are more asymmetrical in form, with very shallow intermediate grooves, the two ridges being more unequally developed; the cochlear facets are flatter, and the other two plantar facets are often united and L-shaped.

The astragali in large-sized paraceratheres are comparatively better studied. The differences from that of *Juxia* may be summarized as follows. 1) They are all much wider than high. 2) The obliquity of the trochleae relative to the bases of astragali is less, almost perpendicular to each other. The surface of the trochleae is less convex-concave in relief, and the two ridges are more asymmetrical in form. 3) The tuberosity situated at the distal end of the medial side of the astragalus is highly reduced. 4) On the plantar side the cochlear facet is much more widened, and the sustentacular facet is laterally shifted so that it does not form the medial border of the astragalus. 5) The distal facet articulating with the cuboid is very wide so that the articulation can be clearly seen from the front. According to Gromova (1959), the astragalus of *Aralotherium prohorovi* is more specialized than those of *Paraceratherium*. It is still lower and broader, with the lateral part of the trochlea widely protruded relative to the base of the astragalus. The ridges are low and the intermediate groove is shallow, etc.

Calcaneus (Pl. XVII 3): There is only a distal part of left calcaneus preserved (V 2891.4).

The part of calcaneus lower than the cochlear process is rather long, with the sustentacular process being less medially projected. Seen from the front, the three facets articulating with the astragalus are of the same forms as the corresponding facets of the astragalus, but with an additional small facet at the superomedial border of the sustentacular facet. In medial view the sustentacular process is very thick on the anterosuperior end, thinning down posteroinferiorly. At the posterolateral corner of the cochlear processes there is a small pit, articulating with the corresponding facet on the distal end of the fibula. The facet articulating with the cuboid is wide, forming an angle slightly smaller than 90° with the dorsal surface of the body of calcaneus.

The calcaneus of *Hyrachyus eximius* differs from that of *Juxia* clearly by two characters: the vertical groove bordered bilaterally by ridges on plantar surface in the lower half of the bone; and the lower positioned sustentacular process which tapers laterally so that the process becomes fan-shaped seen from behind. The calcaneus of *Hyracodon nebraskensis* may be quite close to that of *Juxia*, especially in the lengthening of the distal part of the bone as a whole, and of the sustentacular facet in particular. However, it is reported that there is a distal facet articulating with the navicular, a character uncommon among the rhinocerotoids (Scott, 1896, p. 377). The calcanei in primitive rhinocerotids, such as *Trigonias osborni* and *Subhyracodon occidentalis*, have their distal halves shortened relative to proximal halves, and the L-shaped facet formed by the united sustentacular and distolateral facets. In later rhinocerotids and living rhinos the above listed characters for *T. osborni* and *S. occidentalis* evolve further along the same direction. The calcanei of large-sized paraceratheres show some similarities with that of *Juxia*, as the presence of a facet articulating with the fibula, the presence of three facets articulating with the astragalus, etc. However, the three facets articulating with the astragalus in the former group are all wider than high, and the tongue-shaped facet annexed to the distolateral corner of the cochlear facet is elongated. Furthermore, there is a facet articulating with the tibia on the upper side of the cochlear process. *Aralotherium prohorovi* differs further by having more specialized characters, like the blunt-edged separation between the upper (articulating with tibia) and lower (articulating with astragalus) facets on the cochlear process, and the strong obliquity of the distal facet articulating with the cuboid, as indicated by Gromova (1959).

Navicular (Pls. XVII 4, XVIII 5; Tab. 30): Three specimens are preserved (V 2891, V 2891.7).

It is about equally wide and thick (APD). Seen from the front, it is rectangular in outline, twice wider than high, with its superolateral corner extended more laterally. The proximal articular facet is inversely saddle-shaped as the corresponding facet of the astragalus: weakly convex transversely, and concave anteroposteriorly. The distal side bears three facets articulating with ecto-, meso-, and endocuneiform. The medial one (for entocuneiform) is the smallest (Pl. XVII 4b $_{i}$), rectangular in form, facing laterally and downward, not clearly demarcated from the facet articulating with the mesocuneiform, which is quite large (Pl. 4b $_{m}$), roughly rounded triangular in outline, situated dorsal to the latter. Its medial side forms the medial border of the bone. The lateral one (for the ectocuneiform) is the largest (Pl. XVII 4b $_{e}$), isosceles triangle in form, with its lateral side clearly incised at the middle.

As far as is known, in all the Hyrachyinae, Hyracodontinae, and the rhinocerotids, the naviculars are all thinner and longer (APD) than in *Juxia*, with their height less than 1/2 of the widths. In large-size paraceratheres the naviculars are also thinner (Tab. 30). The facet articulating with the entocuneiform is absent in most cases. The navicular of *Aralotherium prohorovi* is more fan-shaped (Gromova, 1959, Pl. XVIII 2) rather than rectangle-shaped. The facet articulating with the ectocuneiform is much larger than that articulating with the mesocuneiform.

Entocuneiform + MtI (Pl. XVIII 1; Figs. 27 D, 28): Only one specimen is preserved in the holotype.

It is irregular in shape, being an elongated flat bone, with its long axis lying almost vertically, and its short axis extending lateroposteriorly. On proximal end there is a small, transversely concave facet (Fig. 27 D$_{\mathrm{n}}$), elongated elliptical in outline, articulating with the navicular. In dorsolateral side, close to the proximal end is a facet articulating with the mesocuneiform (Fig. 27 D$_{\mathrm{m}}$), with a deep groove below. The plantar side is slightly convex transversely and roughened, with a weak tubercle at its distal side. The medial side is rather sharp, but at its lower part there is a small facet articulating with the MtII (Fig. 27 D$_{\mathrm{II}}$). Max L (oblique) is 60 mm; Max W, 30 mm; APD, 18 mm.

In *Hyrachyus eximius* the entocuneiform + MtI is proportionally large, rounded in form, covering the distal parts of the tarsals and the proximal ends of MtII-MtIII from behind. It articulates additionally with the plantar end of the proximal extremity of the MtIII. The same bone in *Heptodon posticus*, as described by Radinsky (1963, Fig. 3 A), is very similar to that of the former species, but the bone is composed of two small bones: entocuneiform and MtI. The entocuneiform + MtI in *Hyracodon nebraskensis* is very peculiar in form. Scott described it (1896, p. 377, Pl. II 7) as: "Das Entocuneiforme ist sehr gross und hat eine ausserordentlich sonderbare Gestalt. Der proximale Teil bildet einen breiten, ovalen und abgeflachten, schuppenänlichen Knochen, von dem ein langer aber schmalerer Fortsatz ausgeht. Letzterer erstreckt sich abwärts, biegt sich aber auch gegen die Fibular-Seite des Fusses und reicht bis unter das Kuboid; sein freies Ende is verdickt und von dreieckiger Gestalt, mit der Spitze gegen die Tibial-Seite gerichtet. Diser Knochen artikulirt proximal mit dem Naviculare, vorn mit dem Mesocuneiforme und zweiten Metatarsale, und am distalen Fortsatz ist eine kleine Facette für den Plantar-Vorsprung vom oberen Ende des dritten Metatarsale. Trotz seiner Grösse und Wichtigkeit ist dieser Knochen durchaus nach hinten zu gelegen ist kaum in der Vorderansicht des Fusses sichtbar."

This bone in primitive rhinocerotids is poorly known. According to Scott (1941, p. 785), in *Trigonias osborni*: "The entocuneiform is a very large, oval, and scale-like bone, which depends from the plantodistal border of the navicular, and is also applied to an oblique surface of the tibio-plantar angle of MtII." Thus, it lacks an articulation with the mesocuneiform. In later rhinocerotids and living rhinos this bone is highly veriable in shape. It is generally plate-like, with the same number of articular facets, as in *Juxia*. However, its distal process is very prominent, the groove above the distal process is very deep, and the facets articulating with the navicular and MtII are large and rounded in outline (Fig. 27 E).

In large-sized paraceratheres this bone is already greatly reduced in size, with only one or two facets articulating with MtII and occasionally with navicular (Fig. 27 F).

Ectocuneiform (Pls. XVII 5, XVIII 5; Tab. 31): Two specimens of right side are available in the collection.

The bone is very thick. The thickness is greater than 3/5 of its width, seen from the front. Both proximal and distal articular facets are triangular in outline, with lateral borders concave in their middle parts. On the medial side there are three small facets: one upper and two lower. The upper one is the largest and crescent in form, articulating with the mesocuneiform. The two lower facets articulate with the MtII (Pl. XVII 5b$_{\mathrm{mtII}}$). The anterior one is small, while the posterior one is as large as the upper one. Laterally there are two facets articulating with the cuboid.

The ectocuneiform in *Hyrachyus eximius* is even higher in proportion than that of *Juxia* (Tab. 31). This bone in *Hyracodon nebraskensis* is of the same form and articulates with the same bones as that of *Juxia* does. In *Trigonias osborni* this bone bears a facet articulating with the MtIV as well, a character not seen in *Juxia*. In later rhinocerotids and living rhinos this bone is always very thin. In large-sized paraceratheres the ectocuneiforms differ readily from that of *Juxia*. They are proportionally thinner, with their heights being only 1/4 – 2/5 of their widths (Tab. 31). Contrary to the case in *Juxia*, this bone articulates only with MtIII and MtIV, without connection with the MtII. The ectocuneiform of *Aralotherium prohorovi* is even more specialized than that of *Paraceratherium*, being still broader and thinner, articulating with the cuboid by a single anterior facet on the lateral side of the bone.

7) Metatarsals

MtII (Pl. XVIII 2, 5; Fig. 28; Tab. 32): Three specimens are preserved. A complete left MtII is preserved in the holotype. The rest two are only partly preserved.

The bone is slender and long, mesiolaterally flattened, with its distal part diverging laterally from the MtIII. The proximal extremity is transversely narrow, but very long (APD). The proximal facet articulating with the mesocuneiform is semilunar in outline, saddle-shaped, transversely concave, anteroposteriorly slightly convex (Pl. XVIII 2c). Behind it is the plantar process. On mesial side at the proximal end there are two composite facets (Pl. XVIII 2a $_{\text{e, mtIII}}$) articulating with the ectocuneiform (the upper pair) and MtIII (the lower pair) respectively. On posterolateral corner of the shaft, below the proximal end is a facet facing upward and posteriorly, which articulates with the entocuneiform + MtI (Pl. XVIII 2b $_{\text{i}}$). This facet varies considerably in size and position. The proximal 2/3 of the mesial side of the shaft is occupied by a long triangular rough area, the top of which points downward (Pl. XVIII 2a). The upper 1/3 of the dorsal border is sharp, becoming rounded downward. The plantar border of the lateral side is ridge-like, becoming more prominent distally. The distal end is constructed as in McIV.

All the MtII in other rhinocerotoids, except for the large-sized paraceratheres, are morphologically similar to that of *Juxia*. However, they all differ from the latter in being proportionally shorter (Tab. 32). In large-sized paraceratheres the distal end is particularly enlarged. In *Paraceratherium asiaticum* the MtII does not contact with the endo- and ectocuneiforms, whereas in *Aralotherium prohorovi* the MtII has only one anterior facet articulating with the MtIII. Therefore, the proximal facets of the large-sized paraceratheres are in general more reduced than in *Juxia*.

MtIII (Pl. XVIII 3, 5; Fig. 28; Tab. 33): Only a right MtIII with its plantar process of the proximal end broken is preserved in the holotype. In addition, there are three incomplete specimens (V 2891.5, V 2891.7).

The outline of the proximal articular facet is like that of the distal articular facet of the ectocuneiform. The proximal end of the medial side bears two small facets articulating with the MtII (Pl. XVIII 3c $_{\text{mtII}}$). The proximal end of the lateral side bears three facets: the anterosuperior one articulating with the cuboid; the anteroinferior and the posterior ones articulating with the MtIV (Pl. XVIII 3b $_{\text{mtIV}}$). A deep notch is present between the anterior and posterior facets. The plantar process at the proxiaml end is very prominent. The shaft is like that of the McIII. On both sides above the distal trochlea the protuberances and pits for the collateral tendon attachment are extremely developed. Above the trochlea, the groove on dorsal side and the paired pits on plantar side are all very deep and clearly shown. Seen from the bottom, the trochlea is trapezoid in outline, with its anterior border being slightly broader (Pl. XVIII 3f). The sagittal ridge is high, but not sharp, widening posteriorly and diminishing dorsally. It becomes lost only on the dorsal side of the trochlea so that it can be clearly seen from the front. On the other hand, the grooves bordered the sagittal ridge bilaterally, which serve as the place to lodge the sesamoids, are limited only to the posterior half of the trochlea. They can hardly be seen from the front.

So far as is known, in *Hyrachyus eximius* and most of the other rhinocerotoids the MtIII's do not articulate with the cuboids. In this respect, only *Hyracodon nebraskensis* is similar to *Juxia* in having connection between the MtIII and cuboid. However, none of these rhinocerotoids above mentioned have their MtIII proportionally so elongated and robust relative to MtII and MtIV. Furthermore, the sagittal ridges of the distal trochleae in them are never so high and long so that they can hardly be seen from the front.

In large-sized paraceratheres the MtIII becomes very stout and proportionally short. Its proximal width is about 1/3 of the total L of MtIII (1/5 in *Juxia*). The sagittal ridge of the distal trochlea is here highly reduced so that it can not be seen from the front, but the bilaterally situated grooves extend more anteriorly so that they can readily seen from the front.

MtIV (Pl. XVIII 4 – 5, Fig. 28): Only one proximal part is preserved (V 2891.5).

The proximal end is rather stout, with the facet articulating with the cuboid occupying only about half the size of the proximal end. The facet is nearly rectangular in outline, weakly saddle-shaped, with its long axis extending posterolaterally. There is a voluminous posterior protuberance, which is separated from the facet by a depression. At the proximal end of the mesial side there are two facets articulating with the MtIII (Pl. XVIII 4b $_{\text{mtIII}}$). The anterior one is under the proximal facet, facing anteromesially; the posterior one is on the mesial side of the protuberance, facing mesially.

Little can be said about the differences between *Juxia* and other rhinocerotoids in this bone. They are about the same as in the MtII. The MtIV in other rhinocerotoids are proportionally shorter. According to Cope (1884, Pl. LVa 2), the MtIV may have a contact with the ectocuneiform in *Hyrachyus eximius*. The MtIV in large-sized paraceratheres differs from that of *Juxia* more clearly. As the case in MtII, the MtIV is proportionally thinner relative to the MtIII. Furthermore, the proximal end of MtIV is situated higher than that of MtIII and contacts with the ectocuneiform. This is just opposite to the case in *Juxia*.

8) Restoration of pes: Pl. XVIII 5 is a restoration of the left pes of *Juxia sharamurenensis*. The parts restored in plaster (proximal half of calcaneus, mesocuneiform, cuboid, proximal 2/3 of the MtIII, and distal 2/3 of MtIV) are marked by a letter x.

The general characters of the pes of *Juxia sharamurenensis* can be summarized as follows: The pes is high, tridactyl with MtIII as central axis. Tarsal part is higher than wide. Calcaneus bears two separate facets articulating with tibia and fibula. Astragalus is oblique in its trochlear part, intermediate groove deep, and ridges roundly ridge-like. All the tarsal bones of the distal row is relatively high. Cuboid contacts with MtIII. Entocuneiform + MtI long and plate-like, articulating with navicular, mesocuneiform, and MtII, but not MtIII. It retreats to back part of tarsals. Proximal end of MtII is higher than that of MtIII, which is higher than that of MtIV. MtIII is particularly robust relative to MtII and MtIV, which shift backward and mesially relative to MtIII, but with their distal parts diverging from MtIII. Sagittal ridges of distal trochleae are strong enough to be seen from the front. Phalanges are like those of fingers.

In the whole, it is much easier to distinguish the pes of *Juxia* from those of the other rhinocerotoids.

The characters of the pes in *Hyrachyus eximius* distinguishing from that of *Juxia* are the following: 1) Trochlea of astragalus is strongly oblique, with its ridges sharp, and a prominent tuberosity is developed at the distal end of the medial side. 2) The cuboid articulates only with MtIV. 3) The entocuneiform + MtI is large and rounded in form, articulating also with MtIII. 4) The MtII – MtIV are all proportionally short, and their middle ridges and bilaterally situated grooves of distal trochleae are short (APD) and weak. 5) The MtIII is not particularly robust relative to MtII and MtIV. 6) The MtII and MtIV do not clearly shift backward and mesially. 7) Sagittal grooves of proximal facets in PhI's are short and shallow; PhIII is particularly long, without middle clefts on distal borders.

The pes of *Hyracodon nebraskensis* is closer to that of *Juxia* than that of *Hyrachyus eximius* is. The similarity between the former and *Juxia* is especially clearly shown in the slenderness of the tarsals, the weak tuberosity at the distal end of medial side in astragalus, additional articulation of cuboid with MtIII, and the proximal ends descending laterally in relative position. However, *Hyracodon nebraskensis* retains a number of plesiomorphic features shown in *Hyrachyus eximius*, as the general form of the trochlea of astragalus, the form and articulation with other pes bones of the entocuneiform + MtI, and the morphology and proportion of the metatarsals.

The differences between primitive rhinocerotids and *Juxia* in pes are obvious as well. In *Trigonias osborni* the pes is short, with low and wide tarsal part, which is wider than high. Distal part of astragalus is strongly shifted medially relative to trochlea. Cuboid does not contact with MtIII, but MtIV contacts with ectocuneiform. Proximal end of MtIII is situated lower than those of both MtII and MtIV. MtIII is not particularly robust relative to MtII and MtIV. Sagittal ridges of distal trochleae are short and low, and can not be seen from the front. Phalanges are wider than high, without clearly shown middle clefts on distal borders in PhIII's. Although more slender than in *T. osborni*, the pes in *Subhyracodon occidentalis* is morphologically closer to the former than to *Juxia*. In later rhinocerotids and living rhinos the pedes are much shortened in general and more specialized in the features above listed in primitive rhinocerotids.

The differences between large-sized paraceratheres and *Juxia* are striking. All the tarsal bones are much more widened and lower. The trochlea of the astragalus is highly asymmetrical and low. Entocuneiform + MtI is highly reduced in size. Proximal heads of the three Mt's are situated at about the same level. MtIII is particularly robust, articulating also with mesocuneiform. Lateral Mt's are more or less straight, not clearly diverging from MtIII in their distal parts. All the phalanges are extremely low and wide, mostly dish-like, without middle clefts on distal borders in PhIII's. However, in degree of monodactylism they are closest to *Juxia* than to any other rhinocerotoids.

Juxia micracis (Wang, 1976)

(Pl. XIX 1－7; Tabs. 3－4, 15)

Imequincisoria mazhuangensis (partim), Wang, 1976: 104－105, Pl. I 1－2
Imequincisoria micracis, Wang, 1976: 106－107, Pl. III 1－2
Imequincisoria sp. (partim), Wang, 1976: 108 (V 5074.4－8)

Holotype: V 5073, left P2－M3, right P1－M3, and I2－I3.

Other referred specimens: V 5072, upper and lower incisors (originally assigned to *I. mazhuangensis*); V 5474.5, left trapezoid (IVPP Loc. 73013); V 5074.4, left unciform (IVPP Loc. 73013); V 5074.8, left lunar (loc. not indicated). The three carpal bones may belong to the same individual.

Locality and horizon: The village Xiaomazhuang in Wucheng Basin on north slope of the Tongbai Mountains in Henan Province, China; Wulidun Formation, late Middle Eocene.

Emended diagnosis: Size increases from third to first incisors faster than in the type species. Upper incisors more linguolabially flattened, L/W ratio about 1.4－1.5; mesial ridges and lingual cingula in I1－I2 prominent; diastema between the two i1's wider; cristae and supplementary plications in postfossettes in P2－P4 stronger.

Discussion: Dentition of this species was fully described by Wang (1976) under the title of *Imequincisoria micracis* and partly of *I. mazhuangensis*. In view of the poor quality of the pictures provided by Wang, part of the teeth is reproduced in Pl. XIX of the present volume.

A closer comparison of the relevant specimens left no doubt that the above listed incisors are closest to those of *Juxia* than to any other forms. The features commonly shared by them are the special morphology (fattened cone in shape, with mesial and distal ridges and lingual cingula, I1 fan-shaped, distal ridges of upper incisors concave) and the way of implantation (uppers vertical, lowers procumbent, separated by diastemata) of the incisors. Nevertheless, they differ from those of *J. sharamurenensis* in the following ways: 1) The degree of size increasing mesially is greater. 2) The mesial ridges in I1－I2 are not only more robust, but also everted inwardly. 3) The distal edge of I1 and mesial edge of i1 abrade each other, implying an interlocking mode of occlusion between I1 and i1. In *Juxia sharamurenensis* the i1 is almost horizontally positioned and the abrasion facet caused by the I1 is positioned on top and faces anteriorly.

The cheek teeth of the two species are almost indistinguishable. The only minor difference between them is the better development of cristae and supplementary plications in postfossettes shown in P2 – P4 of the former form.

The presence of two sets of limb bones differing in both size and morphology found from the same site in Wucheng Basin is of particular importance in reassessment of the systematic position of these rhinoceroses. A part of the limb bones referred by Wang to *Forstercooperia* sp., a lunar, a trapezoid and an unciform, are of the same size and morphology as in *Juxia* (Pl. XIX 5 – 7). Most important is the unciform, which bears a long facet articulating with McV on distal side, indicating that the manus should be tetradactyl as in *Juxia*. On the other hand, the specimen consisting of some articulated carpal and metacarpal bones of larger size, referred by Wang also to *Forstercooperia* sp., shows clearly the McV is highly reduced and the manus is tridactyl (Pl. XIX 8). This renders it possible that the articulated manus of larger size may really belong to the genus *Forstercooperia*.

Juxia shoui Qi et Zhou, 1989

(Tabs. 4, 15)

Holotype: V 8757, anterior part of skull with C – M2.

Other referred specimen: V 3268, a left lunar

Locality and horizon: V 8757 is found from Ulan Gochu Formation at Urtyn Obo, according to original description; V 3268 is found from "Lower White" of the Urtyn Obo section by Qi Tao, Wang Banyue and others in July 1991; early Late Eocene (or latest Middle Eocene ?).

Emended diagnosis: Nasal notch shallow, with its posterior border lying above P2; C – P1 diastema short, only about 10 mm; separation of hypocone from protocone in P2 – P4 weaker.

Comments: The founders of the present species pointed out that the new species differed from *Juxia sharamurenensis* (considered synonymous with *J. borissiaki* by Qi and Zhou) in being: "smaller in size, P2 – P4 width enlarged, P4 more molariform, and diastema much shorter" (Qi and Zhou, 1989, p. 208). A comparison of the measurements (Tab. 4) shows that the size differences between these two forms are practically negligible, and the seemingly larger breadth of the premolars are evidently due to the senility of the specimen. On the other hand, the latter two features, seem to be valid, i. e., the lower degree of molarization of the premolars as shown in the weaker separation of the hypocone from protocone, and the shorter muzzle part of the skull as shown in the shallow nasal notch and shorter C – P1 diastema. The lunar from the same locality is very close to that of *Juxia sharamurenensis* in both size (Tab. 15) and morphology, with the only difference that the facet articulating with magnum is smaller and the distal angle is nearly 90°. With these minor differences we are inclined to retain Qi and Zhou's species as a valid one of *Juxia*.

Urtinotherium Chow et Chiu (= Zhou et Qiu), 1963

Baluchitherium (partim), Granger and Gregory, 1936 (*vide infra* for more details)
Indricotherium (*parvum*), Chow, 1958: 264 – 265, Pl. I 1 – 4
Indricotherium (*intermedium*), Chiu, 1962: 57 – 60, Pls. I – II
"*Indricotherium*" (cf. *parvum*), Chow *et al.*, 1974: 268 – 269, Pl. I 9
Indricotherium (*qujingensis*), Tang, 1978: 76 – 77, Pl. I 1 – 3
Dzungariotherium (*erdenensis*), Qi, 1989: 301 – 304, Pl. I

Type species: *Urtinotherium intermedium* (Chiu, 1962).

Other included species: *U. parvum* (Chow, 1958).

Geographic and stratigraphic distribution: Urtyn Obo, Nei Mongol, and eastern part of Yunnan in China, Ulan Gochu Formation and upper part of Lumeiyi Formation, Late Eocene.

Emended diagnosis: Size intermediate between *Juxia* and *Paraceratherium*. L of mandible about 0.6–0.87 of that of *P. grangeri* (Grade II). Posterior border of symphysis at the level of anterior part of p3; ascending ramus comparatively low, its height less than 1/2 of total L of mandible, including i1. Lower dental formula complete (3·1·4·3); i1 much enlarged than other lower incisors and canines. P2 hypocone weakly separated from protocone; upper molars with well developed parastyle, paracone, parastyle fold, but weak antecrochet, making the bottom line of the medisinus almost rectilinear. Astragalus comparatively high, with its ratio of W/H <110%, and its sustentacular facet being much higher than wide.

Comments: Prior to the establishment of *Urtinotherium incisivum* (Chow and Chiu, 1963), Qiu (= Chiu, 1962) had described a new species of *Paraceratherium*, and named it *Indricotherium intermedium*. This was partly because of the impossiblility to compare the material of his new species (upper molar and astragali) directly with that of *Urtinotherium* (mandible). With the inclusion of an upper tooth row to *Urtinotherium* (*vide infra*), a closer comparison of the two forms is now possible. The comparison shows clearly that the specimens of *I. intermedium* are of the same size and at about the same level of evolution as that of *Urtinotherium incisivum*. The principle of priority dictates that they be united under the same genus and species, namely, *Urtinotherium intermedium*.

As early as 1989, Lucas and Sobus proposed to transfer *Indricotherium parvum* and *I. qujingensis* to *Urtinotherium*, a point of view adopted in the present volume. Although the type species of *Urtinotherium* is already considerably large and advanced in tooth morphology, its dental formula remains complete, a feature diagnostic of *Urtinotherium*. This led us to conclude that the reduction of the anterior teeth (i2–c) did not occur until the size of the animals increased considerably and the other dental features became rather advanced. A corollary of the above fact is that the small and primitive *I. parvum* should possess a complete dental formula and be grouped in *Urtinotherium* as a primitive species of it. On the other hand, *Indricotherium qujingensis* may well be conspecific with *I. parvum* based on their great similarity in size and morphology (*vide infra*), thus be transferred to *Urtinotherium parvum* as well.

Judged from its size, *Dzungariotherium erdenensis*, described by Qi (1989), is fully comparable to the type species of *Urtinotherium* (*vide infra*), and is also to be transferred to *U. intermedium*.

***Urtinotherium intermedium* (Chiu [= Qiu], 1962)**

(Pl. XXIII 1; Tabs. 12, 29, 35–38)

Baluchitherium (partim), Granger and Gregory, 1936: 11–17, 66; Figs. 7, 44 B
Indricotherium intermedium Chiu, 1962: 57–59, Pls. I 2–3, II
Indricotheriinae gen. et sp. indet., Chiu, 1962: 59–60, Pl. I 1
Urtinotherium incisivum, Chow and Chiu, 1963: 230–236, Pls. I–II
Dzungariotherium erdenensis Qi, 1989: 301–305, Pl. I

Holotype: V 2769, a nearly complete mandible, from Ulan Gochu Formation at Urtyn Obo, Nei Mongol, Late Eocene.

Other referred specimens: 1) V 2384.1, right M2; V 2384.2–4, 3 astragali and a distal end of lateral metapodium; V 2371, an astragalus (originally described as *I. intermedium*), all from Shizong (originally called as Luoping) County, Yunnan, exact locality and horizon uncertain. 2) AM 26026 [772], right radius (Wood, 1938, p. 16, footnote 1, Figs. 6–7), collected from "Middle White" of the Urtyn Obo section (*vide* Osborn, 1929a, Ulan Gochu Formation) by 3CAE in 1928. 3) AM 26390 [914], axis (Granger and Gregory, 1936, Fig. 7), collected from "Houldjin gravels" (Ulan Gochu Formation, *vide infra*) at the locality 11 km west of Camp Margetts by 3CAE in 1930. 4) AM 26389 [840], left McIII, collected from "Houldjin gravels" (Ulan Gochu Formation, *vide infra*) at Camp Margetts by 3CAE in 1930. 5) V 8803, broken maxilla with P2 – M3 of both sides (originally as *D. erdenensis*), from Ulan Gochu Formation at Urtyn Obo, Nei Mongol.

Emended diagnosis: Largest-sized species of the genus. Teeth and limb bones 0.8 – 0.87 as long as those of *Paraceratherium grangeri* (Grade II). i1 similar to that of *Paraceratherium*, much larger than other incisors; canine only larger than i3. Hypocone and protocone not separated in P2 when heavily worn.

Discussion: The mandible of *Urtinotherium incisivum* (675 mm without i1) is 0.87 as long as that of *P. grangeri* (775 mm; AM 26166, Grade II). Exactly the same ratio was found in the M2 of *Indricotherium intermedium* described by Chiu in 1962 (82.5 mm × 89.4 mm) relative to that of *P. grangeri* (95 mm × 102.8 mm, *vide* Tab. 38). This shows that the mandible of the type species of *Urtinotherium* and the M2 of *I. intermedium* are highly compatible in size, or even of about equal size. The validation of the generic name *Urtinotherium* and the specific name *intermedium* (1962) over the postdated *I. incisivum* (1963) justified the usage of *Urtinotherium intermedium*.

The following specimens described under different generic and specific names are here referred to the present species based mainly on size and morphology.

i. The right radius (AM 26026) described first by Wood (1938) was originally identified as belonging to *Embolotherium* in field notes. Wood correctly pointed out some paracerathere features of this radius, as the oblique ridge extending to distal end of the bone, a feature observed only in paraceratheres. We noticed also other similarities between this radius and those of other paraceratheres, such as the smallness of the facets articulating with the ulna. However, this radius is definitely much smaller than those of other large-sized paraceratheres. Our calculation of the ratio between the lengths of this radius (1041 mm) and that of *Paraceratherium grangeri* (1200 mm, Grade II) is exactly 0.87. This strongly supports its referral to *Urtinotherium intermedium*.

ii. The axis (AM 26390) was only briefly described and measured by Granger and Gregory (1936). Its large size, extreme elongation, and other morphological characters reveal clearly its affinity with the paraceratheres. Compared with the other known complete axis of large-sized paracerathere, TP 9401, an axis of *Paraceratherium lepidum* to be described below, AM 26390 is much smaller than the latter. Ratios of some comparable measurements of axis of AM 26390 to those of TP 9401 vary around 0.76 – 0.77 (*vide infra*). In view of the fact that *P. lepidum* is larger and more advanced than *P. grangeri* (*vide infra*), the same ratios of AM 26390 to *P. grangeri* are to be slightly higher, probably around 0.8. This is in accordance with the size differences between *Urtinotherium intermedium* and *Paraceratherium grangeri*. This led us to propose to transfer the axis (AM 26390) to *Urtinotherium intermedium*.

iii. A number of large-sized paracerathere limb-bones were recorded from Camp Margetts, but only one of them, a left McIII (AM 26389), was figured, but not described (Granger and Gregory, 1936, Fig. 44 B). A brief description of this specimen is given below, accompanied by our newly produced pictures (Pl. XXIII 1a – e).

The proximal surface of the McIII (Pl. XXIII 1a) is wider than long (APD), mainly occupied by the fan-shaped facet articulating with the magnum. The facet articulating with the unciform (Pl. XXIII 1a, 1c un) is strip-like, restricted in anterior half. Seen from the front, the angle formed by the two proximal facets is 135°, and upward pointed. The narrowest part of the shaft is at the level 80 mm below the proximal end. Then the shaft gradually widens downwards until the lateral tuberosities above the distal articular facet. The dorsal side of the distal articular facet is rounded and bulging. The sagittal ridge and the bilateral grooves are almost invisible from the front.

In proportion and morphology, this McIII is undoubtedly closer to that of *Paraceratherium* than to any other genera among the large-sized paraceratheres. The McIII of *A. prohorovi* is proportionally shorter, with its narrowest part being at the middle of the shaft. The angle of the proximal end is low and obtuse, and the sagittal ridge of the distal articular facet is wider and flattened (Gromova, 1959, Pl. XX 2). The McIII of *Turpanotherium elegans* (*vide infra*) is more similar to that of *A. prohorovi* than to *Paraceratherium*. Nevertheless the AM 26389 McIII is much smaller than that of *P. grangeri* (Grade II). The ratio of L of this McIII to that of the latter is 0.78 (Tab. 37), just intermediate between the ratio for *U. parvum* and *P. grangeri* (0.65 – 0.75) and that for *U. intermedium* and *P. grangeri* (0.8 – 0.87). It is equally acceptable to attribute this McIII either to *U. parvum* or to *U. intermedium*. We tentatively transfer it to the latter, *U. intermedium*.

iv. When creating the new species, *Dzungariotherium erdenensis*, Qi pointed out that the size of the type specimen (maxilla) was compatible with the holotype (mandible) of *Urtinotherium* in size. The calculated ratio of L of the P2 – M3 of Qi's maxilla (318 mm) to that of *P. grangeri* (Grade II, 388 mm) is 0.82 (Tab. 38), just within the range of variation in the ratios of *U. intermedium* to *P. grangeri*. The main reason that Qi referred this maxilla to the genus *Dzungariotherium* was the seemingly larger antecrochet in the molars. However, this can well be caused by the senility of the described skull. Furthermore, the maxilla in question bears a P1 and the P2 is rectangular in outline. These again are plesiomorphic features in large-sized paraceratheres and different from those of *Dzungariotherium*, where the P1 is lost and the P2 becomes triangular in form. As a result, we are inclined to transfer this species of *Dzungariotherium* to *Urtinotherium intermedium*.

Urtinotherium parvum (Chow [= Zhou], 1958)

(Pl. XX; Tabs. 33, 37 – 40)

Baluchitherium grangeri, Granger and Gregory, 1936: Fig. 44A

Indricotherium parvum, Chow, 1958: 264 – 265, Pls. I 1 – 3, II 1 – 2

"*Indricotherium*" cf. *parvum*, Chow *et al*., 1974: 268 – 269, Pl. I 9

Indricotherium qujingensis, Tang, 1978: 76 – 77, Pl. IX 1 – 3

Indricotherium parvum, Zhang, 1980: 348

Lectotype: Left M2 (uncatalogued), collected from "upper Lunan beds" (now the upper part of Lumeiyi Formation) in Lunan, Yunnan, by Hu Chengzhi in 1958, now kept at the Geological Museum of China.

Other referred specimens: 1) Isolated teeth, including right P3, left P4, left p3 (originally identified as p2), and broken left m1, excluding the P2 described by Chow (Chow, 1958, Pl. I 4), from the same locality and bed as the lectotype, kept in the Geological Museum of China. 2) PGMV 792, a left P2 described by Chow *et al*. (1974), kept in the Geological Museum of China. 3) V 4705.1 – 3, left M2, P2 (?) and P4, collected from upper part of Caijiachong Formation near Yangjiachong in Qujing, Yunnan, by Tang *et al*. in 1972, published in 1978. 4) AM 26190 [686], left McIII, left calcaneus, right MtIII, 1 PhII and 2 PhIII of middle digit, collected from "Baron Sog" beds (now corrected as Ulan Gochu Formation, *vide infra*) at Jhama Obo, by 3CAE in 1928. 5) EMM 0146, right P1 – M3, collected from the "Lower White" in Urtyn Obo section, Nei Mongol.

Emended diagnosis: Smaller than type species. Teeth and limb bones about 0.65 – 0.73 as those of *Paraceratherium grangeri* (Grade II) in length. P1 longer than wide, P2 – P4 wider than long; P2 trapezoid, narrowed anteriorly, hypocone and protocone half-separated; in upper molars antecrochet very weak and bottom line of medisinus almost rectilinear. p3 protoconid and entoconid clearly conical in shape.

(1) Description and Comparison

1) Specimens from Ulan Gochu Formation at Urtyn Obo

EMM 0146 (Pl. XX 1, Tab. 38): The tooth row is rather heavily worn, indicating its senility of age (about 20 years old, *vide infra*).

P1 is triangular in outline, longer than wide. Parastyle long, with the parastyle fold on ectoloph palpable. Para- and metacone part of ectoloph is very wide, occupying more than 1/2 of Max W of P1. Protocone forms a longitudinal strip, slightly convex lingually, without connection with ectoloph in the upper part of the crown. Metaloph is composed of hypocone and metaconule, widely connected with ectoloph. Lingual cingulum is better developed than buccal one, a funnel is formed by the lingual cingulum and the ectoloph anterior to the protocone. P2 is trapezoid in outline, wider than long, with posterior width being the widest part of the tooth. Ectoloph is very wide; as in P1, paracone rib is obvious, while the metacone rib is scarcely developed. Protocone is comma-shaped, with its tail linking with ectoloph. Hypocone is about equally large as protocone, but slightly more lingually situated. Protocone and hypocone are confluent, but with visible separating grooves on buccal and lingual sides. Metaconule is comparatively wide and convex posteriorly, broadly connected with hypocone and ectoloph. Cingulum is rather robust along the lingual half of the anterior side, forming an encircling band. P3 is basically structured like P2 with some minor distinctions. It is more or less rectangular in outline, with its lingual side nearly symmetrically convex. Metacone rib is similarly developed as that of paracone. Protocone and hypocone are completely fused, without separating grooves. P4 is very similar to P3 in size, form and structure, with only minor distinctions, like the weak convergence of the buccal and lingual walls posteriorly so that the tooth is anteriorly broader, and the presence of a cingulum in the lingual half of the posterior side.

M1 is so heavily worn that little can be said about its structure. Paracone, parastyle and parastyle fold are all clearly visible; on the crown surface, a very small circled medifossette and a slit-like postfossette are present. A tiny tubercle at the outlet of the medisinus represents the remaining part of the highly reduced lingual cingulum. M2 is better preserved. Paracone is very prominent on buccal wall; antecrochet is weak; bottom line of medisinus is largely rectilinear, with its buccal end slightly deflected anterobuccally. Anterior and posterior cingula are well developed, more or less ridged, except in buccal side, where the cingulum either lost, or becomes very low; lingual cingulum is as in M1. M3 is trapezoid in outline at the crown base owing to the presence of the posterior end of the ectoloph, but triangular in upper half of the crown because of the complete merging of ecto- and metaloph into an ectometaloph. Paracone is large and widely separated from parastyle. At the boundary between the ectoloph and metaloph on buccal wall a line starts somewhere in the middle height of the crown and intensifies toward the base, culminating in a buttress, which is accompanied by a furrow lingually. The posterior cingulum is ended before reaching the buttress. Otherwise M3 is similar to M2. For measurements see Tab. 38.

2) Material from Jhama Obo (AM 26190)

McIII (Pl. XX 2, Tab. 37): On the proximal end (Pl. XX 2a), the facet articulating with magnum is roughly trapezoid in outline, with its volar border markedly narrower than the dorsal one. The surface is rather flat except the dorsolateral corner where it sharply turns upward. The facet articulating with unciform is triangular in outline, restricted to the anterior half, bordered posteriorly by a deep notch. The angle formed by the above two facets is well pointed upwards. Seen from the front or back (Pl. XX 2b – c), the narrowest part of the shaft is almost immediately below the proximal extremity, then it widens gradually downward, with the Max W being at the bilateral tuberosities above the distal articular trochlea. The tuberosities are not voluminous, but rather pointed. The large rough area on the proximal part of the dorsal side below the proximal facet articulating with magnum so clearly shown in McIII of *Juxia sharamurenensis* is scarcely developed here. The volar side is generally flat, widens gradually downward, bordered bilaterally by ridges. Sagittal ridge of distal articular trochlea is well developed in posterior half, but can still be seen from the front. The upper borders of the trochlea on dorsal and volar sides are equally high.

Calcaneus (Pl. XX 3, Tabs. 39 – 40): Seen medially (Pl. XX 3a), the tuber calcanei (tuber calcis) is very prominent, occupying the whole length of the proximal end of the bone; its upper border extends slightly upward posteriorly, while its lower border, marked by a ridge, slants downward and posteriorly. Seen from the front (Pl. XX 3b), the tuber calcanei forms the widest part of the upper half of the bone. The whole upper surface of the tuber forms a large rough area for attachment of the tendon of m. gastrocnemius. Dorsal border of the upper half of the bone is slightly concave, with its upper end dorsally pointed, while the plantar border is slightly convex. The cochlear process is relatively small, not very far extended forward relative to the body. The larger and lower facet on it, articulating with astragalus, faces primarily dorsally, only slightly downward, while the smaller and upper one articulating with tibia faces mainly upward, slightly dorsally. The tongue-shaped small facet below the larger facet on the cochlear process is small, with its distal end being far away from the distal end of the bone. The sustentacular process is plate-like, horizontally stretching medially. The long axis of the cross section of the sustentacular process extends posteriorly, only weakly slanting downward so that the process is almost horizontally situated relative to the body. The facets articulating with astragalus on cochlear and sustentacular processes are separated from each other by a groove. The distal part of the body below the cochlear process is only a little shorter than the part above the cochlear process. The distal facet articulating with cuboid forms an angle slightly smaller than 90° with the dorsal border of the distal part of the body, making the posterior end of the facet being considerably lower than the cochlear process in position. For measurements see Tab. 39.

MtIII (Pl. XX 4; Tabs. 33, 40): It is stouter and slightly shorter than McIII. On proximal end (Pl. XX 4a), the main facet articulating with ectocuneiform is fan-shaped in outline. The small and triangular facet articulating with mesocuneiform is present anteromedial to the above facet, but no facet articulating with cuboid is observed. The shaft keeps its width unchanged throughout its whole length except for the ends. The distal end is like that of McIII.

PhII of middle digit (Pl. XX 5, Tab. 40): Seen from above, it is nearly semicircular in outline, with its anterior border being convex, but posterior border slightly concave. The proximal surface is concave with a very weak sagittal ridge, while the distal surface is convex with a better developed sagittal groove.

PhIII of middle digit (Pl. XX 6 – 7, Tab. 40): There are two specimens, one is with its both angles broken (Pl. XX 6), the other is better preserved, with only its one angle missing (Pl. XX 7). The extensor process at the middle of the dorsal border of the proximal end is prominent, but rather blunt. Behind the proximal facet articulating with PhII is a small lozenge-shaped smooth area for lodging the distal sesamoid. The dorsal side is convex, with bilaterally situated deep dorsal sulci. Posterior side is rather flat, with the volar (or plantar) sulcus across the whole phalanx. Distal border is slightly concave at the middle, but without a real middle cleft.

(2) Comparison and Discussion

The material based on which Chow (1958) erected the new species *Indricotherium* (now *Urtinotherium*) *parvum* is P2 – P4 and M2. Of them only the P4 and M2 are more or less complete and measurable. Compared with the teeth of the type skull of *P. grangeri* (Grade II), they are only 0.7 – 0.76 in length and 0.65 – 0.73 in width of the latter. Since the width is more reliable in rhinoceros tooth measurements than length (*vide supra*), we choose the width ratios (0.65 – 0.73) as the most representative size differences between *I. parvum* and *P. grangeri* (Grade II). The only comparable material between *I. parvum* and *U. intermedium* are p3 and the anterior part of m1 (or m2?). Those of *I. parvum* are certainly smaller: p3 is 39.5 mm×27 mm (45 mm×35 mm in *U. intermedium*); width of m1 (or m2?) 37 mm (45 or 48 mm in the latter). Morphologically they also show some distinctions. In the former the p3 (originally identified as p2) is more primitive in character, with all the major cusps being clearly cone-shaped (Chow, 1958, Pl. II 2) and the talonid narrower than the trigonid, while in *U. intermedium* only the metaconid of p3 is clearly cone-shaped and the talonid about equally wide as the trigonid (Chow and Chiu, 1963, Pl. I). No records of the incisors of *I. parvum* have ever been reported. However, based on the fact that full number of lower incisors (and probably also the upper incisors) is retained in larger-sized and morphologically more advanced *U. intermedium*, it is likely that *I. parvum* may also have a complete set of incisors, a major character diagnostic for the genus *Urtinotherium*. As a result of the above comparison, *I. parvum* should be considered a valid species of the genus *Urtinotherium*, thus *U. parvum*.

Fortunately, a complete upper tooth row (EMM 0146) was found to supplement the poor specimens of *U. parvum* from the type locality. Firstly, EMM 0146 is very close to these specimens in size. The only comparable teeth between the two samples are P2 and M2. Their sizes are about the same (Tab. 38). Furthermore, the ratio of the length of P1 – M3 of EMM 0146 to that of the type skull of *P. grangeri* (Grade II), which is 0.71 (285 mm / 403 mm), falls within the calculated range of variation of width ratios (0.65 – 0.73) of the P2 and M2 from the type locality to those of *P. grangeri* (Grade II). There are minor morphological differences between EMM 0146 and the specimens of *U. parvum* from the type locality. In EMM 0146 the P2 is evidently trapezoid in outline, posteriorly wider than anteriorly; no groove separating hypocone from protocone is present on lingual wall of P4; and the bottom line of the medisinus in M2 is slightly sharply deflected anteriorly at the buccal part, indicating the slightly larger antecrochet. In specimens of *U. parvum* from the type locality, the P2 is probably rectangular in outline with more or less symmetrical lingual border, a shallow groove is present on lingual wall in P4 and the bottom line of the medisinus is smoothly curved in M2, indicating a smaller antecrochet. We are inclined to consider the above differences as intraspecific variations and to identify EMM 0146 as *U. parvum*.

Some other *Indricotherium* specimens can also be referred to *U. parvum*. The first is the P2 described by Chow *et al*. (1974) as "*Indricotherium*" cf. *parvum*. It is slightly smaller than that of EMM 0146, but certainly larger than that of *Juxia* (compare Tab. 38 with Tab. 4). Morphologically it is rather like that of the Qujing specimen to be discussed below, with its hypocone widely linking with metaconule, but clearly separated from protocone. Together with the Qujing specimens, this P2 is supposed to be attributed to *U. parvum*. The sample described by Tang (1978) as a new species, *I. qujingensis*, is composed of a P2, a P4 and an M2. The P4 and M2 are very near those of EMM 0146 in size (Tab. 38), and almost inseparable from the latter in morphology. However, the P2 is larger in size and really more advanced in morphology than that of *U. parvum*. The lingual length of this P2 measures 34 mm, larger than those measured on other available P2's of *U. parvum*, which are 26 – 28 mm, but comparable to that of *U. intermedium*, the buccal length of which is 37.3 mm (Qi, 1989, p. 302, *vide supra*). Furthermore, contrary to the P2 of *U. parvum*, the hypocone links mainly with metaconule, but widely separated from protocone, As a result, we are certain that the P4 and M2 of the Qujing sample can safely be referred to *U. parvum*, but doubtful as to the P2.

The close affinity of the limb bones of AM 26190 with the large-sized paraceratheres is without doubt. This is particularly clearly shown in the morphology of the PhII of middle digit, which is dish-like rather than column-shaped as in *Juxia*. However, these limb bones are particularly small compared to all the available material so far known of the large-sized paraceratheres. As is shown in Tab. 40, they are only 0.6 – 0.7 as large as those of *P. grangeri* (Grade II), even slightly smaller than the representative ratios calculated from the type specimens of *U. parvum* and *P. grangeri* (Grade II), which are 0.65 – 0.73.

AM 26190 limb bones also differ from typical large-sized paraceratheres in morphology. The McIII and MtIII are more slender in proportion (Tabs. 33, 37, 40), The angle on the proximal end of the McIII is high and pointed, the sagittal ridges of the distal articular trochleae of middle metapodials are sharp, the extensor tuber of PhIII of middle digit is well developed, etc. Taken as a whole, AM 26190 limb bones are closer to *Paraceratherium* rather than to *Aralotherium*, which is more specialized than the former.

The above comparison shows that AM 26190 specimens are the most primitive and smallest of all the known limb bones of the large-sized paraceratheres, and we think it more appropriate to refer them to *U. parvum* now.

Paraceratherium Forster-Cooper, 1911

Paraceratherium, Forster-Cooper, 1911; Lucas and Sobus, 1989 (partim): 393 – 395, Fig. 3A – C, F – H; Lucas and Bayshashov, 1996: 540 – 545, Fig. 2

Indricotherium, Borissiak, 1915a, 1916, 1918, 1923b; Pavlow, 1922; Gromova, 1959

Baluchitherium, Osborn, 1923 (partim): 4 – 9, Figs. 2, 3A, 4 – 5, 6A, 7A; Teilhard de Chardin, 1926; Granger and Gregory, 1936 (partim, *vide* description part); Young and Chow, 1956

[non] *Paraceratherium* (*prohorovi*), Gromova, 1959

[non] *Indricotherium* (*intermedium*), Chiu, 1962: 57 – 59, Pls. I 2 – 3, II

[non] *Indricotherium* (*parvum*), Chow, 1958: 264 – 265, Pls. I 1 – 3, II 1 – 2; Zhang, 1980: 348

[non] "*Indricotherium*" cf. *parvum*, Chow *et al.*, 1974: 268 – 269, Pl. I 9

[non] *Indricotherium* (*qujingensis*) Tang, 1978: 76 – 77, Pl. IX 1 – 3

[non] *Paraceratherium* (*sui*), Ye *et al.*, 2003

Type species: *Paraceratherium bugtiense* (Pilgrim, 1908).

Other included species: *Paraceratherium asiaticum* (Borissiak, 1918); *P. grangeri* (Osborn, 1923); *P. lepidum* Xu et Wang, 1978.

Geographic and stratigraphic distribution: Chelkar-Teniz – North Priaralie, Turgai and Ili river areas of Kazakhstan; middle and eastern parts of Mongolia; Eren region and Qianlishan district of Nei Mongol, Turpan Basin of Xinjiang, China; Baluchistan (Bugti Dera) of Pakistan. All Oligocene in age.

Emended diagnosis: Largest of the known Paraceratheriinae members. Body length around 7.5 m, shoulder height around 4.5 mm. Condyle 30% – 40% of the height of nuchal surface; paroccipito-posttympanic process extremely robust, with their ventral borders below condyle; no unified sagittal crest; zygomatic arch robust, sharply rises upward on posterior part above glenoid cavity; posterior border of nasal notch above P4 – M1; infraorbital foramen faces laterally; muzzle bones (skull part anterior to cheek teeth) very long; I1 cone-shaped, turning directly downward. Lower border of mandible convex under premolars, concave under diastema and stretching anteriorly together with i1. Dental formula 1·1 – 0·4 – 3·3 / 1·0·3·3. P2 semimolariform; P3 – P4 submolariform, with crescent metaconule, linking with ectoloph and hypocone only when considerably worn; lingual side of protocone rounded and antecrochet moderately developed in upper molars. Posterobuccal corner of protoconid often ridged, protruding lateroposteriorly, and entoconid cone-shaped, weakly linking with hypoconid in p3 – p4.

Cervical vertebrae (C1 – C7) very much elongated and widened, 1.5 – 2 times as long as skull L. Bodies of C1 – C6 hollowed by enlarged transverse canals; capita and vertebral fossae of C3 – C7 wider than high, concave at the middle on their upper borders. Alar notch of atlas wide and shallow, forming an obtuse angle; intervertebral foramen lying apart from alar notch, but linked with the latter by a groove; posterior opening of transverse canal situated at lateral border of posterior articular facets; foramen alare inferior small. Posterior end of spinous process of axis little elevated, with a pair of ridges leading to mesial border of postzygapophysis. Transverse processes of C3 – C5 bifurcated, in C6 tripartite. Thoracic vertebrae with very high and robust spinous processes, all slanting backward, with no diaphragmatic vertebra; posterior surfaces of spinous processes of anterior T's deeply excavated, making cross sections V-shaped; spinous processes of posterior-most T's shortened, less deeply excavated posteriorly and with sharp anterior ridges. Bodies of lumbar vertebrae large, spinous processes plate-like, transverse process straight. Cross section of middle thorax ribs plate-like.

Long bones of extremities very robust, straight, columnar in shape. Scapular tuber shifted downward, with its lower border lower than the middle part of glenoid cavity, much enlarged and widened, slightly separated from glenoid cavity by groove. Caput of humerus faces almost directly upward, with reduced lateral tuberosity, upper border of which is lower than the upper surface of the caput, anterior portion of lateral tuberosity scarcely turning medially to cover the bicipital groove; humeral crest and deltoid tuberosity very weak; lateral epicondyle large, extending upward and laterally, with its lateral border being straight; distal trochlea with distinct median groove and ridge on lateral condyle. Radius proportionally robust, W $\geqslant$1/3 of L; crest below the radial tuberosity sharp, extending downward and medially beyond the middle of the shaft. Shaft of ulna robust, with its posterior border almost straight, olecranon shorter, semilunar notch low and broad, especially its upper part. Carpal part (all carpal bones in articulation) wider than high; proximal and distal articular facets of all carpal bones rather flattened, with only weakly expressed "hindering facets" in anterior parts; carpal bones transmitting body weight to lateral metacarpals (cuneiform, unciform, trapezium and trapezoid) diminished and narrowed; distal angle of lunar more or less symmetrical, about equally resting on unciform and magnum; magnum wider than high, becoming the widest bone in carplas. McII – McIV widen downward, with the narrowest part at the lower part of the upper 1/3 shaft; McIII much wider relative to McII and McIV; McV atrophied into a small lump of bone. Phalanges of middle finger particularly low and wide, PhI – PhII oval dish in form, distal border of PhIII without sagittal notch.

Ilium of innominate bone elongated relative to ischium, with its iliac crest slightly convex; acetabulum posteriorly shifted, situated at the posterior 1/3 of the innominate bone. Transition from femoral caput to shaft smooth, without clearly expressed "neck"; greater trochanter small, with its lateral border scarcely beyond shaft, no lesser trochanter, third trochanter represented only by bulging area. Proximal end of tibia not particularly widened relative to mid-shaft; its proximal articular facets spherically concave, dish-like; intercondyloid eminences inconspicuous; tibial tuberosity low, without deep groove for ligament on it; muscular groove lateral to the tibial tuberosity almost absent, but tibial crest very long, extending to the medial side of distal end; distal trochlea separated by low and obtuse anteroposterior median ridge into two about equally large concaved facets; no medial malleolus, no downward pointed process at posterolateral corner of distal end. Astragalus wider than high, ridges of trochlea obtuse, about equally wide, median groove shallow, "neck" under trochlea high, anterior border of facet articulating with cuboid wide, facets articulating with calcaneus on plantar surface all low and wide. Calcaneus articualting with both tibia and fibula by small facets above and lateral to the cochlear process; cochlear facet articulating with astragalus wide and bifacial, bearing a considerably large tongue-shaped facet beneath. Facet articulating with cuboid facing downward and posteriorly so that the lower border of the bone slanting slightly upward posteriorly, seen from lateral side. Entocuneiform + MtI atrophied into a small lump of bone. MtIII wihtout contact with cuboid. Otherwise Mt's and Ph's of toes like Mc's and Ph's of fingers closely.

Comments: The taxonomy at generic level of the large-sized paraceratheres (*Paraceratherium*, *Dzungariotherium*, *Aralotherium*, etc.) has long been a perplexing and knotty problem. The sole specimen on which the genus *Paraceratherium* was established was a mandible from Baluchistan (Forster-Cooper, 1911). The most diagnostic feature of the mandible is the presence of a single pair of much enlarged and connate i1's, stretching forward (slightly downward too) among the incisors. The genus *Baluchitherium* was based purely on postcranial bones of enormous size from the same locality (Forster-Cooper, 1913a–b). The erection of the genus *Indricotherium* was based on richer materials, including large numbers of postcranial bones, but lacking adequate skull and mandible specimens (Borissiak, 1915a). Although better materials including skull and mandible were soon after obtained from Kazakhstan and Mongolia (Pavlow, 1922; Osborn, 1923), uncertainty as to the relationships between these genera lingered on among paleontologists for a long time (Forster-Cooper, 1924b; Granger and Gregory, 1936). In 1939, another genus *Aralotherium* was added (Borissiak, 1939). The situation had not been changed until 1959 when Gromova published her systematic revision of all the materials then known of the paraceratheres. Apart from *Pristinotherium* (Birjukov, 1953) and *Benaratherium* (Gabunia, 1955), which were poorly understood because of the paucity of material, Gromova retained two genera and three species altogether: *Indricotherium transouralicum* (= *I. asiaticum* and *Baluchitherium grangeri*), *Paraceratherium bugtiense* (= *Baluchitherium osborni*) and *P. prohorovi* (= *Aralotherium prohorovi*).

As early as 1936 Granger and Gregory held that *Paraceratherium*, *Baluchitherium* and *Indricotherium* could belong to one and the same genus. They listed 5 points of similarities between them (p. 54–62, *loc. cit.*) with special emphasis on the similarity between the type mandible of *Paraceratherium bugtiense* and AM 26166 mandible of *Baluchitherium grangeri*. However, they chose *Baluchitherium* to represent the whole group of these rhinoceroses. Recently, Lucas and Sobus (1989) explicitly proposed to include *Dzungariotherium* in this group as male representative, and substitute *Baluchitherium* by *Paraceratherium*. Nowadays, most of the American scholars support this view. Spassov (1989) only partly agreed on this point of view. He admitted that *Dzungariotherium* may be included in *Paraceratherium*, but insisted in retaining *Indricotherium* as an independent genus. McKenna and Bell (1997), Dashzeveg (1991), and most of Chinese colleagues (Ye *et al.*, 2003; Qiu *et al.*, 2004a) held the opinion that *Indricotherium* and *Paraceratherium* should be two separate genera.

However, the recent discovery of a skull in association with mandible and most of the vertebral column (TP 9401) in situ in Turpan Basin (*vide infra*) gave the last impetus to change our previous view. The mandible (TP 9401) is almost a replica of the type specimen of *Paraceratherium bugtiense*, and the associated skull shows the most diagnostic feature of *Baluchitherium grangeri* skull, i.e., the elongated muzzle with enlarged and downturned I1. Combination of similar features in upper and lower jaws can also be found in materials of *Indricotherium transouralicum* described by Pavlow (1922) from Turgai area, where some teeth of *Indricotherium asiaticum* were described by Borissiak (1923b). All of this convinced us that the skull from Loh Camp and the material from Turgai area should be congeneric with the type mandible of *Paraceratherium bugtiense* and the generic name *Paraceratherium* has undoubted priority (1911) over the others.

One of the corollaries of the above conclusion is the rehabilitation of the genus *Aralotherium*. The monotypic *Aralotherium prohorovi* as defined by Borissiak (1939) and fully described by Gromova (1959) is so different in muzzle and symphysis from *Paraceratherium* as now understood that it is highly inappropriate to group them into one and the same genus.

Paraceratherium grangeri (Osborn, 1923)

(Pls. XXI–XXII, XXIII 2–6; Tabs. 1, 7–9, 12, 14–17, 27, 29, 33, 35–45)

Baluchitherium grangeri (partim), Osborn, 1923: 4–9, Figs. 2, 3A, 4–5, 6A, 7A

[non] *Baluchitherium grangeri*, Teilhard de Chardin, 1926: 11–16, Fig. 6, Pls. I 3–7, II 1–9, 11–12

Baluchitherium grangeri (partim), Granger and Gregory, 1936 (*vide infra*)

[non] *Baluchitherium grangeri*, Young and Chow, 1956: 449 – 451, Figs. 2 – 3, Pls. I A – B, II

[non] *Indricotherium* cf. *grangeri*, Chow and Xu, 1959: 93 – 94, Pl. I

Indricotherium transouralicum (partim), Gromova, 1959: 33 – 38

Paraceratherium (partim), Lucas and Sobus, 1989: 367 – 373, Figs. 19.5B, 19.6B, 19.7B

Holotype: AM 18650, skull and mandible, largely restored and completed based on muzzle with right maxilla containing P1 – P4, left half of middle and posterior parts of skull, pieces of posterior half of left ramus of mandible, collected from Shand Member of Hsanda Gol Formation, 3.2 km SW of Loh Camp in Tsagan Nor Basin, Mongol, Early Oligocene.

Redescribed specimens: 1) AM 21618 [539], left and right manus and right pes of the same individual from about the same layer at a locality 0.8 km east of the type locality. 2) AM 26166 [745], mandible, and 26179 [731], left and right calcanei from Upper Naogangdai Formation ("Baron Sog·Baluchitheres" bed) at Urtyn Obo. 3) AM 26387 [874], left and right astragali, right cuboid, right MtIII, right PhI of middle toe and PhIII of lateral digit, from "Houldjin gravels" near Overnight Camp, 8 km east of Camp Margetts (= Daoteyin Obo).

Emended diagnosis: Size similar to *Paraceratherium asiaticum*, about 1/8 larger than *P. bugtiense* in length, but slightly smaller than *P. lepidum*.

Mandible differs from that of *P. bugtiense* in having slightly enlarged mandibular angle and slanting posterior border of ascending ramus, and the p2 less reduced in size.

Differs from *P. asiaticum* (features in brackets) in: lacking noticeable groove between hypocone and protocone on lingual side in P3 – P4 (weak, but present); hypocone situated posterior to metaconule in P4 (anterior to); presence of entolophid in p3 – p4 (entoconid isolated); development of deltoid tuberosity (scarcely noticeable) and ridge on lateral condyle of distal trochlea being very weak (clearly shown) in humerus; most carpal bones being wider (narrower) and anteroposteriorly shorter (longer); proximal facet of cuneiform articulating with radius being narrower (wider), facet of magnum articulating with McII being smaller (larger); astragalus proportionally wider and lower (narrower and higher); McII and McIV obviously shorter (nearly equally long) than McIII; proximal angles of PhIII of middle digit prominent (lacking).

Differs from *P. lepidum* in the following points (characters of *P. lepidum* in brackets): 1) Occipital condyle high, about 2/5 of nuchal surface (1/3); 2) paroccipito-posttympanic process smaller, total width of processes of both sides about equal with that of occipital condyles (wider than that of condyles) when seen from ventral side; lower border of process only slightly lower than that of occipital condyle (much lower); 3) posterior border of nasal notch situated above P4 – M1 (above M1 – M2); 4) muzzle part of skull robust and elongated, with much enlarged I1 (slender, I1 reduced); 5) posterior border of ascending ramus of mandible slanting posteriorly and mandubular angle lobate in form (vertical, no protruding angle); 6) upper dental formula: 1·1 – 0·4·3 (1·0·3·3); 7) P2 trapezoid in outline (triangular), antecrochet in M1 – M3 weak (stronger); 8) p2 larger, double-rooted, cone-shaped entoconid still observable (confluent with entolophid); 9) C1 – C7 about 1.5 times longer than skull length (close to twice), capita and vertebral fossae of C3 – C7 slightly wider than high (very flattened, dumb-bell in shape); 10) spinous processes of thoracic vertebrae comparatively short and narrow (particularly high and wide); and 11) limb bones comparatively longer and slenderer (shorter and more robust), proximal width less than 1/3 of length in tibia (>1/3), Mc's and Mt's longer (possibly shorter).

(1) Supplementary Description and Comparison

1) Material from Loh Camp, Mongolia

AM 21618, right carpal bones (lacking pisiform and trapezium)

Scaphoid (Pl. XXI 1, Tab. 14): The bone is irregularly cubic in form, with its distolateral angle on dorsal side very much protruded. It is only slightly longer (APD) than high and wide. Seen from dorsomedial side, it is trapezoid in form, with its dorsal border slanting dorsodistally, but the most protruding part of the volar border being at the middle (Pl. XXI 1a). The proximal articular facet is roughly rectangular in outline, wider posteriorly (Pl. XXI 1b). The anterior part of the surface is strongly convex, forming a wide and rounded transverse ridge, descending medially. Posterior to the ridge the surface is deeply concave. At the dorsomedial corner of the articular facet there is a small flattened part, which is the rudimentary "hindering facet". The distal end bears two facets articulating with magnum and trapezoid (Pl. XXI 1c $_{m,\ td}$). The small, semicircular facet articulating with trapezium is shifted mainly on the volar side (Pl. XXI 1e $_{tm}$). There are three facets articulating with lunar on the lateral side: two uppers and one lower (Pl. XI 1d). The posterior one of the upper two facets is situated lower and extends distoposteriorly.

The above described scaphoid is sharply different from that of *Juxia* in general form and morphology (*vide supra*). Taken as a whole, the scaphoid is closer to that of *P. asiaticum* than to *Aralotherium prohorovi* and *Turpanotherium elegans*. 1) The scaphoid of AM 21618 is proportionally higher. Its H/L ratio is 74.5%, falling within the range of variation in *P. asiaticum* (63.7% – 78.4%), lower than in *J. sharamurenensis* (79.4% – 84.7%), but higher than in *A. prohorovi* (67.3% – 69%) and *T. elegans* (62.7%). 2) The facet articulating with trapezium is present on the volar side of the bone in AM 21618 and in *P. asiaticum*, whereas it is very small in *T. elegans*, and absent in *A. prohorovi*. On the other hand, in *J. sharamurenensis* it is situated on the distal side, at the posterior end, facing distoposteriorly. 3) There are three facets articulating with lunar in AM 21618, whereas there are only two in the other forms. However, in *P. asiaticum* the posterior part of the upper facet turns downward similer to the case as in AM 21618.

The differences between AM 21618 and *P. asiaticum* are shown in greater width of the proximal facet articulating with radius and the presence of the rudimentary "hendering facet" in AM 21618.

Lunar (Pl. XXI 2, Tab. 15): It is pentagonal in dorsal view, with its lower angle more or less symmetrical in position. The proximal facet articulating with radius is strongly convex in anteroposterior direction, wider (104 mm) than long (80 mm), without posterior extension onto the volar process.

The lunar of AM 21618 is markedly differnet from that of *J. sharamurenensis*, where the bone is very high and narrow, its distal end primarily rests on unciform, and the proximal articular facet extends backward onto the volar process. In this respect, AM 21618 is closer to those of the large-sized paraceratheres so far known. The lunar is particularly close to that of *P. asiaticum* with the only exception that the proximal facet is slightly longer (113 mm) than wide (101 mm) in the latter. On the other hand, a "hindering facet" is developed at the anterior part of the proximal articular facet in all the other three forms, *P. bugtiense*, *A. prohorovi* and *T. elegans*.

Cuneiform (Pl. XXI 3, Tab. 16): Seen from lateral side, the cuneiform is roughly rectangular in form, with its lower border strongly concave. Proximally, the facet articulating with ulna is very large and the facet for radius is very small (Pl. XXI 3b $_{r}$). The facet articulating with pisiform is also small (Pl. XXI 3b $_{p}$, 3d $_{p}$), triangular in form, facing posteromedially. Distally, there is only one large articular surface for unciform, strongly concave anteroposteriorly. On medial side there are two facets for lunar: a circular upper one and a strip-formed lower one (Pl. XXI 3b $_{l}$).

The cuneiform of AM 21618 is distinct from that of *J. sharamurenensis* in size and general form. That of the latter is much smaller and very high in proportion. In size and proportion the cuneiform of AM 21618 falls within the range of variation of *P. asiaticum*, while those of *P. bugtiense*, *A. prohorovi* and *T. elegans* are all proportionally narrower and longer (Tab. 16 ratios 1 – 2). However, in relative sizes of the three proximal facets, AM 21618 is quite distinct from all other large-sized paraceratheres so far known. In the latter forms the facet articulating with radius and pisiform are considerably larger so that the combined surface of the two facets is about equally large as the main facet for the ulna, whereas they are much smaller in AM 21618. In this respect, AM 21618 is rather similar to *J. sharamurenensis*, where the facet for the radius is also very small, but that for the pisiform is proportionally larger. Therefore, the cuneiform of AM 21618 seems to be more plesiomorphic.

Trapezoid (Pl. XXI 4, Tab. 41): A small bone, triangular in outline when seen from above, but semicircular when seen laterally. The proximal facet articulating with scaphoid is very strongly convex anteroposteriorly, smoothly merging with the facet articulating with trapezium on volar side. Distally, there is only one flat facet articulating with McII. On lateral side the facets articulating with magnum forms a lain down letter Π.

Again, AM 21618 is closer to that of *P. asiaticum* than to those of other large-sized paraceratheres, especially in H/W and H/L ratios, whereas in all the other large-sized paraceratheres the trapezoid is higher, narrower and shorter in APD (Tab. 41 ratios 2－3).

Magnum (Pl. XXII 2, Tab. 42): Seen from the front, the magnum is roughly rectangular in form, wider than high. The concave upper border is shorter than the convex lower one, the lateral border slants distolaterally, and the upper lateral angle pointing upward. Proximally, there are two facets articulating with scaphoid and lunar respectively (Pl. XXII 2a $_{sc,\ l}$). The medial facet (for scaphoid) is fan-shaped, situated in anterior half of the bone; while the lateral one (for lunar) is strip-shaped in anterior half, but widened in posterior part on the prominent volar knob or "head." Distally, there is only one facet articulating with McIII. No contact with McII can be observed. The hook-like volar process is highly reduced, pointing slightly downward. This process can clearly be seen from ventral side, behind the facet articulating with McIII.

Direct comparison of this bone with that of *J. sharamurenensis* is impossible because of its lacking in the latter form. However, the restoration of the manus of *J. sharamurenensis* (Pl. XIII 3) shows clearly that its magnum is very narrow and high, in sharp contrast with the wider than high magnum in AM 21618 and all the other known large-sized paraceratheres. AM 21618 magnum differs from those of other large-sized paraceratheres in lacking a contact with McII, which is present in all the known specimens in the latter group. AM 21618 and *P. asiaticum* share one common plesiomorphic feature in magnum, i. e., the clearly demarcated volar processs, which is highly reduced in other known forms of large-sized paraceratheres.

Unciform (Pl. XXII 3, Tab. 17): In dorsolateral view, the bone is very irregular in form, wider than high (Pl. XXII 3a). Seen from above or below, the bone is roughly triangular in form, anteroposteriorly longer than wide, with protruded volar tuberosity. Both proximal articular facets (with lunar and cuneiform) are saddle-shaped, convex anteroposteriorly. In mediodistal side, the facets articulating with magnum, McIII and McIV are confluent, with a small facet articulating with McV shifted onto the posterior side of the bone. The volar tuberosity is well developed, protruded posteriorly and separated from the anterior articular facets.

The most remarkable feature of AM 21618 is its greater width relative to height and length (APD). No other paraceratheres have such a wide unciform (Tab. 17). AM21618 unciform is similar to those of *P. asiaticum* and *T. elegans* in having well separated volar tuberosity and the small facet articulating with McV on volar side. In *A. prohorovi*, both volar tuberosity and McV facet are highly reduced: the former is lost and the latters were found in 2 of 7 specimens.

2) Material from Upper Naogangdai Formation at Urtyn Obo

AM 26166, a mandible (Pl. XXII 1, Tab. 36): This specimen was briefly mentioned and figured by Granger and Gregory (1936, p. 3, Fig. 4 A－B). The right half of the symphysis is better preserved with the right i1 in situ (not so heavily broken as illustrated in Fig. 4 A by these authors). It is clear that the posterior border of the symphysis is situated at the level of the posterior end of p3. The i1 stretches primarily anteriorly, and the two i1's are not in direct contact with each other. The lingual cingulum of i1 is well developed and curved, extending mesially to form a basal projection, separated from the mesial border by a shallow notch. The p2 is double-rooted, without fully developed talonid, which is composed of a short hypolophid and an rudimentary entolophid. The posterolingual ridge of the metaconid is weak. The anterior border of the p3 is broad, but with the paralophid shortened, without reaching to the lingual cingulum. The posterobuccal corner of the protoconid is angular in form, but without rugosities. The entoconid remains conical in form, but connects with the low entolophid. The p4 is similar to p3, with its paralophid longer, reaching to the lingual cingulum.

In general morphology the mandible of AM 26166 is quite similar to those of *P. asiaticum* and *P. lepidum*, especially in the direction of the lower border of the symphysis, the anteriorly stretching i1 and the morphology of the premolars. However, the basal projection of the lingual cingulum in i1 is intermediate in strength between the above mentioned two forms. In *P. asiaticum* it is less distinct as described by Borissiak (1923b) and Gromova (1959), whereas in *P. lepidum* it is much more prominent.

AM 26179, two calcanei (Pl. XXIII 2, Tab. 39): The two calcanei are very similar in morphology, the right one is larger, but the left one is better preserved (Pl. XXIII 2). In dorsal view, the part above the cochlear process is the thinnest part of the body, widening gradually toward the tuber calcis. In plantar view (Pl. XXIII 2b), the lateral side of the distal part below the sustentacular process bulges strongly. In lateral view (Pl. XXIII 2a), the upper border of the tuber calcis is straight, and slightly rises posteriorly; the lower part below the cochlear process slightly narrows downward, with its anterior border slanting backward toward the distal end and the distal border rising more markedly than the upper border of the tuber calcis, but with its posterior end lying much lower than the cochlear process. On cochlear process there are two facets, the upper one (for articulation with tibia), and the lower one (with astragalus), forming a two-sided angle when seen laterally. The tongue-shaped facet extended from the large facet on cochlear process is very small in size, with its lower end lying far from the distal end of the bone.

AM 26179 is generally close to that of *P. asiaticum* described by Borissiak (1923b, Pl. IX 1b, 6a–b) in the following points: 1) The two parts of body above and below the cochlear process are about equally long. 2) The upper border of the tuber calcis is more or less straight, slightly ascending posteriorly. 3) The tongue-shaped small facet below the cochlear process is very small and short, with its distal end lying far from the distal end of the bone. 4) The posterior end of the distal facet articulating with the cuboid lies far below the level of the cochlear process. The minor differences between AM 26179 and that of *P. asiaticum* are the abrupt widening of the tuber calcis relative to the body below it and the larger size of the facet on the cochlear process relative to the sustentacular facet in *P. asiaticum* (Borissiak, 1923b, Pl. IX 6a).

3) Material from Overnight Camp, 8 km east of Camp Margetts (Daoteyin Obo)

AM 26387 [974], two astragali, a cuboid, an MtIII and some phalanges

Astragalus (Pl. XXIII 3, Tab. 29): The trochlea is slightly oblique, with the angle of obliquity being 100°. In anterior view (Pl. XXIII 3a), the trochlea is rahter symmetrical, with wide ridges, but narrow intermediate groove. The medial ridge is symmetrically convex, and the lateral ridge is higher than the medial ridge, and its convexity is asymmetrical, with its lateral half being rather flat. The distal border of the trochlea is clearly demarcated from the neck by a step-like ridge, which forms an asymmetrical notch under the intermediate groove. Seen from medial side (Pl. XXIII 3c), the medial ridge spans more than 1/4 circle, facing mainly upward. Seen from lateral side (Pl. XXIII 3e), the lateral ridge covers less than 1/4 circle, the radius of which is longer than that of the medial ridge, facing upward and dorsally. On plantar side (Pl.

XXIII 3d), there are four facets articulating with calcaneus: the largest one is the cochlear facet (3d c1), which is concave vertically; a small tongue-shaped facet lying beneath the former (3d a) facing posterodistally; the medial one is the sustentacular facet (3d b), which is rather large and oval in form, with its long axis stretching laterodistally, separated from the other facets; and the strip-shaped laterodistal facet (3d c2). On distal side (Pl. XXIII 3f), there are two facets: the major one is the medial facet articulating with navicular, which is saddle-shaped, transversely weakly concave, but anteroposteriorly strongly convex; the lateral one is strip-shaped, articulating with the cuboid, with its plantar end being downturned.

AM 26387 is closer to that of *P. asiaticum* than to *A. prohorovi* in a number of points: 1) The ridges are high over the rather deep intermediate groove; in contrast, these ridges are low and intermediate groove is shallow in *A. prohorovi*. 2) The lateral ridge of the trochlea is only weakly protruded laterally relative to the neck; whereas it is strongly protruded in *A. prohorovi*. 3) The boundary between the trochlea and the neck is sharply defined in contrast to not so sharply defined boundary in *A. prohorovi*. 4) Both cochlear and sustentacular facets are about equally wide and high, but these are wider than high in *A. prohorovi*. However, AM 26387 is relatively low in proportion, with its W/H ratio being 126.8%, higher than those in *P. asiaticum* (104% – 116%), but comparable to the lower values of the range of variation in *A. prohorovi* (125.2% – 150%).

Right cuboid (Pl. XXIII 4, Tab. 43): It is irregularly cubic in form, with a laterally situated plantar process (Pl. XXIII 4d). In dorsal view, the bone is rectangular in outline, slightly wider than high. There are two proximal facets articulating with astragalus (medial) and calcaneus (lateral), the medial one being strip in form and rather wide; whereas the lateral one being irregularly oval, with its medial border straight, but lateral border convex. On distal end there is only one facet articulating with MtIV, which is roundly triangular in form.

In general form and size, this bone is closer to that of *P. asiaticum* than to those in other known large-sized paraceratheres. In *A. prohorovi* the cuboid is rather long (APD) and narrow (Tab. 43 ratio 3), while in *D. orgosense* it is much wider than high when seen from the front (Tab. 43 ratio 1).

Right PhI of middle toe (Pl. XXIII 5, Tab. 44): This phalanx is comparatively high and long (APD), but narrower (transversely). The proximal facet is asymmetrically oval in outline, with the medial part longer than the lateral half, and weakly concave. The distal surface is shorter (APD) than the proximal one, but about equally wide as the latter, with shallow sagittal groove.

This phalanx is again closer to that of *P. asiaticum* described by Borissiak (1923b, Pl XI 3). In *A. prohorovi* this phalanx becomes much thinner and wider in proportion, with rather flattened proximal and distal articular facets.

PhIII of lateral digit (Pl. XXIII 6, Tab. 45): The bone is asymmetrical and high, with prominent proximal and distal lateral angles. The morphology of the PhIII's of lateral digits in *Paraceratherium grangeri* is almost unknown because of their poor presentation by Granger and Gregory (1936, Figs. 27, 30). In morphology the described phalanx (AM 26387) is rather close to the PhIII of lateral digit illustrated by Borissiak (1923b, Pl. XI 13). But it is smaller and proportionally slightly higher than the latter (Tab. 45). The PhIII of lateral digit of *Aralotherium prohorovi* as described and illustrated by Gromova (1959, p. 135 – 136, Fig. 23) is much larger, proportionally lower, with very long distal angle on lateral side. The PhIII of *Turpanotherium elegans* are highly reduced (*vide infra*), thus clearly distinguished from that of AM 26387.

(2) Discussion

Since 1959, when Gromova transferred *Baluchitherium grangeri* into *Indricotherium transouralicum* (corrected as *Paraceratherium asiaticum* by the present authors), most paleontologists have accepted this point of view. Although Chiu (1962) proposed to retain these two forms as separate species of *Indricotherium*, no positive response has been echoed.

Granger and Gregory (1936) lumped all the paracerathere materials found by the 3CAE from the Eren region into the single species *Baluchitherium grangeri*. At the same time, they fully admitted the large range of variations in size of that species, with the largest individuals being 1.4 times larger than the smallest ones, except for AM 26190 from Jhama Obo, the generic status of which was doubted by these authors. Several problems have arised as to the systematic position of the above mentioned materials. 1) Whether all the above mentioned materials could be attributed to one and the same species as Granger and Gregory did? 2) Whether *Baluchitherium grangeri* typified by the holotype skull from Loh, Mongolia (AM 18650) and *Indricotherium transouralicum* from Kazakhstan are to be synonymized into one species as Gromova did? 3) If the materials from Mongolia and Kazakhstan represent different species, which species the Eren materials should belong to?

In order to clear up these problems, we tried to reexamine as much of the 3CAE paracerathere materials from Eren region as possible. Owing to some practical problems (the storage rooms were being renovated, and some of the specimens are locked in the showcase, etc.), only a part of these materials were accessible for our examination. The main conclusions concerning the above problems are as follows. 1) Based on current taxonomy, the specimens from Mongolia plus Eren region and Kazakhstan are to be referred to two separate species of the genus *Paraceratherium*: *P. grangeri* and *P. asiaticum*. 2) Most of the specimens from Eren region listed by Granger and Gregory (1936), especially those from the "Baron Sog·Baluchitheres bed" at Urtyn Obo, and possibly from Overnight Camp, are attributable to *P. grangeri*, but there are others which should belong to other forms of paraceratheres, as stated below.

i. The Loh skull (AM 18650), compared to the newly discovered skull from Xinjiang (TP 9401), is undoubtedly referable to the genus *Paraceratherium* (*vide infra*). The manus and pes found from the same layer not far from the holotype skull (AM 21618) were only sketchily described, measured and figured by Granger and Gregory (1936). The pes is locked in the showcase and inaccessible for further study. However, the Fig. 30 in Granger and Gregory's paper (1936) seems to illustrate the pes rather faithfully. On the contrary, the Fig. 27 (*loc. cit.*) is far from being accurate in showing the form and interrelationship of the carpal bones. Fortunately, six of the carpal bones were accessible to us, and were thus redescribed (*vide supra*). Our study shows clearly that the carpal bones (AM 21618) are basically *Paraceratherium* in pattern, but differ from those of Kazakhstan described by Borissiak (1923b) in a number of morphological features, supporting the separation of the Loh materials from those from Kazakhstan as a separate species.

ii. Our research tends to also show that the material referrable to *P. grangeri* is principally confined to those found from the "Baron Sog·Baluchitheres bed" at Urtyn Obo and Nom Khong (Holy Mesa), and possibly from the "Houldjin gravels" at Overnight Camp. The paracerathere specimens found from Overnight Camp are slightly smaller than those from the "Baron Sog·Baluchitheres bed," however, they may well be referred to the same species as the latter ones. On the contrary, the paracerathere specimens from other localities represent other forms of paraceratheres. The materials from Jhama Obo and from the lower part of the Ulan Gochu Formation at Urtyn Obo section are to be referred to *Urtinotherium parvum* (*vide supra*); those from the upper part (?) of the Ulan Gochu Formation at Urtyn Obo section, including the radius mentioned by Wood (1938), and those from Camp Margetts (= Duhminbo'erhe; AM 26389, McIII) and from a locality 11 km west of Camp Margetts (Nuhtingbo'erhe; AM 26390, an axis) are referable to *Urtinotherium intermedium* (*vide supra*). On the other hand, the materials currently found from the typical "Houldjin gravels" around the city Erenhot are referred by us to *Aralotherium* sp. (*vide infra*).

Paraceratherium lepidum Xu et Wang, 1978

(Pls. XXIV-XXIX, XXX 1－3; Tabs. 1, 6－8, 11－12, 27, 35－38)

Paraceratherium zhajremensis, Lucas and Bayshashov, 1996: 540－545, Fig. 2
Paraceratherium tianshanensis, Zhang, Abuduresule, Liu *et al.*, 1997: 18－27, Figs. 1－2

Neotype: TP 9401, skull, mandible, C1－C7, T1－T17, Lm1－Lm3, left 1－17 ribs, right 1－2, 7－11 ribs, of the same old individual (~35 years old, *vide infra*), found from upper part of Taoshuyuanzi Formation at a locality ~1 km west of Feiyue Railway Station (possibly IVPP Loc. 64081), Late Oligocene.

Other referred specimens: 1) Turpan Basin, upper part of Taoshuyuanzi Formation, Late Oligocene: TP 9402, right tibia, found together with the neotype; TP 9403, right McIII, exact locality unknown; V 3194, left P4－M2, from near Feiyue (donated by Xinjiang Bureau of Petroleum); V 3195. 2, right humerus, IVPP Loc. 64080; V 3196, PhI－III in association with distal end of right MtIV and PhI－II of middle digit, IVPP Loc. 64081. 4; V 3300, PhI－III in association with distal end of right McII (or MtII?), IVPP Loc. 64081. 4; V 3303, right tibia with both ends of fibula, IVPP Loc. 64082. 2) West slope of Qianlishan Mountains, Nei Mongol, IVPP Loc. 78018, 8 km southeast of railway station of Taositu on east bank of Huanghe River, from upper part of Ulanbulak Formation, late Early－early Late Oligocene: V 3305, anterior part of right horizontal ramus of mandible, with p3－m1. 3) Atasui, middle Kazakhstan, Late Oligocene: KAN 2/632, posterior half of mandible, with talonid of m1 and m2－m3.

Diagnosis: Differs from *P. bugtiense* (features in brackets) in: being larger (mandible 4/5 as long as that of TP 9401); having very broad (APD) and transversely thick paroccipito-posttympanic process (narrow and thin); and a deep incisura vasorum on lower border of horizontal ramus anterior to the mandibular angle. Differences from *P. grangeri* (features in brackets) are: 1) Height of condyle about 1/3 of that of occiput (2/5). 2) Paroccipito-posttympanic process broader, with its posterior border slanting anteroventrally (vertically) and its lower end lying far lower than condyle (slightly). W of skull at paroccipito-posttympanic processes greater than that at condyles (about equally wide). 3) Posterior border of nasal notch lying above M1－M2 (above P4－M1). 4) Muzzle part of skull composed of the premaxilla and the anterior part of maxilla reduced, becoming slender and short (robust and long); L from anterior border of I1 to anterior border of P2 equals that of P2－M1 (equals P2－M2). 5) Posterior border of ascending ramus of mandible approximately vertical (slanting posteroventrally), without prominent angle (angle prominent). 6) Upper dental formula 1·0·3·3 (1·1－0·4·3). 7) P2 triangular in outline (trapezoid), upper molars with clearly shown antecrochet (very weak). 8) p2 highly reduced, single-rooted (large, double-rooted), entolophid fully formed in p3－p4 (entoconid partly separated from entolophid). 9) Cervical vertebrae particularly lengthened, L of C1－C7 almost twice as long as that of skull (1.5 times), capita and vertebral fossae in C3－C7 much wider than high, dumbbell in shape, with deep notches at the middle of upper border (slightly wider than high, oval, shallow middle notch). 10) Spinous processes of thoracic vertebrae particularly high and wide (comparatively low and slender), with very wide V-shaped rough areas on tops (narrower). 11) Limb bones may be short and thick (longer and slender), proximal widths of tibia, McIII and MtIII more than 1/3 lengths of these bones respectively (less), narrowest portions of McIII and MtIII in the middle 1/3 (at the level between the upper and middle 1/3).

(1) Description and Comparison

1) Specimens kept in Turpan Museum (TP 9401－9403)

TP 9401

Skull (Pl. XXIV, XXV 3－5; Tab. 1): The skull is laterally compressed, with its premaxilla and I1 destroyed during excavation. M1 is worn to the crown base, and M3 is in its middle wear stage.

Occipital view (Pl. XXV 3): It is bell-shaped, with its upper border being arched. Horizontal part of occipital crest is very rough, forming a rather wide band, attenuating bilaterally. Under the middle part of the occipital crest there is a deep depression of triangular form (not fully prepared), width of which at upper border measures 70 mm. The widest part of the upper half of the occipital surface lies at the level of the lower border of the depression, measuring 210 mm. The lateral border of the occipital surface becomes concave below this widest part. The surface below the depression strongly bulges, forming a two-sided, wide and rounded ridge. The condyle is about equally high and wide, both being about 104 mm. The linea divisa condyli (vide Flerow, 1957) is rather clearly shown, stretching laterally and upward. The foramen magnum is rectangular in form, 80 mm wide and 110 mm high. No sagittal notch on the upper border of the foramen, instead a pointed projection is present. The width of both condyles is 270 mm, while the widest part of the occipital surface, which lies slightly above the level of condyle, measures 300 mm.

Dorsal view (Pl. XXIV 2, XXV 4): The occipital crest is convex, forming almost a semicircle, seen from above. A sagittal groove is present on the parietal portion of the skull, 20 mm wide, extending anteriorly to the level of the glenoid cavity. The groove is bordered bilaterally by a pair of prominent ridges, the narrowest width of which is 55 mm. Bilateral to the ridges is a pair of lines for attachment of temporal muscles, the narrowest width of which is 95 mm. The sagittal part in the frontal portion is clearly bulged, bordered bilaterally by a pair of depressions extending anteriorly onto the posterior part of the nasals, probably for the attachment of the m. levator nasolabialis. The postorbital tuberosity is not prominent, and the supraorbital one is broken, but probably developed. The fronto-nasal suture is W-shaped, with the depth from the anterior sagittal point to the posterior-most part of the base measuring about 50 mm. The distance from the anteiror sagittal point of the fronto-nasal suture to the occipital crest is 605 mm. The width of the nasals at the level of the posterior end of the nasal notch is 120 mm. The distance from occipital crest to the anterior border of the I1 is estimated as 1290 mm. The width at the supraorbital tuberosities is 320 mm (lesser than actual one because of lateral compression of the skull). The premaxilla extends posteriorly toward the mesial side of the maxilla (Pl. XXV 4 $_{\text{pm}}$), with its posterior end reaching the level of the infraorbital foramen. The left and right premaxillae converge anteriorly and united at the level 50 mm anterior to the P2. The muzzle part was destroyed during the excavation (according to recollection of some participants). The part of the muzzle anterior to the dashed line (Pl. XXV 4) is thus restored in plaster.

Lateral view (Pl. XXIV 1): The profile of the parietal-frontal region is slightly concave, while the nasal slightly ascending anteriorly. The occipital crest overhanges little over the occipital surface, still lying anterior to the condyle. The lateral part of the occipital crest stretches downward onto the lateral side of the posttympanic process. The paroccipito-posttympanic process is very large: 200 mm high, 83 mm thick (transversely), 170 mm long (APD) at upper side, and 120 mm long at lower end, which lies 80 mm below the condyle. The posterior part of the zygomatic arch ascends sharply, with the lateral surface of this part roughened. No clear postorbital tuberosity is visible. The anterior border of the orbit lies above and slightly posterior to the anterior border of the M3. The nasal notch is deep, extending posteriorly close to the orbit, lying above the middle of M2. A lacrimal tubercle is seen at the anterosuperior border of the orbit. The infraorbital foramen is round, 25 mm high and 20 mm long, situated above P4 – M1, 105 mm away from the posterior end of the nasal notch, horizintally measured. The lateral border of the nasal bone turns downward. The posterolateral part of the nasal expands onto the facial part, forming a branch lying below and posterior to the nasal notch. The cross section of the nasal is bean-shaped (Pl. XXIV 3). Anterior to P3 the premaxilla lies above the maxilla, becoming thickened transversely, reaching 43 mm in width. The premaxilla-maxilla suture descends anteriorly, ends 80 mm anterior to the P2. The premaxillar body is roughly horizontal in direction, with its anterior end turned downward. A groove is present on dorsal side between the two premaxillae. L from anterior border of I1 to P2 is 270 mm, while that from posterior border of I1 to P2 is 230 mm.

The measurements not included in Tab. 1 are (in mm): Distance from posterior border of postglenoid process to posterior border of condyle, 280; from posterior border of condyle to anterior border of orbit, 750; from posterior border of condyle to posterior border of M3, 685; from occipital crest to broken point of nasal, 845; from occipital crest to posterior border of nasal notch, 710; from posterior border of condyle to P3, 1050; to M2, 880; from posterior border of nasal notch to anteiror border of I1, 580; and height from the most convex part of nasal to alveolar border, 385.

Upper teeth (Pl. XXV 5, Tab. 38): I1 is missing. The I1 shown in Pl. XXIV 1 is a restored one in plaster. The upper cheek tooth series lacks a P1. P2 is triangular in crown outline, with its buccal wall convex. Parastyle and parastyle fold are almost invisible. Metoloph is thin in middle part, but thick and convex at lingual end. Medifossette is small and round in form, and the medisinus is very shallow. The anterior cingulum is obliterated due to wear, but the lingual cingulum is well developed. The buccal cingulum is complete, ascending toward crown surface at posterior end. The convexity of the buccal wall of P3 is weaker than that of P2. Protoloph stretches lingually and posteriorly, while metaconule is semilunar in from, widely connected with ectoloph, but thinly with anterior part of hypocone. Medifossette triangular in form, and the outlet of medisinus is narrow and pointed. The lingual cingulum is complete and well developed, ascending posteriorly. The buccal cingulum is weakly W-shaped. The buccal wall of P4 is flat, while the lingual wall is rounded. The metaconule is thicker than that in P3. The medifossette is irregularly triangular in form, with weakly expressed crista. The medisinus is shallow. The buccal cingulum is similar to that of P3. The anterior cingulum is clearly shown in its buccal half, but weak and thin in lingual half. The anterior part of the lingual cingulum forms a tubercle, while posteriorly the lingual cingulum becomes confluent with the posterior cingulum.

M1 is heavily worn, with a shallow anterior constriction fold of hypocone and rounded triangular medifossette. The buccal cingulum is W-shaped, with its middle peak low and rounded. The lingual cingulum is only seen at the outlet of the medisinus. The buccal wall of M2 is flat. The parastyle, parastyle fold and paracone rib are closely situated. The antecrochet closes the medisinus, and forms a closed medifossette at the crown base. The lingual side of the protoloph is round, with weak anterior constriction fold. The lingual side of the metaloph is narrow, with clear anterior constriction fold. The anterior cingulum ends lingually at the anterolingual angle of the protocone. The weak lingual cingulum is present only at the outlet of the medisinus. The posterior cingulum is high and prominent, but separated from the ectoloph by a deep notch. The buccal cingulum is W-shaped as well. The parastyle, parastyle fold and paracone rib of M3 are all very prominent. The posterior constriction fold of protocone becomes clearer towards its base. No clear boundary is visible between the ectoloph and metaloph. The ecto-metaloph is curved. A tubercle is present at the posterior part of the outlet of the medisinus. The anterior cingulum is very wide, while the lingual cingulum extends to the lingual side of the hypocone. The buccal cingulum begins posterior to the paracone rib, strengthening posterolingually, and ends posterobuccally to the hypocone.

Based on a skull (V 4322), Xu and Wang (1978) established a new species, *Paraceratherium lipidus* (corrected as *P. lepidum*, *vide infra*). Judged from Zhai's description (1978), this skull could be collected from the upper 100 m of the Taoshuyuanzi Formation in the same small area as TP 9401 did. The skull is now on exhibit at the Beijing Museum of Natural History. V 4322 is close to TP 9401 in size (Tab. 1). They are similar in the morphology of occiput, paroccipito-posttympanic process and M2 – M3, in the position of nasal notch and orbit, etc. However, V 4322 differs from TP 9401 in having narrower space between the paired parietal ridges and stronger lingual cingulum in M2 – M3 (Xu and Wang, 1978, Pl. I 2, 4). Unfortunately, V 4322 lacks its muzzle part, so that the most important part of the skull can not be directly compared between these two specimens.

Although similar to TP 9401 in a number of features (sagittal crest, occiput, loss of P1, P2 morphology, etc.), the holotype skull of *Dzungariotherium orgosense* differs from TP 9401 widely in having much more reduced muzzle part with atrophied I1, very much widened paroccipito-posttympanic processes, more posteriorly retreated nasal notch, etc.

Mandible (Pl. XXVI, Tabs. 35 – 36): The lower border of the mandible is rather straight from below the p4 backward until to the point slightly posterior to the anterior border of the ascending ramus. Anterior to the straight part the lower border is deeply concave until to a point slightly posterior to the base of the i1. The straight part is posteriorly bordered by a wide and deep concavity, possibly corresponding to the incisura vasorum in horse, anterior to the narrow angle of the mandible. The lateral surface of the horizontal ramus is flat, but the medial surface is convex. In dorsal view, the symphyseal part is narrow and short, suddenly narrowed anterior to the p2 (Pl. XXVI 3), with its posterior border lying at the level of the middle part of the p4. Its lingual surface is trough-like, deeply concave transversely, but slightly convex longitudinally. The alveolar border anterior to the p2 is blunt first, then becoming sharp and steeply downturned (Pl. XXVI 1). The lower border of i1 remains slightly higher than the straight part of the lower border of the mandible. The mental foramen lies below the p2.

The lower half of the posterior side of the ascending ramus is very wide and roughened (Pl. XXVI 2), facing posterolaterally, with its widest part lying at the lower end. This rough area serves obviously as the attachment of the m. sterno-massetericus (the lower branch of the m. sterno-cephalicus). The postcotyloid process (Pl. XXVI 2 c) is prominent, articulating with the postglenoid process of the skull by its mesial surface. The anterior side of the ascending ramus is mostly sharp. The coronoid process is short, with its base very wide but the top posteriorly curved and pointed. The mandibular notch between the coronoid process and the condyle is wide and shallow. The condyle forms a semicylindrical beam slanting slightly downward and medially. The masseter fossa is rather large, but shallow. The mandibular foramen is voluminous, with its posterior groove stretching toward the lower part of the condyle.

The measurements not included in Tab. 35 are (in mm): horizontal L of i1 – p2 diastema, 95; H of horizontal ramus under the posterior half of the m3, 180; D between m3 and the posterior border of ascending ramus, 290; Min H of ascending ramus, 370; H of coronoid process, 100; W of articular surface of condyle, 205; Max W of rough surface for the m. sterno-massetericus, 85; Max H of symphysis, 88; and H of i1 alveolus, 63.

Lower teeth (Pl. XXVI 1, 3 – 7; Tabs. 35 – 36): Seen from lateral side, the lower border of the i1 is about horizontal, while its upper border slanting downward anteriorly. On lingual side there are two ridges converging anteriorly. The mesial cingulum is very prominent, forming a tubercle at the posteroventral corner of the tooth (Pl. XXVI 4). The cross section of the i1 is oval, with its longer diameter lying in superolateral-inferomesial direction. The p2 is very small, single-rooted, but the lingual side of the root is grooved. The crown surface is triangular in outline, anteriorly pointed (Pl. XXVI 7). The paraconid is already separated, while the talonid groove is formed by the posteromedial ridge of the metaconid and the entolophid. Both buccal and lingual cingula are well developed. The crown surface of the p3 is trapezoid, double-rooted. The posterobuccal angle of the protoconid is blunt. The lingual cingulum is complete, while the buccal one is well developed and weakly W-shaped. The p4 and m1 are heavily worn. In m2 the talonid is half closed by weakly developed lingual cingulum, while the buccal cingulum is more developed, but only very slightly W-shaped. The crown surface of the m3 is the best preserved one among the lower cheek teeth. The paralophid is comparatively thin, but with a strong bulging in its middle part so that the trigonid basin is blocked here when heavily worn (Pl. XXVI 6). The talonid is very long relative to the trigonid, bordered by a crested lingual cingulum and the ridges descended from the metaconid and entoconid. The posterior part of the buccal cingulum is only weakly developed, while the posterior cingulum is well developed, forming a convexly curved line.

As stated above, the mandible of TP 9401, especially its symphyseal part, is very close to the holotype of *Paraceratherium bugtiense* and the specimen AM 26166 of *P. grangeri* (Granger and Gregory, 1936, Fig. 4A – B; Pl. XXII 1 in this volume). The features commonly shared by TP 9401 and the holotype of *P. bugtiense*, but not by AM 26166 of *P. grangeri*, are: 1) The posterior border of the ascending ramus is vertical, without a prominent mandibular angle. 2) The anteriorly positioned mental foramen below and anterior to the p3. 3) The highly reduced and single-rooted p2.

It is highly interesting to note that the posterior part of a mandible (KAN 2/632) described by Lucas and Bayshashov (1996) as a new species of *Paraceratherium*, *P. zhajremensis*, is almost identical with that of TP 9401. This is not only clearly shown in the morphology of m2 – m3, but particularly so in the presence of a wide and deep notch (incisura vasorum) on the lower border of the horizontal ramus anterior to the mandibular angle.

Atlas (Pl. XXVII 1, Tab. 6): The atlas is completely preserved. The part containing the anterior articular cavities is very much anteriorly protruded, about 90 mm away from the anterior border of the wing. The alar notch forms an obtuse angle. The anterior border of the dorsal arch bears a shallow U-shaped sagittal notch, bordered bilaterally by a pair of prominences. Together with the rough area lying behind, the prominences form a triangular rough area representing the spinous process, which ends roughly at the boundary between the anterior 2/3 and the posterior 1/3 of the dorsal arch. The paired posterior articular facets form a wide curve, which is wider than the anterior articular cavities, seen from above. The dorsal arch ends posteriorly 10 mm anterior to the posterior articular facets, instead of being at the same level as the latter (Pl. XXVII 1a). The intervertebral foramen (Pl. XXVII 1a) is situated slightly anterior to the level of the anterior border of the wing.

The wings are rather long anteroposteriorly, implanted obliquely relative to the central part of the atlas, with its dorsal surface facing upward and posteriorly. The anterior border of the wing is very short and slants backward, confluent with the lateral border, forming a smooth curved line, thickened and roughened posteriorly. A short groove links the alar notch with the intervertebral foramen. On the posterior side of the wing, at the upper 1/3 of and close to the lateral border of the posterior articular facet, is the small posterior orifice of the vertebrarterial canal. The ventral side is perforated by the foramen alare inferior at the anteromesial corner of the wing (Pl. XXVII 1b).

The Max projected L is 315 mm, H at the anterior articular cavities is 215 mm.

So far only a few specimens of atlas are known in paraceratheres: two more or less complete ones for *Aralotherium prohorovi*, one complete for *Paraceratherium bugtiense*, and one for *P. asiaticum*. The atlas of *P. bugtiense* (Forster-Cooper, 1924a, Figs. 1 – 2; Fig. 16 in this volume) is very peculiar in form and differs widely from others. Its wing is particularly narrow transversely, the alar notch is deeply incised, the posterior orifice of the vertebrarterial canal has shifted upward to the dorsal side of the wing, and a pair of large tuberosities are developed at the anterior margin of the dorsal arch. It is important to note that similar, but smaller, tuberosities, are also found in TP 9401, but not in other forms. The atlas of *A. prohorovi* is also quite different in form. In this species, the anterior part containing the anterior articular cavities is further protruded relative to its wings, the intervertebral foramen is very large and posteriorly shifted, the wing is more or less widened laterally, and the vertebrarterial canal is already considerably inflated (Gromova, 1959, Pls. V – VI). According to Gromova, in *P. asiaticum* the posterior opening of the vertebrarteial canal is situated lateral to the posterior articular facet, the vertebrarterial canal is only slightly inflated, the anterior border of the wing is directed laterally and slightly posteriorly, but the alar notch forms an acute angle (Gromova, 1959, p. 35). Taken as a whole, TP 9401 is more similar to that of *P. asiaticum* in general, with the only difference in the acute angled alar notch in the latter. TP 9401 is similar to *P. bugtiense* in having a pair of anterior prominences on dorsal arch, though weaker, but otherwise the two forms are quite different. TP 9401 is similar to *A. prohorovi* only in the widening of the wing and the confluent anterior and lateral borders; otherwise they differ widely.

Axis (Pl. XXVII 2): The body of the axis is very elongated, with a long and pointed odontoid process. The paired anterior articular facets inversely conform to the posterior ones of the atlas. The vertebral fossa is shallowly concave, and takes the form of a dumb-bell with its middle parts of the dorsal and ventral sides slightly concave (Pl. XXVII 2e). The ventral side of the body is weakly concave in its anterior 2/3, with a weakly expressed mid-ventral keel in its posterior 1/3 (Pl. XXVII 2c). The spinous process is not very high, but very thick transversely. Its dorsal side is roughly lozenge-shaped, with its anterior end forming an arrowhead. Posteriorly, the dorsal side is gradually widened, reaching the maximum width at the posterior end of the anterior 2/3 of the total length of the axis, then sharply narrowed down. The sagittal portion of the dorsal side is sunken, bordered by a pair of prominences at the widest part of spinous process and a pair of sharp and narrow ridges in the posterior 1/3 of the process (Pl. XXVII 2a). In lateral view, the spinous process has a deeply concave anterior border, making the anterior end of the dorsal side pointed and overhanging the anterior articular facets. The dorsal side forms a gently arched curve at the anterior 2/3, suddenly dropped down at this point and then sloped gently until to its posterior end of the postzygapophysis, which extends far away posterior to the axis body (Pl. XXVII 2b). The vertebrarterial canal (= canalis transversarius) is very long, situated in the middle part of the body. Both of its anterior and posterior openings are large. The transverse process is small, begins at the middle part of the vertebrarterial cannal, then extends posterolaterally, forming a slender posterior process (Pl. XXVII 2c).

Some of its measurements are (in mm): Total L, 660; Max H, 340; L of body + odontoid process, 580; L of odontoid process, 110; W of anterior articular facets, 300; W of vertebral fossa, 220; Max H of it, 145; H at its middle part, 120; Max W of axis with transverse processes, 335; Max W of spinous process, 160; Min L of vertebrarterial canal, 125.

The axes of paracerathere are very poorly known. The axis described by Granger and Gregory(1936) as *Baluchitherium grangeri* (AM 26390) has turned out to belong to *Urtinotherium parvum* (*vide supra*). Compared with it, TP 9401 is much larger (660 mm versus 486 mm of total L, etc.). Morphologically they are also different. In AM 26390 the dorsal side of the spinous process ascends more steeply in its anterior 2/3 and its climax is situated above the anterior part of the postzygapophysis, whereas in TP 9401 the profile is almost horizontal and the climax is situated anterior to the postzygapophysis. Secondly, in AM 26390 the posterior 1/3 of the spinous process is ridge-like, whereas in TP 9401 it is trough in shape. Furthermore, its vertebral fossa is roughly oval in shape, whereas in TP 9401 it is dumb-bell in shape. The preserved anterior part of the axis of *Aralotherium prohorovi* (Gromova, 1959, Pl. VII 1) is rather similar to that of TP 9401, but is certainly samller than the latter.

C3 (Pl. XXVIII 1, XXIX 1; Tab. 7): The caput of the body takes the form of a broadened dumb-bell, with its H at lateral side 132 mm and 105 mm at the middle. It is strongly convex centrally, with its lateral portions being rather flat. The vertebral fossa has the same form, but concave, W of which reaches 230 mm, lateral H 130 mm. The ventral side of body is longitudinally concave, but flat transversely, with a weak mid-ventral keel in the anterior 2/3.

In dorsal view, the plate formed by the pre-and postzygapophyses forms roughly an elongated rectangle. The prezygapophyses do not go beyond the caput, with deep and wide notch between them; while the postzygapophyses extend 90 mm further backward than the vertebral fossa, and the notch in-between is covered by the posterior end of the spinous process. The articular facet of the prezygapophysis faces upward and slightly mesially, while that of the postzygapophysis, downward, slightly laterally and posteriorly (Pl. XXVIII 1a-b). The angle formed by the planes of the pre-and postzygapophyses is about 10° (Pl. XXVIII 1a). The dorsal surface of the part of the neural arch between the pre-and postzygapophyses is flat or weakly concave and bears a number of nutrient foramina. The spinous process is very low and crested, widening posteriorly, with its dorsal side covered by irregular crests and rugosities.

The transverse process is bifid. The anterior branch is long and plate-like, with its distal end being strongly rugose. It extends anteroventrally and slightly laterally. The posterior branch is very short and pointed, extending principally laterally. The two branches are linked by a strongly curved lateroventral ridge. The vertebrarterial canal is 185 mm long, with its anterior opening located 46 mm posterior to the anterior border of the caput, and the posterior opening 129 mm anterior to the lateral border of the vertebral fossa.

Some measurements of the C3 not included in Tab. 7 are (in mm): L of body measured from the caput centre, 445; Max W at posterior branch of transverse process, 400; W at anterior branch of transverse process, 375; L of anterior branch of transverse process from base to tip, 108.

C4 (Pl. XXVIII 1, XXIX 1; Tab. 7): Its form is very close to that of C3, but differs in a few points. It is shorter and wider than C3 (Tab. 7), more clearly shown in dorsal view (Pl. XXVIII 1b). Its spinous process is lower and narrower than that in C3. The articular facet of the prezygapophysis faces not only upward and slightly mesially, but also slightly anteriorly, so that it is about parallel with that of the postzygapophysis, although both are oblique to the dorsal surface of the neural arch. Both branches of the transverse process are better developed than in C3 (Pl. XXVIII 1a-b), and the vertebrarterial canal is more inflated as illustrated by its larger anterior and posterior openings. Max W at posterior branch of transverse process is 480 mm.

C5 (Pl. XXVIII 2, XXIX 1; Tab. 7): It is further shortened, shorter than C4 (Tab. 7). The caput is more convex, especially in transverse direction, but with a weaker concavity at the middle of the upper border. Both pre-and postzygapophyses are larger, and their articular facets are bean-shaped and diagonally oriented. The median notch between the prezygapophyses is more or less V-shaped, rather than wide U-shaped as in C3-C4. The spinous process is present only in the anterior half of the vertebra. The anterior branch of the transverse process is more developed than in C3-C4, but the posterior branch is narrower and more pointed. Otherwise the C5 is similar to C4.

C6 (Pl. XXVIII 2, XXIX 1; Tab. 7): It is shorter than C5 (Tab. 7). In dorsal view, the plate formed by the pre-and postzygapophyses are trapezoid in form if the median notches between the zygapophyses were not taken into consideration. The trapezoid is wider than long and narrowed posteriorly, and the median notches are particularly wide (Pl. XXVIII 2b). The transverse process is bifid, separated not into anterior and posterior branches, but into horizontal and vertical ones, both of which are more or less plate-like. The upper or horizontal branch slants slightly downward. The lower or vertical branch is plate-like and thin, only very weakly separated into anterior and posterior lobes. A plate of irregular form links the horizontal and the vertical branches at their anterior bases. The verterarterial canal is short, but inflated. Its posterior opening is wider (85 mm) than high (50 mm), and bordered below by a horizontal plate, which is the posterior extension of the plate linking the horizontal and the vertical branches.

C7 (Pl. XXVIII 3, XXIX 1; Tab. 7): C7 is the shortest of the cervical vertebrae (Tab. 7). The caput is wider than high, and semispherically convex. The vertebral fossa is deeply concave, bean-shaped, without clear median notch on its upper border, but that on the lower border being more or less clearly expressed. In dorsal view, the width of the prezygapophyses reaches 500 mm, the widest among all the cervical vertebrae. The planes of the articular surfaces of the pre- and postzygapophyses are subparallel, strongly oblique relative to the long axis of the body. The transverse process is column-like, extending slightly downward. Neither vertebrarterial canal nor posterior facets for the articulartion of the first ribs are present.

The total L of the mounted 7 cervical vertebrae measured from the anterior-most point of the atlas to the upper border of the vertebral fossa of the C7 is 2440 mm. The estimated length of all the cervical vertebrae, minus 270 mm (the extra spaces between the vertebrae left in the mounted skeleton), is about 2170 mm.

Very few articulated and complete cervical vertebrae of paraceratheres have so far been described. The better material may be the C4, C6 and C7 of *Paraceratherium grangeri* reported by Granger and Gregory (1936). Compared with that of TP 9401, the C4 of AM 26168 (*loc. cit.*, Fig. 8) is not only smaller and proportionally wider (Tab. 7 ratio 1), but differs also in morphology. The caput (and the vertebral fossa) in C4 of AM 26168 is about semicircular in outline, with its upper border more or less straight and lower border strongly convex, while that in TP 9401, dumb-bell in shape. Further differences of the cervical vertebrae of TP 9401 from those of *P. grangeri* (features in brackets) can be pointed out as follows: The two branches of the transverse process in C4 are well separated (little differentiated), the posterior branch is much smaller than the anterior branch (not so much smaller). On the other hand, the transverse process in C6 is bifid (clearly trifid; *loc. cit.*, Fig. 9). The C7 is longer (shorter; *loc. cit.*, Fig. 10).

Of the material of *Paraceratherium bugtiense* there are only a C3 (or C4) and a fragmentary C6 (Forster-Cooper, 1924a). Compared with those of TP 9401, the C3 (or C4) is smaller, but with a very inflated vertebrarterial canal expressed by the large anterior and posterior openings of that canal (*loc. cit.*, Fig. 5). The C6 described by Forster-Cooper (*loc. cit.*, Figs. 6 – 7) has a bean-shaped caput, with little expressed median notches on upper and lower borders, while in TP 9401 the caput takes the form of a dumb-bell. Furthermore, the vertebrarterial canal in the C6 of the former form is so inflated that the vertebra becomes totally hollowed as illustrated in Forster-Cooper's Fig. 7, which is certainly not the case in TP 9401.

The cervical vertebrae of *Aralotherium prohorovi* are poorly known because of the poor state of their preservation. Taken as a whole, the cervical vertebrae of *Aralotherium prohorovi* are smaller (Tab. 7) and possess more inflated vertebrarterial canals than those in TP 9401, as stated by Gromova (1959).

Thoracic vertebrae (Pl. XXIX 2): Altogether there are 17 preserved, most of which are apparently associated, and T1 – T3, T4 – T5, T6 – T8 and T9 – T10 are still adhered together. Since all of the thoracic vertebrae are fixed in the mounted skeleton, it is not possible to picture them separately, although closer observation is generally allowed.

The thoracic vertebrae can be summarily described as a whole as follows:

The L's of the bodies change little. The body of T1 is the longest, shortened slightly backward to T3, and from then on the L's of the bodies become more or less constant, varying between 95 – 115 mm. The L's are as follows (in mm): T1: 145, T2: 130, T3: 125, T4: 110, T5: 110, T6: 115, T7: 100, T8: 95, T9: 100, T10: 90, T11: 115, T12: 110, T13: 105, T14: 100, T15: 95, T16: 100. The bodies of the anterior several T's are broad and low, becoming narrower and higher backward. At least the body of the T5 is still wider than high.

The transverse processes in the anterior several T's are very robust, making the vertebrae particularly wide, but diminish rapidly until T5. The Max W of T1 is 510 mm, while that in T5, 310 mm. The T's posterior to the T5 remain more or less equally wide. The mammillary tubercles on the prezygapophyses appear from the T5, and become very high and prominent from the T10 posteriorly.

The cranial costal facets are confluent with the facets articulating with the tubercles of the ribs on the ventral sides of the transverse processes in T1, otherwise both cranial and caudal costal facets are normally developed in majority of the T's except for the last several T's, where possibly only the cranial costal facets are present. The costal facets are situated highest in the middle T's, shifted lower both anteriorly and posteriorly. The caudal costal facets are situated at the ventral border of the vertebral fossa in T1, shifted upward posteriorly, already at the upper border of the vertebral fossa in T5.

All the spinous processes are high and robust, especially in the anterior T's. They slant posteriorly, thus, no diaphragmatic vertebra is present. On the lower 2/3 of the anterior sides, median ridges are formed, becoming sharper and crested posteriorly. The spinous processes are particularly high, all around 550 mm high, in T1 – T5. They become gradually shorter posterior to the T5. The shortest spinous process is higher than the height of the body in posterior T's. The spinous process of T1 is the widest and thickest. They become narrower and thinner posteriorly.

The following is a brief description of some of them separately.

T1 (Pl. XXIX 1 – 2, Tab. 8): The caput is smaller than that of C7, strongly convex, kidney-shaped with its upper border slightly concave. The vertebral fossa is wider than the caput, and bordered by a pair of round facets articulating with the heads of the second ribs (caudal costal facets). The prezygapophysis is very robust, flaring widely upward and laterally. The articular facet on it is more or less rectangular in form, 125 mm wide and 120 mm long. The facet is weakly convex, facing upward and anteriorly. The transverse process is very robust, extending slightly downward, with its cross section being rectangular, 140 mm long and 85 mm thick. Its lateral surface is rugose, while its ventral side is concave, with a large surface articulating with the tubercle of the first rib. No cranial costal facets are present in the anterior part of the body or at the borders of the caput. The spinous process is extremely long and robust, 550 mm long measured from the top of the vertebral canal, and 185 mm wide at its base, slanting backward. The process becomes gradually widened upward, reaching 245 mm wide at its top. It is deeply excavated posteriorly, thus the cross section of the process forms a two-sided angle, which is about 120° at the base. The median ridge on the anterior surface of the spinous process is clearly shown in most part of the anterior side, fading out only at the uppermost part. The top of the process is very rough and thick, 70 mm at the thickest part.

T2: It is similar to T1 in morphology. Max W of T2 at the transverse processes is 480 mm. The costal facets face mainly downward. L of body: 130 mm; W of caput: 190 mm, with cranial costal facets, 200 mm; while W of vertebral fossa with caudal costal facets: 340 mm. H of spinous process measured from the upper border of the transverse process 530, with its top 110 mm higher than that of T1.

T3: L of body: 125 mm. Max W of T3 at the transverse processes: ~400 mm. The caudal costal facets are separated from the vertebral fossa and situated in the upper half of the body, facing posteriorly and laterally. W of vertebral fossa: 180 mm. The top of the spinous process is 90 mm higher than that of T2, and its W: 195 mm.

T4 (Tab. 8): W of caput without cranial costal facets: 170 mm. The transverse process is situated posterior to the caput. The spinous process is the highest of the thoracic vertebrae, with its top 110 mm higher than that of T3. The total H of T4 from ventral side of body to top of spinous process: 720 mm.

T5: L of body: 110 mm; H of vertebral fossa: 150 mm; and Max W of T5 at the transverse processes: 310 mm. The caudal costal facets are situated at the upper border of the vertebral fossa. Top of spinous process is 60 mm higher than that of T4. The highest point of the skeleton is at the tops of the T4 – T5, where the H taken from ground to the tops of the spinous processes is 3730 mm.

T6 – T13: From T6 backward the spinous processes become gradually shorter and thinner, and the slant becoming stronger. From the T9 backward the tops of the spinous processes become more robust than the parts immediately below them. The transverse processes are smaller and rode-like.

T14 – T16: They are heavily plastered so that no useful information is afforded.

Posterior to the T16 there are three other vertebrae, even more heavily plastered, without transverse processes preserved, nor ribs attached to them. It is difficult to determine whether they are thoracic or lumbar vertebrae based on such a poor state of preservation.

The T1 is the best known among the paracerathere thoracic vertebrae. Borissiak, Forster-Cooper and Granger and Gregory described the T1's of *Paraceratherium asiaticum*, *P. bugtiense* and *P. grangeri* respectively. All these T1's are smaller than that of TP 9401 (Tab. 8). Compared with other T1's, that of TP 9401 has wider body and vertebral foramen, and much more robust spinous process.

The T2 – T16 were described by Borissiak (1923b) for *Paraceratherium asiaticum*, and Granger and Gregory (1936) for *P. grangeri*. All of them are smaller in size (Tab. 8), and have weaker spinous processes, which are less deeply excavated posteiorly.

Ribs: Of the right side the ribs 1 – 16 and the 18th are original, but the 17th is a restored one.

Rib 1 (Pl. XXIX 3): It is fan-shaped, 700 mm in total length. The head turns medially away from the long axis of the shaft of the rib, whereas the tubercle is aligned with the shaft. The articular facets of the head and tubercle are confluent into a larger one of dumbbell in shape, Max W of which is 128 mm. The narrowest part of the rib immediately below the tubercle is 76 mm (APD), and the widest part of the rib at its distal end is 235 mm, 55 mm thick.

Rib 2: It is oval in cross section (80 mm × 30 mm in middle part), distal end broader (110 mm × 55 mm). Rectilineal L of the rib: 745 mm, while its curvilineal L: 800 mm.

Rib 3: The rib is strongly curved, with its head and tubercle well separated, but its distal end not particularly robust. Rectilineal L of the rib: 1035 mm, while its curvilineal L: 1160 mm. W (APD) of proximal end: 135 mm, at middle: 100 mm, 20 mm thick.

Rib 4: The proximal end is robust with large head and tubercle, 135 mm wide, 40 mm thick. The rib becomes thinner distally, with its distal end being concave and roughened, 100 mm wide and 40 mm thick. Rectilineal L of the rib: 1180 mm, while its curvilineal L: 1330 mm.

Rib 5: The rib remains plate-like. Its proximal 1/3 is 90 mm wide and 25 – 30 mm thick. Rectilineal L of the rib: 1370 mm, while its curvilineal L: 1590 mm.

Rib 6: The tubercle is small, and lying far away from the head. The cross section of the proximal half of the rib takes the form of a comma, with its anteromedial border pointed and posterolateral border convex. The rib becomes thinner distally. Rectilineal L of the rib: 1400 mm, while its curvilineal L: 1730 mm.

Rib 7: It is close to the rib 6 in morphology, but thinner in general. This is the longest among the ribs. Rectilineal L of the rib: 1480 mm, while its curvilineal L: 1920 mm.

The ribs 7 – 9 are about equally strong and long. Posterior to rib 9 the shafts of the ribs become thinner and shorter more rapidly backward, with the separation of the tubercles from the heads becoming wider. The rib 17 is much more reduced than its preceding ones.

There is only one complete first rib of *Paraceratherium asiaticum* described by Borissiak (1923b). It is smaller than that of TP 9401: L: 600 mm, W of proximal end: 116 mm, and distal end: 188 mm (700 mm, 128 mm and 238 mm in TP 9401). The only complete third or fourth rib of *P. asiaticum*, described by Borissiak (1923b), is about as long as that of TP 9401, but apparently thinner in distal end (88 mm × 35 mm versus 100 mm × 40 mm). The longest rib (rib 8) of *P. grangeri*, described by Granger and Gregory (1936), is about 1700 mm (calculated curvilineal length based on Fig. 22, *loc. cit.*).

TP 9402, right tibia (Pl. XXIX 4, Tab. 27): It was excavated from the same site of the skeleton, but may not be of the same individual because of its younger age than that of the skeleton as evidenced by the partial coalescence of the distal epiphysis with the shaft. The tibia is very short and robust, with its ends much wider than the middle part of the shaft.

The medial condyle of the proximal end is shallowly concave. The lateral condyle is broader, but shorter in anteroposterior direction than the medial one. The intercondyloid eminences are low, with a narrow and shallow median groove. The tibial tuberosity is very wide, occupying about 2/3 width of the proximal end, with its lateral border close to the lateral border of the shaft. The groove lateral to the tibial tuberosity is very shallow. The facet articulating with the fibula is located 50 mm underneath the proximal surface.

The shaft is roughly triangular in cross section, with its lateral border forming a crested ridge, posterior side flattened and anterior side being convex. The distal end is relatively small. Its cross section is trapezoid in shape, with a shorter posterior side. The tibial crest is only about 200 mm long, without reaching the distal end. On distal side the medial groove of the trochlea is deeper but narrower than the lateral one, which is much flatter and wider. The intermediate ridge slants posteromedially, with its posterior end further downward extended than its anterior end.

TP 9402 seems to be shorter and comparatively more robust than most tibiae of known paraceratheres except for the EMM 0009 of *Aralotherium* sp. to be described later (Tab. 27). Morphologically, it is more similar to that of *P. grangeri* than to *P. asiaticum* in having a shorter tibial crest and the unequally developed trochlear facets and the more obliquely directed intermediate ridge.

TP 9403, right McIII (Pl. XXIX 5, Tab. 37): It was found in 1994 while excavating the TP 9401 skeleton, but allegedly separately from the skeleton. The posterior part of its proximal end is damaged (Pl. XXIX 5c). In proximal view, the facet articulating with the magnum is fan-shaped, 135 mm wide at anterior border, while that for the unciform forms a narrow band, which is wider anteriorly (42 mm). In dorsal view, The former facet slants slightly distomedially, forming a 140° angle with the latter facet. The metacarpal tuberosity (for the attachment of the m. extensor carpi radialis) is only weakly developed under the facet articulating with the unciform. The narrowest part of the shaft is in its upper 1/5, gradually widening distally. The volar side of the shaft is concave, while the medial side slightly convex and the lateral side flat. The upper borders of the distal trochlea on dorsal and volar sides are about equally high. The sagittal ridge is mainly developed in the posterior 2/3 of the trochlea, but visible from the dorsal side. The anterior portion of the articular surface without sagittal ridge faces dorsodistally. A rather wide rough area encircles the upper border of the trochlea on dorsal side.

As the TP 9402, the McIII of TP 9403 is closer to that of *Paraceratherium* than *Aralotherium* in general form, expressed in having its narrowest part in the upper part of the shaft (in the middle in *Aralotherium*). However, in the flatness of the proximal articular facets and the posterior part of the sagittal ridge of the distal trochlea, TP 9403 is more similar to that of *Aralotherium*. Nevertheless, TP 9403 is the shortest and the most robust one compared to the other McIII's referred to *Paraceratherium* (Tab. 37).

2) Specimens kept in IVPP

The IVPP material includes the specimens collected by Zhai *et al*. in 1964, probably from the same level of the same area as the skeleton TP 9401. Most important of them are the following:

V 3194, a left maxilla with P4 – M2 (Pl. XXV 1, Tab. 38): All the teeth are heavily worn. What is clear is the presence of a large antecrochet and a narrow anterior protocone constriction groove in the M2. Taken as a whole, this specimen is close to the P4 – M2 of TP 9401.

V 3195.2, a right humerus (Pl. XXX 1, Tab. 11): The humerus is basically complete, with only minor parts damaged. It is very short and robust. The caput tilts backward, facing upward and backward. It is wider than long, strongly convex anteroposteriorly, but little in transverse direction. In posterior view, the upper border of the caput slopes slightly down laterally. The lateral tuberosity is weakly developed, not overhanging above the bicipital groove anteriorly, and with its upper border not higher than the caput. The medial tuberosity is hardly noticeable.

The deltoid tuberosity is shifted downward, reaching the middle of the shaft. The lateral epicondyle is very prominent, extending high and laterally. The medial epicondyle is small, hardly extending posteriorly. The medial condyle of the distal trochlea is larger than the lateral one, and the blunt ridge of the lateral condyle is situated in the medial 1/3 of the condyle. The intercondylar groove is shallow and asymmetrical.

Compared with the other known humeri of paraceratheres, V 3195.2 is proportionally the most robust one, closer to that of *Aralotherium* (Tab. 11). In length it is closer to that of *Paraceratherium bugtiense*, but shorter than those of *P. asiaticum* and *P. grangeri*. Furthermore, V 3195. 2 is similar to *Aralotherium* in having the weak curvature of the caput in transverse direction, but closer to *Paraceratherium* in the morphology of the distal trochlea, especially in having a clearly expressed longitudinal ridge on the lateral condyle.

The rest of the limb-bones, collected by Zhai and his colleagues in 1964 and referred to the present species, are not very diagnostic and their description is omitted in this English summary. Nevertheless, part of them is shown in Pl. XXX 2 – 3.

We note that a large number of limb-bones (altogether 45) collected by Zhai and his colleagues in 1966 were already mentioned by Xu and Wang (1978) as belonging to *P. lipidus*, unfortunately, without any description and measurements. Later, these specimens were transferred to the Beijing Museum of Natural History. Among them only one right humerus (V 4328.1), which is mounted in the reproduced cast skeleton of TP 9401, is available for us to study. The humerus (V 4328.1) is almost identical to the above described humerus (V 3195.2).

3) Specimens from Qianlishan Mountains area

V 3305, anterior part of right horizontal ramus with p3 – m1 (Pl. XXV 2, Tab. 36): The lower part of the horizontal ramus is damaged, but it is clear that the ramus is rather high. Judged from the concavity of the lower border below the mental foramen, which lies under the p2, the anterior part of the symphysis should have been mainly anteriorly extended, possibly slightly downward. The posterior border of the symphysis lies at the level of the middle of p4. Of the p2 only a fragment of root is preserved, which is certainly single-rooted. The p3 is pointed anteriorly. The posterobuccal angle of the protoconid is rather ridge-like and followed by a deep ectoflexid. The buccal cingulum is well developed and W-shaped, while the lingual one is also rather developed. The p4 is trapezoid in crown form. The buccal cingulum is as that in p3, but the lingual one is broken at the metaconid. The buccal cingulum of m1 is also W-shaped, but weaker than in p4, and the lingual one is almost absent.

(2) Discussion

The genus *Paraceratherium* was founded (Forster-Cooper, 1911) based mainly on the peculiar morphology of the symphysis and the lower tusks of a single mandible, and the materials of these parts in other large-sized paracerathere genera (*Indricotherium*, *Baluchitherium* and *Aralotherium*) were originally either rather poorly preserved, or not in association with the skulls. This has been the major obstacle for unravelling the relationships between these genera for a long time in the past. Being crucial to understanding the relationships of these genera, the discovery of an associated skull with mandible of a single individual, such as TP 9401, is especially satisfying.

In TP 9401, the morphology of the symphysis and the lower tusks is almost the same as the type species of the genus, *P. bugtiense*. Similar type of the symphysis and lower tusks has been variously described also in *Indricotherium asiaticum* (= Pavlow's *Indricotherium transouralicum*, PIN n. 2029) and

Baluchitherium grangeri (Granger and Gregory, 1936, AM 26166). Furthermore, the skull of TP 9401 has an elongated premaxilla with down-turned upper tusks (although restored, probably a correct restoration, *vide supra*), just as the holotype skull of *Baluchitherium grangeri* and the muzzle part of the skull of *Indricotherium asiaticum*, additionally described by Pavlow (1922). This is in sharp contradiction against the down-turned symphysis and the highly reduced upper muzzle part in *Aralotherium* (Borissiak, 1939), and the strong reduction of both upper and lower muzzle parts in *Dzungariotherium* (Chiu, 1973). This strongly proves that the materials referred to *Paraceratherium* (Forster-Cooper, 1911) and *Indricotherium* (Borissiak, 1915), and possibly also *Baluchitherium* (Forster-Cooper, 1913), belong to one and the same genus, and the latter two generic names are junior synonyms of the former.

As to its specific status of TP 9401, it should be noted that the mandible is closer to the type mandible of *P. bugtiense* in a number of commonly shared features, such as the vertical posterior border of the ascending ramus, the strongly reduced p2, the formation of the entolophids in p3 – p4, etc. However, TP 9401 is generally larger in overall size, with a deep incisura vasorum on the lower border of the ramus in front of the mandibular angle, a feature not found in *P. bugtiense*.

It appears rather difficult to deal with the skull material referred to *P. bugtiense* and the postcranial bones attributed to *Baluchitherium osborni* by Forster-Cooper in 1923 – 1924. Since both skulls described by Forster-Cooper (skull B and D) lack the muzzle parts, it cannot be sure whether they do possess elongated premaxillae with down-turned upper incisors as TP 9401 does, but the paroccipito-posttympanic processes are certainly much narrower (APD) and widely separated from the postglenoid one in these skulls. Futhermore, the nasal notch of the skull B seems to be more posteriorly retreated, lying above the anterior border of the M2 (Forster-Cooper, 1924b, Fig. 3). If these skulls really belong to *P. bugtiense* as Forster-Cooper suggested, the validity of *P. bugtiense* as an independent species is to be admitted.

Whether the postcranial bones of *B. osborni* are also to be referred to *P. bugtiense* as Gromova suggested, is still problematic. Some of them are comparable with their corresponding bones in *P. lepidum*, especially the cervical vertebrae. As stated above, the atlas of *B. osborni* has particularly narrow wings, the form of the alar notch and the position of the posterior opening of the vertebrarterial canal are also different from those of the atlas of TP 9401. However, the paired tuberosities on the anterior border of the dorsal arch, so characteristic of the atlas of *B. osborni*, can also be found in TP 9401 atlas, though smaller in size. Other cervical vertebrae of *B. osborni* are greatly hollowed by strongly inflated vertebrarterial canals, whereas the hollowing in the cervical vertebrae of TP 9401 is moderately developed. The humerus of *B. osborni* (Fig. 9, *loc. cit.*) is different from that of V 3195.2 in having a larger medial but smaller lateral tuberosity (reverse in V 3195.2), and in lacking the longitudinal ridge on the lateral condyle of the distal trochlea. The tibia of *B. osborni* has the same width at its proximal and distal ends, whereas in TP 9402 the proximal end is much wider than the distal one (Tab. 27). In conclusion, it would be safe to say that the referred skulls of *B. bugtiense* are basically close to that of TP 9401 and could well be considered different from the latter at species level. However, it is hard to determine now whether the postcranial bones of *B. osborni* should belong to the same species as the better known mandible and skulls, i.e., *P. bugtiense*, or to another species, or even to another genus.

Compared with *P. grangeri* and *P. asiaticum*, *P. lepidum* is evidently more advanced and specialized. This is clearly expressed in skull and teeth. In *P. lepidum*, the muzzle part is further reduced, becoming slenderer, with smaller I1; the paroccipito-posttympanic process becomes particularly robust, with its lower end far beyond the lower border of the condyle; the nasal notch is further posteriorly retreated, reaching the level of M1; P1 is completely lost; P2 takes the form of a triangle; and the antecrochets are well developed in M1 – M3.

Another problem pertains to the reason why we referred the above described specimens to *P. lepidum*, rather than to other forms found from the same basin. As is well known, three forms were reported from the same small area of the Turpan Basin, namely: *Paraceratherium* (or *Dzungariotherium*?) *tienshanense*, *P. lepidum*, and *Dzungariotherium turfanense*. In addition, a new form is to be established in the present volume below, *Turpanotherium elegans*. Thus, altogether four species of large-sized paraceratheres lived in this small area of Turpan Basin. Which form should TP 9401 belong to?

First of all, the new form, *Turpanotherium elegans*, is characterized by its particularly small size and high-crowned teeth, and thus could easily be excluded from further comparison with TP 9401.

Next is *D.*? *tienshanense*, which may also be a valid species, although the only material of this species remains very poor (a broken M3 and a fragment of mandible with p4 - m2) and its stratigraphic position remains uncertain. However, the teeth are much larger than those of TP 9401, in fact, larger than those of all known paraceratheres (Tab. 36), and are higher crowned as well.

TP 9401 cannot be referred to *Dzungariotherium turfanense* either. The holotype of the latter species is an anterior half of skull (V 4340; Xu and Wang, 1978, Pl. II 1). Based on the original description, the skull has a very strongly reduced muzzle part, with its I1 strongly atrophied. Furthermore, the skull is much smaller than that of TP 9401, with its length of P2 - M3 being only 380 mm, only about 0.88 as long as that of TP 9401 (430 mm).

As discussed above, TP 9401 skull more closely resembles the holotype skull of *Paraceratherium lipidus* (V 4322; Xu and Wang, 1978, Pl. I 1). Therefore, we referred TP 9401 to that species. In addition, we note here that the species name (*lipidus*) is apparently a lapse of pen, or printing error of the Latin adjective *lepidus* (pleasant, neat, fine). Such kind of error and the wrong gender ending can be corrected according to Article 32 (d) of International Code of Zoological Nomenclature (third ed., 1985). Hence the name after correction should be *Paraceratherium lepidum*.

The postcranial bones of *P. lepidum* once kept in IVPP, altogether 45 pieces, were only listed by Xu and Wang (1978), without description and measurements. All of these postcranial specimens were collected from the same small area yielding the skull V 4322, by Zhai and his colleagues in 1964. Attribution of them to *P. lepidum* is mainly based on their occurrence in the same small area where the skull V 4322 was found, and on size and robustness, clearly expressed in humerus, tibia and metacarpal bones in particular. Whether such an attribution is tenable is a matter to be substantiated in the future.

The referral of the mandible fragment of V 3305 from the western slope of the Qianlishan Mountians to the same species is also tentative and needs to be proved by additional material yet to be found.

Paraceratherium sp.

(Pl. XXXI 1 - 2; Tabs. 32, 36)

Material: 1) V 3322, An incomplete mandible, from Huangyangtou, Lanzhou Basin. 2) V 3369, left MtII, collected by IVPP and Gansu Provincial Museum joint field team in 1993, from Simagou, Gaolan County, Lanzhou Basin (IVPP Field no. GL 9310); all from yellow sandstones of Lower Member of Xianshuihe Formation, late Early Oligocene.

Description

V 3322, mandible (Pl. XXXI 1, Tab. 36): The right horizontal ramus is more or less complete, but the left one has only its anterior part preserved. Of the teeth the right p3 - p4 and m2 - m3 and the left p2 - p4 are preserved. The right m1 had been dropped out before death with its alveolus absorbed and the ramus below it pathologically deformed, becoming abnormally thicker but shallower.

The symphysis is damaged so that its real form cannot be properly restored, but seemingly contracted anteriorly. Very small i1 alveoli can be seen on the fractured surface of the symphysis. The mental foramen is situated below the p2. The p2 is small, its talonid is L-shaped, composed of hypo- and entolophid, with lingual and buccal cingula well developed. The p3 is triangular in form, pointed anteriorly, without entoconid separated from hypocoinid. The posterobuccal angle of the protoconid is smoothly convex, without tubercles. The p4 is similar to, but larger than p3.

V 3269, left MtII (Pl. XXXI 2, Tab. 32): The proximal surface articulating with mesocuneiform is semicircular in form and flat. No facet articulating with entocuneiform is visible. A prominent tuberosity is present at the plantar side. In lateral view, the thinnest part of the shaft is located ~ 100 mm below the proximal end.

Comparison and discussion

The lower border of the mandible of V 3322 is quite similar to that of TP 9401, especially in the slight convexity under the premolars. Furthermore, the degree of reduction of the p2 and the development of the entolophids in the p3 – p4 are also similar to those in TP 9401. However, the symphysis of V 3322 is weaker and the i1 may be more reduced than in TP 9401. Whether it is a female individual of *P. lepidum* is hard to say. For the moment, we prefer to place it in this genus as an indeterminated species.

The MtII came from the same layer of Lanzhou Basin as the above mandible. It is shorter but more robust than that of *P. asiaticum* (Tab. 32). This is in accordance with the other limb bones referred by us to *P. lepidum*. For the moment, we refer it to the same indeterminated species of *Paraceratherium* together with the above mandible.

Paraceratherium? sp.

(Pl. XXX 4, Tab. 36)

Material: V 3306, a fragment of left mandible with m2 – m3, handed over to IVPP by 109 Brigade of the Department of Petroleum Exploration at Yinchuan in 1965, collected from Wulanamnnai valley (Teilhard de Chardin's locality of Saint-Jacques); exact stratigraphic position is unknown.

Description and discussion: The m2 and m3 are rather peculiar in morphology. The buccal wall of the protolophid is flat, or even slightly concave, with a weak groove anterior to the protoconid and numerous tubecles anterior to the groove. The posterobuccal angle of the protoconid is smoothly angled, making the ectoflexid deep and clearly expressed. On the lingual side, at the outlet of the talonid basin there are also tubercles. Similar structure can only be seen in some lower premolars of *P. asiaticum* as stated by Gromova (1959, p. 86 – 87, Fig. 11). The buccal cingulum is well developed at the anterior and posterior ends. Although V 3306 is well distinctive in morphology, it seems premature now to erect a new species based on such poor material.

Dzungariotherium Chiu (= Qiu), 1973

Paraceratherium (partim), Lucas and Sobus, 1989: 367 – 373

[non] *Dzungariotherium erdenensis*, Qi, 1989: 301 – 305, Pl. I

Type species: *Dzungariotherium orgosense* Chiu, 1973.

Other included species: *D. turfanense* Xu and Wang, 1978 and *D.? tienshanense* (Chiu, 1962).

Geographic and stratigraphic distribution: Ordos, Nei Mongol; south part of Junggar and east part of Turpan basins, Xinjiang Uygur Autonomous Region, late Early-Late Oligocene.

Emended diagnosis (based on type species): Seen laterally, dorsal profile of cranial part of skull straight. No single sagittal crest is formed, leaving wide and flat interspace between parietal lines. Paroccipito-posttympanic process thick transversely, with its lateral border far external to condyle. Nasal notch extends posteriorly beyond the anterior border of the orbit, lying above M2 – M3, with its posterior border being angulated. Nasal shortened, with its tip lying above P2. Infraorbital foramen is located above the middle of P4, facing upward. Anterior part of maxilla and premaxilla strongly reduced, only as long as the L of P2 – P4. Alveolar border is strongly curved, convex downward; the line linking both ends of alveolar border, when horizontally placed, is markedly lower than condyle. Mandibular angle little protruded posteriorly, with its posterior border almost vertical. Anterior part of lower border below premolars ascends anteriorly. Dental formula: 1·0·3·3 / 1·0·3·3. I1 is rudimentary, while i1 is small, with its root ended anterior to p2. P2 crown is triangular, wider than long; ribs on buccal walls of upper premolars weak; protocone constriction grooves are present in upper molars. p2 strongly reduced, single-rooted; p3 crown triangular in form, pointed anteriorly; p3 – p4 with posterobuccal angles of protoconids curved and smooth, with fully formed entolophids. No diaphragmatic vertebra is present. Four lumbar vertebrae. Articular facets on pre- and postzygapophyses in Lm's are concave-convex transversely. At least the spinous processes of the first two lumbar vertebrae are close to those of the posterior T's, with crested anterior ridges and deep excavation throughout the whole lengths of the posterior sides. The transverse processes of the Lm3 and Lm4 are articulated with each other. Limb bones may be very short and robust.

Comments: The generic validity of *Dzungariotherium* has been doubted by a few paleontologists. As a major representative of them, Lucas proposed a hypothesis of sexual dimorphism. According to him, the skulls with long muzzle and enlarged and downturned I1 as represented by the type skull of *Baluchitherium* (corrected to *Paraceratherium*) *grangeri* are male individuals, while those with reduced muzzle and atrophied I1 as represented by skulls belonging to *Dzungariotherium* (also *Aralotherium*), are female individuals of the same form. In this case, the latter two genera are merely female representatives of the same genus *Paraceratherium*, who has the priority over the former two.

Lucas' hypothesis seems highly tempting and worthy of further testing. The Chinese paracerathere material seems to provide information both in favor of, and against, such a hypothesis. The factors in favor of it are: 1) The skulls, mandibles and the cheek teeth of *Dzungariotherium* and *Paraceratherium* are really closely similar in morphology, difficult to separate, except for the muzzle parts. 2) There existed both *P. lepidum* and *D. turfanense* (*vide infra*) in the upper 100 m of the Taoshuyuanzi Formation within a small area of about 10 km^2 in east part of Turpan Basin. The former is larger than the latter. From the ecological point of view, it seems more reasonable to consider them as representatives of both sexes of one and the same form instead of different genera.

The factors unfavorable to Lucas' hypothesis are: 1) This is contradictory to the observation of other features commonly thought as sexual manifestation. For example, the enlarged postorbital process and robust zygomatic arch covered with heavy rugositites are usually considered male features, but they are present in Lucas' female individual with strongly reduced muzzle and atrophied incisors (*D. orgosense*). On the other hand, male individuals of *P. lepidum* in Lucas' hypothesis (with elongated muzzle and enlarged incisors), the postorbital process and the zygomatic arch are both rather weak. 2) The distinction between *Dzungariotherium* and *Paraceratherium* is not only reflected in the above mentioned sexual features, but also in other characters whose sexuality is not evident. For example, the differences in the development of paroccipito-posttympanic process, the morphology of the nasals and the degree of retreat of the nasal notch, etc. 3) The newly found material (*vide infra*) has further proved that in *Dzungariotherium* the mandibular symphysis is strongly shortened, with its lower border ascending anteriorly, and the i1 highly reduced. This made the distinction between *Dzungariotherium* and *Paraceratherium* even more clear-cut. 4) The evolutionary trend in *Paraceratherium* seems to be the gradual reduction of the muzzle and the incisors as illustrated in the earlier *P. grangeri* and later *P. lepidum*. This could easily be explained by the losing of function of the incisors as the gathering apparatus replaced gradually by the development of the more flexible lips in later forms. On the contrary, if the incisors were interpreted as an organ of mate competition, there would be difficulty to explain why this sexually important organ went to its reversed direction. 5) Finally, no similar sexual dimorphism expressed in muzzle and incisors has ever been observed in recent mammals.

As a result of the above deliberation, we prefer to retain their generic status for now in the absence of more decisive evidences in favor of Lucas' hypothesis of sexual dimorphism.

Dzungariotherium orgosense Chiu (= Qiu), 1973

(Pl. XXXI 3)

Holotype: V 3190, skull and mandible, with symphysis partly damaged and ascending ramus poorly preserved, 20 km south of Anjihai bridge, south border area of Junggar Basin, from Shawan Formation; Late Oligocene.

Additional material: 1) V 3323, a fragmentary mandible; 2) V 3324, left M2, with its posterior half of ectoloph broken away; 3) V 3325, left calcaneus; 4) V 3326, medial half of right astragalus. All are from Pitiaogou valley of Dongyuan Village, Dongxiang County, Gansu (IVPP field no. LX 199804), basal conglomerates of Jiaozigou Formation; Late Oligocene.

Emended diagnosis: Large-sized species of the genus, inferior only to *D*.? *tienshanense*. L of P2 – M3 about 430 mm. Alveolar border bends upward anteriorly. Premolars comparatively small; lingual wall of protocone flattened, often with vertical groove on it, and with clearer anterior and posterior protocone constriction folds in upper molars.

Description: Of the above mentioned specimens only the mandible (V 3323, Pl. XXXI 3) is worthy of brief description. Of the mandible only the left horizontal ramus and a small part of symphysis are preserved, with crowns of almost all teeth broken away. The mandible is heavy and robust. Its lower border ascends anteriorly, particularly so under p2 – p3. A pair of small cavities represents sockets of small i1 on anterior broken surface. Both the morphology of the symphysis and the small i1's sockets tend to show the strong reduction of the anterior part of symphysis and the i1 in this specimen.

Comparison and discussion: V 3323 mandible is rather distinctive in having its lower border generally ascending anteriorly. As far as is known, in all known mandibles of *Paraceratherium*, the lower border is more or less horizontal, convex under premolars, concave under diastema, but stretching anteriorly at the anterior end of the symphysis. The above character is in good accordance with the general morphology of the holotype mandible of *D*. *orgosense* (V 3190), symphyseal part of which is even more badly damaged.

Dzungariotherium turfanense Xu et Wang, 1978

(Pls. XXXII – XXXIV, XXXV 2 – 3; Tabs. 8 – 9, 24, 29, 36, 38)

Dzungariotherium turfanensis (partim), Xu and Wang, 1978: 134 – 136, Pl. II 1, 2a, 3

Holotype: V 4340, anterior part of skull with mandible, from upper part of Taoshuyuanzi Group, near Feiyue Railway Station, east part of Turpan Basin; Late Oligocene.

Included material: 1) IMM-1995-IMBLG-1, fragmentary skull with mandible, 7 thoracic and 4 lumbar vertebrae, pelvis with some broken sacral and several coccygeal vertebrae, a piece of articulated bones containing a left astragalus, and distal ends of tibia, fibula and calcaneus, possibly of the same individual, excavated in Teilhard de Chardin's first white sandstone layer of the locality of Saint-Jacques (now Wulanmannai Valley, 3 km east of Balagong township on east bank of the Huanghe River); Late Oligocene. 2) V 3304, right horizontal ramus with p3 – m3, collected from the Upper Member of the Wulanbulage Formation at a place south to Yikebulage Brigade, 8 km southeast of Taositu Railway Station (IVPP Loc.

78018); late Early-early Late Oligocene. 3) V 3195.1 (IVPP field no. 64080.2), right horizontal ramus with m2 – m3; V 3301 (IVPP Loc. 64080), left astragalus, both collected from the lower part of the upper 100 m of Taoshuyuanzi Formation near the Feiyue Railway Station in east Turpan Basin; Late Oligocene.

Emended diagnosis: The smallest species of the genus, with its P2 – M3 L < 380 mm. Upper alveolar border weakly convex downward; lingual side of protocone rounded, without clear protocone constriction folds in upper molars.

Description and Discussion

1) Material from Wulanmannai Valley

Description

Skull and mandible (Pl. XXXII 1; Tabs. 36, 38): The skull is very fragmentary, with its dorsal part and cranium mostly shattered. It belongs to an aged individual, judging by its heavily worn teeth, of which only the M3 preserves its crown features clearly. The zygomatic arch is slender and thin, without clear postorbital process on it. The anterior border of the orbit is situated above the posterior half of M2. The posterior end of the nasal notch, so far as it can be seen, is at least posterior to P4. Although curved, the alveolar border is much less so than in the holotype of *Dzungariotherium orgosense* and *A. prohorovi* (Gromova, 1959, Fig. 2 A). The mandible (Pl. XXXII 1a – b) is better preserved than the skull, with only the upper part and posterior border of the ascending ramus damaged. The lower border of the ramus is rather straight under the ascending ramus, slightly concave below the m3, but convex below the p3 – m2, and then ascends steeply anteriorly until the very end of the symphysis. The posterior border of the ascending ramus is more or less vertical.

The number of cheek teeth is six on each half of the maxilla. The P2 is triangular in outline. The protocone in M3 is rounded lingually, with only very weak anterior protocone constriction fold, but large antecrochet. A pillar-like tubercle is present at the place where the posterior end of the ectoloph should be. The lower cheek teeth (Pl. XXXII 1e) are likewise heavily worn. The p2 is single-rooted, with a small talonid basin. The talonid basins are deeper than the trigonid basins in m2 – m3. The buccal cingulum is weakly W-shaped in lower molars.

Six posterior T's anterior to the last T (Pl. XXXII 2 – 3, XXXIII 1 – 3; Tab. 8): The first T counting from the front is very fragmentary. Its position in the thoracic part of the vertebrae cannot be determined. The three T's posterior to the first one (Pl. XXXII 2 – 3, XXXIII 1) are more or less similar in morphology, with wider and lower bodies, high spinous processes and large transverse processes. They may be the T11 or T12 – T14? judged from their morphology. The L of the spinous processes of T11 or T12 measured from the anterior side is 410 mm, while the L's of the spinous processes of T13? and T14? measured from the posterior sides are 300 mm and 290 mm respectively. The fifth one counting from front (Pl. XXXIII 2) may be the T15. Its spinous process is 270 mm high measured from its posterior side, but slender, with its top not particularly enlarged. The last one of them (Pl. XXXIII 3) is the penultimate T because it was found tightly united with the last T. This vertebra is quite similar to the last one described below. L of its spinous process measured from behind is 230 mm.

The last T (Pl. XXXIII 4, Tab. 8): It is adhered together with the first Lm, therefore, there is no doubt as to its position as the last T. The caput and the vertebral fossa are only weakly convex-concave, both are wider than high. The caput is roughly heart-shaped, with its upper border concave in the middle. The lateral surfaces of the body is markedly concave, bordered by protruded margins of the caput and the vertebral fossa. The ventral keel is doubled, weakening posteriorly. The transverse process is irregular in form, and very short. Anteroventral to it is a cavity for the articulation with the rib caput. The posterior notch of the neural arch is very deep, forming a voluminous intervertebral foramen with the Lm1 (Pl. XXXIII 4b). The metapophysis (or mammillary process) has a rounded upper border, which is lower than the upper border of the postzygapophysis. The articular facet of the prezygapophysis is situated in fact on the base of the spinous process, extending to the mesial surface of the metapophysis. The articular facet of the postzygapophysis faces ventrocaudally, concave in lateral portion, but convex in mesial portion. The spinous process is rather high, higher than the body, slanting posteriorly. Its anteroposterior length diminishes upward, but is suddenly enlarged at the top. The lower 2/3 of the anterior side forms a clear ridge, fading out in the upper 1/3 of the process. The posterior side of the spinous process is shallowly excavated, so that the cross section of the process forms a Y-shape.

Lm1: (Pl. XXXIII 4, Tab. 9): The vertebral fossa is wider than high. The transverse process is plate-like, bending slightly upward (Pl. XXXIII 4a). Its anterior border curved backward in the lateral half, forming a pointed end with the posterior border (Pl. XXXIII 4c). The articular facet on the prezygapophysis is transversely concave, while that on the postzygapophysis is mainly convex, but slightly concave at lateral marginal area. Otherwise this vertebra is similar to the last T.

Lm2 (Pl. XXXIV 1; Tab. 9): The ventral keel is blunt and robust. The curvature of the articular facets on both pre- and postzygapophyses are stronger. The transverse process is longer, but less obliquely extended, with more pointed lateral end, forming a tongue-shaped trowel. The spinous process slants backward weaker.

Lm3 (Pl. XXXIV 2, Tab. 9): The spinous process is largely broken and the transverse processes preserve only their bases. The body becomes more flattened, its caput is roughly oval in shape, much wider than high, with the middle part of the upper border slightly concave. The vertebral fossa is pentagonal in outline. An oval, flat facet articulating with that of the fourth lumbar vertebra is present on the mesial part of the posterior side of the transverse process.

Lm4 (Pl. XXXIV 3, Tab. 9): The spinous process is not preserved. The body is even more flattened. A facet of similar form articulating with the preceding vertebra is present on the anterior border of the transverse process. The facet articulating with the first sacral vertebra on the mesial end of the transverse process is even larger.

Innominate bones (Pl. XXXIV 4, Tab. 24): The innominate bone is wide and short. Its greatest L is 890 mm, while the total W of the two innominate bones is 1120 mm. The ilium is longer than the combined length of both ischium and pubis. The iliac crest is more or less straight, about 560 mm long. Both sacral and coxae tuberosities are not very prominent, and the trihedral corpus of the ilium is very short and wide. The length of the acetabulum is 200 mm, while its width is 160 mm (Pl. XXXIV 4 ac). The ischium is 290 mm long, 200 mm wide, with very strong posterolateral ischium tuber (Pl. XXXIV 4 ti). The ischia and pubes are not fully coalesced, leaving a clear sagittal suture. Judging from the wide ischiadic arch, hence the wide posterior pelvic aperture, and the presence of the sagittal suture between the ischia and the pubes, it is possible that the present pelvic girdle is of a female individual.

Left astragalus (Pl. XXXIV 5, Tab. 29): Among the specimens of IMM-1995-IMBLG-1 there is a piece of articulated bones of left ankle, of which only the astragalus is more or less completely preserved. It is rather low (Tab. 29). The upper border of the medial ridge of the trochlea is convex, while the middle groove is deep. The boundary between the trochlea and the distal part of the astragalus is clearly demarcated on dorsal side (Pl. XXXIV 5a). On plantar side the sustentacular facet takes the form of a comma, with its pointed part situated distomedially (Pl. XXXIV 5b). On distal side the facet articulating with the navicular is roughly triangular in form, with its widest part being at the middle of the posterior side (Pl. XXXIV 5c).

Comparison and discussion

Judged from the main features of the skull and mandible (the strong reduction of the muzzle and the symphysis, the loss of P1, the triangular P2, the small size and single-rooted p2, the development of the antecrochets in upper molars, etc.), IMM-1995-IMBLG-1 can only be attributed to *Dzungariotherium*. They are evidently smaller and more primitive than the type species, *D. orgosense*. They are even slightly smaller than the other species of the genus, *D. turfanense*, established by Xu and Wang in 1978, probably because of their older age, but closer to the latter in morphology.

If all the specimens from Wulanmannai are of the same individual as stated above, the vertebrae and the limb bones would be the first find of their kinds. Compared with other known postcranial bones of the paraceratheres, those of Wulanmannai really show some peculiar features.

Borissiak (1923b) described four last T's of *P. asiaticum*. The last T of Wulanmannai differs from them in a number of points: 1) In the Wulanmannai specimen the spinous process has a crested anterior border in its lower 2/3, deeply excavated posterior side, and an enlarged tuberosity on the top. In *P. asiaticum*, the spinous process is much slender, with ridged anterior border, but the excavation on the posterior side is limited only in its lower 2/3, without particularly enlarged top tuberosity (Borissiak, 1923b, Pl. V 1a–b). 2) In the Wulanmannai specimen, the metapophysis is rather thick, while it is very thin and plate-like in *P. asiaticum*.

The Lm1 of *P. grangeri* described by Granger and Gregory (1936, Fig. 16) may also be the last T, because it has only one irregular transverse process on the right side. This vertebra differs from that of Wulanmannai also quite distinctly. The spinous process is more plate-like, posterior excavation little developed, and the articular facets on both zygapophyses are still rather flat, without clear curvature.

Although the exact position of the other T's from Wulanmannai is difficult to define, their general form is different from the known T's of other paraceratheres. Taken as a whole, the Wulanmannai specimens are closer to the last T of *P. lepidum* rather than to those of *P. asiaticum* and *P. grangeri*.

Similar case also holds true for the Lm's. Those from Wulanmannai have similar spinous processes as the T's. Their transverse processes also extend upward more strongly. Borissiak gave the number of lumbar vertebrae in *P. asiaticum* as only three. This may not be true for such a primitive form. The Wulanmannai material tends to show that the paraceratheres may have four lumbar vertebrae.

There is only one record of the innominate bone of paraceratheres, described by Borissiak in 1923 for *P. asiaticum*. Compared with it, the specimen from Wulanmannai is smaller in general size, but with narrow and straight iliac crest, while in that of *P. asiaticum* the iliac crest is strongly curved and much longer (890 mm versus 560 mm in the Wulanmannai specimen).

2) Material from Turpan Basin kept in IVPP

V 3195.1, left horizontal ramus with m2–m3: The lower border of the ramus is downwardly convex, clearly ascending anterior to the m2. The m2 is moderately worn and well preserved. It is large (L at base on buccal side 105.5 mm) and rather high crowned (H of hypolophid 61.9 mm). Judging from the curvature of the lower border of the mandible, V 3195.1 is here tentatively referred to *D. turfanense*.

V 3301, left astragalus (Pl. XXXV 2, Tab. 29): The part of the trochlea lateral to the neck is moderately protruded over the distal end. The trochlea is asymmetrical, with the lateral condyle much larger than the medial one, medial half of upper border of which is almost horizontal in orientation. Accordingly, the middle groove of the trochlea is very shallow. On dorsal side, the boundary between the trochlea and the neck is moderately defined. The facet articulating with the cochlear process of the calcaneus on plantar side forms a right angle with the small, tongue-shaped facet below it. The facet articulating with the sustentacular process of the calcaneus is oval, obliquely positioned. The distal surface articulating with the navicular is triangular in form, while the facet articulating with the cuboid is narrow and strip-like.

This astragalus is similar to the above described one of IMM-1995-IMBLG-1 in size and general morphology, slightly differing forme the latter in being higher in proportion (Tab. 29 ratio 1) and the flatter upper border of the medial ridge of the trochlea. The smaller of the two astragali described by Teilhard de Chardin as belonging to *Baluchitherium grangeri* forme *minor* was presented by a picture (Teilhard de Chardin, 1926, Pl. II 8). It is morphologically very close to the above described astragalus, but smaller in size. No picture was given by Teilhard de Chardin for the larger one. However, it is closer to the above described astragalus in size. Max W's of both are about 160 mm. They were found from the same valley of Wulanmannai, and may all belong to the same species, i.e., *Dzungariotherium turfanense*.

3) Material from west slopes of Qianlishan District

V 3304, Right horizontal ramus (Pl. XXXV 3, Tab. 36): The mandible is the best preserved specimen from the IVPP locality 78018. The ascending ramus is well preserved, with only the top of the coronoid process missing, while the horizontal ramus preserved only its posterior part up to the p3, with its lower border broken anterior to the m2. The horizontal ramus is comparatively low, probably because of its young age (m1 moderately worn). The posterior border of the ascending ramus is largely vertical, except for the part beneath the articular condyle. The mandibular angle is rounded, without any indication of posterior protrusion. No incisura vasorum can be seen on the lower border of the mandible. All the cheek teeth are comparatively high crowned, with rough enamel surface. The trigonid of p4 is U-shaped, with its paralophid not reaching the lingual border, and the metaconid the most robust cusp of the tooth. The hypolophid and entolophid are confluent, but with a small bulge in the middle on its lingual side. The entolophid is thin, descending lingually so that its lingual end is lower than that of the paralophid. The talonid basin is wider and deeper than the trigonid one. The extoflexid is deep, and the posterobuccal angle of the protoconid is smoothly curved.

V 3304 differs from the early species of *Paraceratherium*, *P. asiaticum* and *P. grangeri*, in having higher crowned cheek teeth and fully developed entolophids in p3 – p4, from the later species, *P. lepidum*, in lacking incisura vasorum on lower border of the mandible and the secondary structures in the trigonid basins in lower molars. V3304 is more similar to *D. turfanense* in size and morphology. We tentatively refer this specimen to *D. turfanense*.

Dzungariotherium? *tienshanense* (Chiu [= Qiu], 1962)

(Tab. 36)

Indricotherium cf. *grangeri*, Chow and Xu, 1959: 93 – 96, Pl. I
Paraceratherium tienshanensis, Chiu, 1962: 62, 64, 68

Holotype: IVPP V 2370, an incomplete right M3 and a part of left horizontal ramus with p4 – m2, reportedly found near the Feiyue Railway Station, east Turpan Basin, without indication of exact locality and stratigraphy, possibly either Late Oligocene or even earliest Miocene (?).

Diagnosis: The largest-sized paracerathere. Cheek teeth high crowned, p4 with fully formed entolophid, rounded posterobuccal angle of protoconid, but low talonid. Lower molar with protolophid steeply descending anteriorly and low paralophid.

Comments: So far V 2370 is the only known material of this species. In fact, the V 2370 teeth are super-sized among the paraceratheres. Chiu (1962) transferred them to the genus *Paraceratherium* (*sensu* Gromova, now should be *Aralotherium*) and established a new species for it, *P. tienshanense*. The V 2370 teeth do possess features close to both of *Dzungariotherium* and *Aralotherium*. The commonly shared features are the higher crowned cheek teeth and the smooth and rounded posterobuccal angles of the protoconids in p3 – p4. However, some features of these teeth, as the steep sloping of the protolophid and the low paralophid in lower molars, seem closer to those of *D. turfanense* (V 3304 and V 3195.1, *vide supra*). As a result of the above discussion, the attribution of V 2370 to *Paraceratherium* is probably wrong, and its attribution to *Aralotherium* seems also short of enough convincing evidence. It may be more reasonable to refer it to the genus *Dzungariotherium*.

Aralotherium Borissiak, 1939

Baluchitherium (partim), Forster-Cooper, 1924b: 377, Fig. 7
Paraceratherium (*prohorovi*), Gromova, 1959
Paraceratherium (partim), Lucas and Sobus, 1989: 367–373; Figs. 19.6. C, 19.7. A
Paraceratherium (*sui*), Ye *et al.*, 2003

Type species: *Aralotherium prohorovi* Borissiak, 1939.

Other included species: *Aralotherium sui* Ye, Meng et Wu, 2003, and *Aralotherium* sp.

Geographic and stratigraphic distribution: North Priaralia, Kazakhstan; northern part of Xinjiang and eastern part of Nei Mongol, China; from late Early Oligocene (?) to latest Oligocene.

Emended diagnosis (excerpted from Gromova, 1959, p. 38 – 39): "Skull: postglenoid and posttympanic processes widely separate. Zygomatic arch slender, weakly curved. Parietal crests not converged. Nasal notch deep: reaching middle of M2 posteriorly. Nasal bones thin, with their tips against anterior border of P2. Infraorbital foramen slightly higher than lower border of orbit, against middle part of P4. Maxilla anterior to molars moderately long: L of diastema P2 – I1 about equal to L of P2 + P3, with anterior end of the maxilla bending upward. Facial part positioned lower relative to cranial part: tangent across alveolar border extending backward situated lower than condyle. Mandible: posterior border of mandibular angle almost vertical, with strongly down-turned symphysis. Alveolus of i1 reaches anterior border of p2. Coronoid process thin, bending backward at top. A pair of small, atrophied I1. Two very large and robust lower tusks (i1), with very lately closed roots and large crowns. P1 absent. P2 elongated, with pointed anterior border, longer than wide, or hardly wider than long; hypocone oval, obliquely oriented. Ectolophs of upper premolars high, higher than long (when unworn). Ribs of paracone and metacone on buccal surface of ectoloph weakly differentiated. Parastyle long, overlapping on preceding tooth considerably. Metaconule in premolars linked nearly at the middle of hypocone in early stage of wear. Protocone in premolars moderately developed, less protruded lingually than hypocone, so that the crrowns are asymmetrically triangular in form. Protocone in molars flattened on lingual side, even with high vertical groove at base. Posterobuccal angle of protoconid in lower premolars rounded, with hardly observable fold. Entoconid almost never isolated, taking part in formation of entolophid. p3 pointed anteriorly. Lingual side of entoconid in lower molars conically rounded. Top parts of metalophid and entolophid bending anteriorly moderately."

"Atlas considerably hollowed within wings. Scapula comparatively short and wide. Scapular tuber descended to the level of glenoid cavity. Distal trochlea of humerus with hardly noticeable ridge on its lateral condyle. Olecranon of ulna massive, curvature of semilunar notch weak. Radio-carpal and inter-carpal articular facets weakly concave-convex, with anterior "hindering facets" preventing dorsal over-extension. Proximal surface of lunar longer than wide, strongly descending laterally. Trapezium strongly reduced, not articulating with scaphoid. Relief of surface articulating with patella on distal end of femur shallow. Patella asymmetrical, with strongly protruded superolateral angle. Tibial tuberosity situated at the middle of the anterior border, while tibial crest extends no lower than middle of shaft. Astragalus very wide, with its trochlea strongly protruded laterally relative to its distal portion. Cochlear facet low and flattened, extending downward into another long facet, forming a two-sided angle with the main facet. Body of calcaneus comparatively long, with weak tuber calcis, and cochlear facet inversely similar to that of astragalus. Its facet articulating with cuboid is flattened. Entocuneiform small. Relief of inter-tarsal facets rather flattened. Middle metapodia narrowest at the middle of shaft. McV very small, seldom articulating with unciform. Articulation of metapodia with phalanges and between phalanges flattened, with sagittal ridges and grooves little expressed. Articulation of PhI with PhII in middle digits faces downward. Angles of PhIII long, especially so are the posterior ones of the lateral digits. Distal border of PhIII of lateral digits convex."

Comments: While combining *Aralotherium prohorovi* and *Paraceratherium bugtiense* into one genus and using *Paraceratherium* as the valid generic name for this group of paraceratheres, Gromova (1959) apparently did not fully realize the importance of the differences in the symphyseal part of the two forms. She listed "strongly down-turned symphysis" in her diagnosis of *Paraceratherium*. However, this is in contradiction with the type mandible of *Paraceratherium bugtiense*, where the symphysis is evidently extending anteriorly. The skull of *Aralotherium prohorovi* is also radically different from that of *Paraceratherium*, as represented by the Loh skull (formerly referred to *Baluchitherium* or *Indricotherium*), a fact well known to Gromova herself. Therefore, *Aralotherium prohorovi* cannot be transferred to the genus *Paraceratherium*, and *Aralotherium* should be retained as a valid generic name.

Nevertheless, the diagnosis given by Gromova for *Paraceratherium* based mainly on the material of *Aralotherium prohorovi* remain the best and the most detailed one for the genus *Aralotherium*, and hence is adopted here without change.

Aralotherium sui (Ye, Meng et Wu, 2003)

(Tab. 36)

Paraceratherium sui, Ye, Meng et Wu, 2003

Holotype: V 13382, a heavily damaged mandible, with both i1's, left p2 – m3 and right p3 – m3, collected from Tieershabahe Formation, Halamagai village, Fuhai County, Xinjiang, China; Late Oligocene.

Comments: The ventrally curved symphysis of the above specimen renders its attribution to the genus *Aralotherium* doubtless. It differs from the other only known species, *A. prohorovi*, in being much larger in overall size, having higher crowned cheek teeth and stronger curved symphysis.

Aralotherium sp.

(Pls. XXXV 1, XXXVI – XXXVII, XXXVIII 1 – 2; Tabs. 27, 35 – 36, 38, 42)

Material: 1) EMM 0016, symphysis and part of left horizontal ramus with p3 – m1; 2) EMM 0012, right maxilla fragment with M2 – M3; 3) EMM 0013, right M2; 4) EMM 0058, right M3; 5) EMM 0011, right M2 with ectoloph and metaloph partly broken; 6) EMM 0071, ectolophid of left p3; 7) EMM 0076, left m3; 8) EMM 0077, right m2; 9) EMM 0087, left m1 or m2; 10) EMM 0032, anterior part of axis; 11) EMM 0135, posterior half of axis; 12) EMM 0136, a part of left scapula and caput of humerus; 13) EMM 0022, distal end of right humerus; 14) EMM 0003, proximal end of right radius; 15) EMM 0145, left magnum; 16) EMM 0054, proximal end of left McIII; 17) EMM 0143, left patella; 18) EMM 0009, right tibia and fibula. All the materials were collected from the Houldjin Formation by the Erenhot Dinosaur Museum staffs in east and north suburb areas of Erenhot, latest Eocene (?)

(1) Description

EMM 0016 (Pl. XXXV 1, Tabs. 35 – 36): Symphysis is ventrally curved, with its long axis forming an angle of about 30° with the alveolar border. Its dorsal surface is trough-like, and its posterior border is situated at the level of the anterior half of the p4. The alveolar border of the diastema is weakly ridged (damaged). Mental foramen large, situated below the p2. L of i1 – p2 diastema is 150 mm.

Crowns of both i1's are broken. The root is oval in cross section, with its longest diameter lying in dorsolateral to ventromesial direction. It ended before reaching the p2, and its shrinkage toward the posterior end is very slow. The L of the longest preserved part of i1 is 97 mm. No p1 is present. The p2 is double-rooted, with its crown broken away. The p3 is trapezoid in form, roundly pointed anteriorly. The posterobuccal angle of the protoconid is smooth, without tubercles. The entoconid is inseparable from the entolophid, which reaches the lingual side of the tooth. Both lingual and buccal cingula are developed and W-shaped, with the buccal one stronger. The p4 is nearly rectangular, with straight anterior border. Paralophid is thin, with its lingual end stretching posteroventrally. Cingula are similar to those of p3, but stronger. The m1 is too heavily worn to show any details of morphology.

EMM 0071, buccal wall of left p3 (Pl. XXXVI 4): The ectoflexid is hardly observable, but the buccal cingulum is well developed and W-shaped. L is 55 mm.

EMM 0077, 0087, two m2 (Pl. XXXVI 5 – 6, Tab. 36): The paralophid is very thin, trigonid basin disappears earlier than talonid one when tooth is not very heavily worn. Buccal cingulum is almost continuous, weaker at the most convex part of protolophid and posterior part of hypolophid. Lingual cingulum is well developed at the outlets of the trigonid and talonid basins, tubercular in form.

EMM 0076, left m3 (Pl. XXXVI 7, Tab. 36): Taken as a whole, the m3 is very similar to the m2 above described. The trigonid is comparatively long relative to the talonid, wide U-shaped, with rather long protolophid. Paralophid, being the lowest among the lophids, slopes down slightly lingually, with a ridge descending form its lingual end posteriorly. Although the crowns of the talonid and trigonid are about equally high, the talonid is situated lower than the trigonid as a whole, so that the top of the lophids and the crown base of the talonid are considerably lower than those of trigonid. The buccal cingulum is as in the m2, but the lingual cingulum is developed weaker than in the m2.

EMM 0012, right maxilla with M2 – M3 (Pl. XXXVI 1, Tab. 38): The length taken from lingual side of M2 – M3 is 160 mm. The antecrochet of the M2 is rather prominent, the lingual side of the protocone is rounded, no constriction folds are observable. The M3 is trapezoid in outline, with the rudimentary posterior end of the ectoloph expressed by a rounded bulge, a groove lingual to it, accompanied by suddenly widened cingulum. The antecrochet is weak. Weak cingulum surrounds almost the whole tooth, with the lingual part of the anterior one better developed.

EMM 0013, right M2 (Pl. XXXVI 2, Tab. 38): The M2 is the least worn among the upper teeth. Its H at paracone is 73 mm. The antecrochet and the constriction folds of protocone are all weakly expressed. There is no real postfossette owing to the low posterior cingulum, which does not close the embrasure from behind. Otherwise it is similar to that of IMM 0012.

EMM 0058, right M3 (Pl. XXXVI 3): The M3 is heavily worn, and different from that of IMM 0012 in some parts. It is triangular in form, with more posteriorly slanting protoloph. The protocone is flattened lingually, with well developed anterior and posterior constriction folds and the antecrochet is strong (Pl. XXXVI 3b). The rudiment of the posterior end of the ectoloph is expressed only by a sudden rise of the cingulum accompanied by a very small fovea lingual to the highest part of the cingulum (Pl. XXXVI 3a).

EMM 0032, anterior half of axis (XXXVII 1): Compared with that of TP 9401, the axis shows a number of differences. The odontoid process is short and widened, 70 mm long measured from ventral side (110 mm in TP 9401), 70 mm high (120 mm in TP 9401) and 105 mm wide (100 mm in TP 9401), with rounded anterior end. The anterior articular facets form an angle of ~140° (125° in TP 9401), thus more perpendicular to the long axis of the odontoid process. Their total W is 320 mm (300 mm in TP 9401). What is remarkable is the presence of a pair of large hollowed areas separated by a thin sagittal septum within the body of the axis (Pl. XXXVII 1c).

EMM 0135, posterior half of axis (Pl. XXXVII 2): In dorsal view, the spinous process forms a flat and roughened surface pointed posteriorly. The posterior border of the postzygapophysis is more or less rectilinear, stretching posteromesially. In TP 9401 the spinous process ends at the level of the anterior border of the postzygapophysis, then followed by a pair of ridges slightly converging posteriorly (vide Pl. XXVII 2a). In AM 26390 the posterior end of the spinous process forms a wide, convexly curved line (*vide* Granger and Gregory, 1936, Fig. 7).

EMM 0136, distal end scapula and caput of humerus of left side (Pl. XXXVII 3): The W of the caput of the humerus is ~300 mm, about the same size as V 3195.2 referred to *P. lepidum* (Tab. 11). The scapular tuber is prominent and clearly separated from the glenoid cavity.

EMM 0022, distal end of right humerus (Pl. XXXVII 4): The longitudinal ridge of the lateral condyle is blunt, making the lateral half of the lower border of the condyle ascending laterally, rather than horizontally. The median groove is rather deep and almost symmetrical.

EMM 0145, left magnum (Pl. XXXVII 5, Tab. 42): The dorsal side is roughly rectangular in outline, wider than high and higher at lateral border. On proximal side there are two articular facets: a larger medial one articulating with scaphoid and a smaller lateral one articulating with lunar. The former facet is fan-shaped, narrowing posteriorly, with a narrow strip extending on the medial side of the knob-like prominence ("head" or posterosuperior process). This facet can partly be seen from the front. The latter facet is a narrower S-formed strip, widened posteriorly, occupying the major part of the knob-like prominence. The ridge separating the above two facets is clearly shown. In lateral view, the anterior half of the proximal side ascends slowly posteriorly, and the posterior half is occupied by the slightly higher knob-like prominence, posterior border of which lies anterior to the volar process. The facet articulating with unciform is large and rectangular in form (Pl. XXXVII 5d). On medial side the articulation with trapezoid is composed of two facets: a U-shaped one and a smaller oval one, separated from each other by wide depressed rough area (Pl. XXXVII 5e). The distal side is mainly articulated with McIII, accompanied medially by two smaller facets articulating with McII, anterior one of which is narrow strip-like, and the posterior one, triangular. The volar process is damaged, but may be posteroventrally curved.

EMM 0054, proximal part of left McIII (Pl. XXXVII 6): The facet articulating with magnum is rather flat, and that articulating with unciform is comparatively large. The angle formed by the above two facets on the dorsal side is rather blunt, ~145°.

EMM 0143, left patella (Pl. XXXVIII 1, Tab. 26): It is irregularly pentagonal in shape in dorsal or posterior view, with its lateral border more or less straight and lower border pointed. The medial border is irregularly curved, with its middle portion strongly protruded. The dorsal surface is heavily rugose, and the posterior one has a large saddle-shaped facet articulating with femur. The sagittal ridge is blunt and high transversely, but vertically it is slightly concave in its upper 2/3 and strongly convex in its lower 1/3. The articular facet medial to the ridge is wider than that lateral to the ridge. Both facets have the same curvature as the ridge.

EMM 0009, right tibia and fibula (Pl. XXXVIII 2, Tab. 27): A tibia of juvenile individual (epiphyses are not completely coalesced with diaphysis). It is very short and thick. The tibial tuberosity is very wide, but not very high above the shaft, with the muscular groove (sulcus muscularis) very shallow and wide, shifted laterally. The tibial crest is blunt and short, developed only in the upper 1/3 of the shaft, and does not link with the muscular line developed on the anteromedial border of the distal half of the shaft. The medial and posterior sides of the shaft are rather flat, while the anterior and lateral sides are transversely convex. A long depressed area of triangular form is developed in the distal part of the lateral side, where the fibula is to be coalesced with the tibia. The trochlea on distal end articulating with the astragalus is asymmetrical, with its lateral groove anteroposteriorly longer (130 mm) than that of the medial one (105 mm). The coalesced fibula and tibia leaves a small fissure only at the level of the tibial tuberosity.

The rest of the observed specimens are not described here because of their poor state of preservation.

(2) Comparison and Discussion

The anterior part of the mandible (EMM 0016) is the only specimen that can be referred to the genus *Aralotherium* for certain. The ventrally curved symphysis and incisors are the features uniquely diagnostic of the latter genus. However, it differs from *A. prohorovi* and *A. sui* in having a 13 mm wide diastema between the left and right i1's, while in the latter two species the incisors contact with each other at their bases. The distinction between EMM 0016 and *A. sui* is even more remarkable. The latter species is much larger in size, with a much more strongly bent symphysis. It is interesting to note that morphologically, EMM 0016 is very similar to one of the mandibles referred to *Paraceratherium bugtiense* by Forster-Cooper (1924b, Fig. 7). They have the same degree of bending of the symphysis, the i1 – p2 diastema about equally long as that of p3 – m1, the p1 being absent, and the same well developed buccal cingula on p2 – p3. However, EMM 0016 is larger than the latter. There is no doubt that the Dera Bugti mandible in question is to be transferred to the genus *Aralotherium*. However, it is hard to decide to which species this mandible should belong. Similarly, it is premature to establish a new species based on such poor information provided by the EMM 0016 mandible. The Erenhot specimen is here treated simply as an indeterminated species of *Aralotherium*.

The other specimens recently found from the Houldjin Formation, including all the other teeth and postcranial bones, are only tentatively referred to the same *Aralotherium* sp. Although similar to *Aralotherium* as a whole, most of these specimens differ from the known species of *Aralotherium* to a certain degree. It is hard to determine whether they should belong to the same form as the EMM 0016 mandible or not. They are tentatively referred to *Aralotherium* sp. primarily because they were found from the same "Houldjin gravels" of the same small area in the suburb of Erenhot.

In the forms of the odontoid process and the hollowed body, the axis from Erenhot is similar to that of *A. prohorovi*, but differs from those of *Urtinotherium intermedium* and *Paraceratherium lepidum*, where the odontoid processes are pointed and the bodies are apparently little hollowed (*vide supra*). However, the peculiar form of the spinous process in the Erenhot specimen is sharply distinctive from those in all the other forms (*vide supra*).

The distal end of the scapula and the proximal end of humerus of EMM 0136 seems to be the largest so far known of the paraceratheres. In morphology, they are more or less similar to those of *P. asiaticum* in having clearly separated scapular tuberosity from the glenoid cavity. However, EMM 0136 is similar to those of *A. prohorovi* in having weakly curved cavity and caput in transverse direction.

There is a good specimen of magnum in the Erenhot material (EMM 0145). It differs from that of *P. asiaticum* in having a low, knob-like prominence and small volar process (both larger in *P. asiaticum*), in separation of the facet articulating with the trapezoid into two, and in the anterior half of the proximal surface of the magnum being almost horizontal. The magnum of *Turpanotherium elegans* (*vide infra*) is particularly wide relative to height (Tab. 42 ratios 2 – 3), so that they differ from each other widely. The magnum described by Forster-Cooper (1924b) as belonging to *P. bugtiense* seems to be shorter (APD) and wider (Tab. 42). EMM 0145 differs from that of *A. prohorovi* also noticeably. In the latter form the knob-like prominence is shifted more posteriorly, becoming the most posteriorly situated element of the magnum, with the volar process completely lost, and the anterior part of the proximal surface being horizontal. Taken as a whole, EMM 0145 is more similar to that of *A. prohorovi*.

Similar cases hold true also for the proximal part of McIII (EMM 0054) and tibia (EMM 0009). In EMM 0054, the proximal facets articulating with magnum and unciform are flatter, and the angle formed by these two facets is obtuse and situated low, features similar to those in *A. prohorovi*, but different from those in *Paraceratherium*. EMM 0009 tibia is particularly short and has a very short tibial crest disconnected from the muscular line on the medial margin in the distal half of the shaft. An extremely long tibial crest is one of the features diagnostic of *P. asiaticum*, as illustrated by Borissiak (1923b).

In addition, the calcaneus described by Osborn (1923, Fig. 8 A) as belonging to *Baluchitherium grangeri* (= *Paraceratherium grangeri*) is also to be transferred to the genus *Aralotherium*, probably to *Aralotherium* sp. This is clearly shown in the brevity of the part of the calcaneus below the cochlear process, the strong slanting of the distal articular surface, and the longer tongue-shaped articular facet below the cochlear facet. All these features are characteristic of the genus *Aralotherium* as clearly demonstrated by Gromova (1959).

Turpanotherium **gen. nov.**

Type species: *Turpanotherium elegans* gen. et sp. nov.

Other included species: *Turpanotherium*? *yagouense* (Qiu, Wang et Deng, 2004) and *Turpanotherium* sp.

Geographic and stratigraphic distribution: So far only known from Turpan Basin, Xinjiang; Lanzhou and Linxia basins, Gansu; Late Oligocene – Early Miocene.

Diagnosis (only for symphysis, lower premolars and manus): Size slightly smaller than *A. prohorovi*. Symphysis and i1 extend anteriorly, with their lower borders forming an almost straight line. A diastema is present between left and right i1's. Cheek teeth rather high-crowned. Both p1 and p2 lost, crowns of unworn p3 and p4 higher than long. Lunar with anterior "hindering facet," two distal facets are unequally developed, with distal angle shifted strongly medially. Angles of PhIII's are strongly reduced.

Turpanotherium elegans **sp. nov.**

(Pls. XXXVIII 3 – 8, XXXIX-XLII; Tabs. 14 – 18, 35 – 37, 41 – 42, 44 – 49)

Holotype: V 3191.1, anterior part of mandible, with two i1's and left p3 – m1 (broken), collected from the upper 100 m of the Taoshuyuanzi Group in IVPP Loc. 64081.3, west of Feiyue Railway Station in eastern part of Turpan Basin, Xinjiang; Late Oligocene.

Other described material: 1) Turpan Basin: V 3191.2 (IVPP Loc. 64081.3) complete left manus; V 3191.3 (IVPP Loc. 64081), left unciform, broken astragalus, cuboid and MtIII; V 3192.1 (IVPP Loc. 64080. collected by the Bureau of Petroleum, Xinjiang), broken posterior part of skull; V 3192.2 – 3 (IVPP Loc. 64080.6, 8), PhI's of middle and lateral fingers; V 3193 (IVPP Loc. 64082), right scaphoid and PhII of lateral finger. All the above listed specimens were collected from the same area and the same level as the holotype. 2) Lanzhou Basin: V 3317, right p3 and p4 of the same individual, collected from Zhangjiaping, Gaolan County in 1987; V 3318, left m3, probably of the same individual as V 3317, purchased from Yantonggou, Gaolan County in 1995; V 3319, left P4, collected from Duitinggou, Gaolan County, in 1988; V 3320, right m1 and V 3321, left m2. All the above listed fossils from the Lanzhou Basin came from the Zhangjiaping Local Fauna at the base of the Middle Member of the Xianshuihe Formation, of Early Miocene age (Qiu *et al.*, 1997, 2001).

Diagnosis: As for the genus.

(1) Description and Comparison

1) Description of the holotype

V 3191.1, anterior part of mandible (Pl. XXXVIII 3, Tabs. 35 – 36): The posterior border of the symphysis is situated at the level of the posterior half of p4. Its dorsal surface is trough-like, and no evident constriction can be seen at the middle part of the symphysis and diastema. In lateral view, the upper border of the symphysis slopes down anteriorly, forming a straight line with the upper border of the i1. Mental foramen is large, located below the middle of p3, close to the lower border of the ramus.

The two i1's are large, widely separated from each other, with a 25 mm diastema between them. No other alveoli can be seen between the two i1's. In dorsal view, their roots diverge a little anteriorly, but their crowns diverge more markedly, with their mesial borders forming a 90° angle. The cross sections of both roots and crowns are oval in shape, with their longest axis stretching in the dorsolateral to ventromesial direction. The enamel of the i1 is very thin, with almost no indication of basal cingulum, except in the posteromesial corner. No wear facets are present on the i1. On right side, a small hole is located slightly posterior to the i1, which may be the alveolus of the rudimentary i2 or i3.

The p3 is triangular in outline, sharply pointed anteriorly. The crown is moderately worn, with its height close to its length. The paralophid is very short, hardly separated from the protolophid. The buccal wall of the protolophid is flat, with a vertical groove at the basal half of the middle part, making the posterobuccal corner of the protolophid rather angular. The metalophid is high and thick, extending posterolingually. The hypolophid is similar to the protolophid in robustness and height, but the entolophid is very thin, sloping lingually, and no separate entoconid is formed. The ectoflexid is narrow and deep. Both lingual and buccal cingula are well developed, with only the part on the buccal wall of the hypolophid being weakly expressed. The p4 is trapezoid in outline, narrower anteriorly, with crown slightly higher than that of p3. The paralophid is evidently longer, but still thin and shorter than metalophid. The trigonid is U-shaped, with the posterobuccal corner of the protolophid angular. The entolophid is more robust than in p3. Both trigonid and talonid tend to be closed lingually, and the ectoflexid is deeper. The cingulum is slightly weaker than in p3. The m1 is poorly preserved, with its cingulum even less developed than in p4.

The wear pattern of the p3 – m1 is rather peculiar, with the lingual part of the wear facets turning lingually, so that a large part of enamel on the lingual side is worn away, especially in p4 and the anterior part of the m1 (Pl. XXXVIII 3b).

2) Other materials from Turpan Basin

V 3191.2, a left manus (Pl. XLII 1): All the bones of the manus (except trapezium) are in natural articulation, with only a few of them slightly damaged (scaphoid, distal part of McIII, and PhIII, etc.).

Scaphoid (Pls. XXXIX 1, XLII 1; Tab. 14): The anterodistolateral projection is broken away. In dorsal view, the scaphoid is about equally high and wide (including the missing projection). In medial or lateral view, it is longer (APD) than high. The most bulged parts of the dorsal and volar sides are situated in the lower 1/3 of the bone. The proximal facet articulating with the radius is rectangular in outline, flat in the anterior-most part, then convex, and concave posteriorly. The distal side bears two large facets articulating with magnum and trapezoid (Pl. XXXIX 1d$_{m,\ td}$). The facet articulating with the trapezium is very small, round in form, retreated to the volar side of the bone (Pl. XXXIX 1d$_{tm}$). On lateral side there are two facets articulating with the lunar (Pl. XXXIX 1b$_{l1,\ l2}$). The upper facet forms a horizontal strip, while the lower one is semilunar in form, restricted to the anterior half.

In the whole, this scaphoid is more similar to that of *A. prohorovi* than of *P. asiaticum* in having the same general proportion (longer than high), the presence of a "hindering facet," and the form of the upper facet articulating with the lunar. In *P. asiaticum*, the bone is higher but shorter in proportion (Tab. 14 ratio 2), without "hindering facet," and the posterior end of the upper facet articulating with the lunar turns evidently downward (Borissiak, 1923b, Pl. VII 6c). V 3191.2 differs from *A. prohorovi* in being smaller, narrower and longer (Tab. 14), and the presence of a facet articulating with the trapezium, which is present in *P. asiaticum*, but wanting in *A. prohorovi*.

Lunar (Pls. XXXIX 2, XLII 1; Tab. 15): Both sides of the proximal articular facets are slightly damaged. There is a clear, almost horizontal "hindering facet" in the anterior part of the proximal facet (Pl. XXXIX 2a – 2c p). Behind this "hindering facet" is an enormous hemispherical knob-like prominence or "head." In proximal view, the lateral side of the "head" is rather straight, while the medial side is strongly convex. On distal side there are two large facets articulating with magnum and unciform (Pl. XXXIX 2d m, u). They are separated from each other by an S-shaped ridge, and each facet has a transverse ridge in the middle. The anterior halves of the facets are more or less flat, while the posterior halves are hemispherically concave, so that the separation between the two halves is sharp, forming an angle, which can be seen from medial or lateral side. The anterior end of the S-shaped ridge forms the angle bordered by the two distal articular facets. The angle is rather obtuse, and only shallowly inserted into the magnum and unciform. Seen from the front, the insersion of the lunar between the magnum and unciform is asymmetrical so that the lunar rests largely on the unciform (Pl. XLII 1). The articular facets on the medial and lateral sides of the bone are conformable to those in scaphoid and cuneiform respectively. The volar process is voluminous, stretching posteriorly.

The lunar of V 3191.2 is close to that of *A. prohorovi* in having a "hindering facet," and lacking the small posteroventral facet on medial side articulating with the scaphoid. On the other hand, it is similar to *P. asiaticum* in general morphology of the distal facets articulating with magnum and unciform. The anterior halves of the two facets are more or less flat, angularly separated from the posterior halves of the facets clearly seen in medial or lateral view (Borissiak, 1924b, Pl. VIII 1d). However, the lunar of V 3191.2 is unique in dorsal view of its distal side, i.e., the facet articulating with unciform is much wider than that with magnum, so that the angle separating the two distal facets is shifted strongly medially and its insertion into the second row of the carpals is very shallow.

Cuneiform (Pls. XL 1, XLII 1; Tab. 16): The bone is roughly semicylindrical in form, longer (APD) than high, and higher than wide. In lateral view, the bone is higher anteriorly than posteriorly. The proximal end bears three facets articulating with radius (anteromedial), ulna (central and lateral) and pisiform (posteromedial) respectively. That for the ulna (Pl. XL 1a u) is the main facet, fan-shaped, concave longitudinally, while those for the radius (Pl. XL 1a r) and pisiform (Pl. XL 1a p) are smaller and triangular, of about equal size, facing upward and medially respectively, and separated from each other widely. On medial side the facets articulating with the lunar (Pl. XL 1c l1, l2) conforms to those on lunar. The distal end bears only one large facet articulating with unciform. It is flat in anterior part, followed by a transverse bar-shaped prominence and strongly concave behind the bar.

As a whole, the above described cuneiform is rather close to that of *P. asiaticum* (Borissiak, 1923b, Pl. VIII 2). This can be seen in the following points: 1) Both are moderately higher anteriorly in lateral view, with the most part of its lower border being flat. In *A. prohorovi* the anterior side is much higher than the posterior side, and the lower border is strongly convex anteriorly (Gromova, 1959, Pl. XIV 1B). In *P. bugtiense* the difference in height is hardly noticeable (Forster-Cooper, 1924a, Fig. 13). 2) The facet articulating with radius is small and widely separated from that articulating with pisiform. In *A. prohorovi* the two facets are almost connected (Gromova, 1959, Pl. XIV 1A), whereas in *P. bugtiense* the facet articulating with radius is much longer than that articulating with pisiform (Forster-Cooper, 1924a, Fig.

18). However, the cuneiform of V 3191.2 is somewhat similar to *A. prohorovi* in being proportionally longer and narrower and having a rather pointed anterior edge.

Pisiform (Pl. XLI 2, Tab. 46): In lateral view, the bone looks like a long teardrop, becoming higher posteriorly. At dorsal end there are two articular facets for ulna and cuneiform respectively (Pl. XLI 2a $_{u,\ c}$). Both facets are wider than high, forming a dihedral angle between them. The former is slightly concave longitudinally, while the latter, slightly convex. Posterior to the facets is a neck, on medial side of which is a wide and deep groove where a tendon of some flexor muscle passes through. The volar part of the bone is higher, without bending medially. Its lateral surface is highly vermiculated.

So far only the pisiform of *A. prohorovi* has been described of the paraceratheres (that of *P. asiaticum* was only measured by Gromova, 1959, Tab. 20). The pisiform of V 3191.2 is smaller than both of them (Tab. 46), and it is more or less straight in dorsovolar direction, without bending medially in its volar end (Pl. XLI 2b). According to Gromova (1959), in *A. prohorovi* the volar end of the bone bends medially (Gromova, 1959, p. 48). In proportion, V 3191.2 is closer to that of *A. prohorovi* (Tab. 46), but it is similar to that of *P. asiaticum* in being straight anteroposteriorly, and in having both articular facets being wider than high (in *A. prohorovi* these facets are either equally high and wide or higher than wide).

Trapezoid (Pl. XL 2, Tab. 41): It is semicylindrical in form. In proximal view (Pl. XL 2c), its dorsal and laterovolar ends are angular, its dorsomedial border is straight, and its lateral border is convex. The proximal facet for scaphoid is convex dorsovolarly, extending to volar side of the bone, confluent with the tiny facet for the trapezium. Distally there is only one facet for the McII, which is flat. There is also a small process bulging from the laterovolar corner of the distal side. The dorsomedial side of the bone is vermiculated, covered by numerous tiny foramina. The lateral side of the bone bears a horseshoe-formed facet for the magnum, distovolar part of which is separated from the other part by a V-shaped notch (Pl. XL 2b).

Again, it is the smallest one among the known trapezoids of large-sized paraceratheres (Tab. 41). In proportion it is rather close to that of *A. prohorovi* (Tab. 41 ratios 2 – 3). The curvature of the proximal facet in *A. prohorovi* is also similar to that of V 3191.2 (in *P. asiaticum* the curvature is stronger). However, in the form of the facet for the magnum, V 3191.2 is closer to that of *P. asiaticum*. In both species this facet takes the form of a horseshoe, whereas in *A. prohorovi* this facet is completely separated into an upper and a lower one. The laterovolar process presented in V 3191.2 is absent in all the other known trapezoids of the large-sized paraceratheres.

Magnum (Pls. XL 3, XLII 1; Tab. 42): This is the largest of the carpal bones. It is highly irregular in form. In dorsal view, it is roughly rectangular in form, much wider than high (Pl. XLII 1). Seen from proximal or distal side, the bone is roughly fan-shaped. On proximal side there are two facets articulating with scaphoid and lunar respectively. The former is fan-shaped, situated only in the anterior half of the bone (Pl. XL 3a $_s$). The latter forms a narrow strip, extending posteromedially, transformed into a semispherically convex surface occupying the whole width of the knob-shaped "head" of the bone (Pl. XL 3a $_l$). The medial side bears the facet for trapezoid, which conforms with its counterpart on trapezoid. The anterior part of the lateral side of the bone is occupied by a rectangular articular facet for the unciform (Pl. XL 3a – b $_u$). Distally, the bone is articulated mainly with the McIII, but accompanied by an anterior and a posterior facet articulating with the McII on the medial side. The volar process is robust, stretching slightly downward, separated from the "head" by a wide notch.

Taken as a whole, the magnum of V 3191.2 is unique in being small in general size and much wider in proportion on dorsal side. V 3191.2 is closer to those of *P. asiaticum* and *P. grangeri* in having a larger "head," separated by a notch from the prominent volar process, which stretches more posteriorly than the "head." The magnum of *P. grangeri* (AM 21618) further differs from that V 3191.2 in lacking the articular facet for the McII. The magnum of *Arolotherium prohorovi* differs from V 3191.2 in having very pronounced "head" shifted more posteriorly than the volar process. The magnum of *Aralotherium* sp. (EMM 0145) is distinguished from V 3191.2 in being much larger in general size and much longer and higher in proportion.

Unciform (Pls. XLI 1, XLII 1; Tab. 17): The laterodorsal side forms a continuous convex surface. In proximal or distal view, the bone is fan-shaped. On proximal side there are two articular facets for the lunar and cuneiform respectively (Pl. XLI 1a c, l). The former facet is roughly rectangular in outline, with its longer axis extending posterolaterally. The latter facet is triangular in form, slightly larger than the former. Both facets are saddle-shaped, with their anterior parts more or less concave, forming the "hindering facets," and the posterior parts markedly convex (APD). The mediodistal side bears three facets forming a continuous convex surface: for magnum (medial), McIII (middle) and McIV (lateral), the last of which being the largest (Pl. XLI 1c m, mcIII, mcIV). A narrow and pointed volar process is present at laterodistal corner on the volar side. On the distal border of the lateral side of the bone, lateral to the volar process, is a small oval facet for the McV (Pl. XLI 1b mcV).

The unciform of V 3191.2 is close to that of *P. asiaticum* in three points. 1) There is a clearly shown volar process. 2) The facet articulating with McV is still present. 3) The L/W ratio in V 3191.2 (80.5%) falls within the range of variation of the ratios in *P. asiaticum* (65.5% – 92.8%). However, the presence of the "hindering facets" in V 3191.2 is the diagnostic character of *A. prohorovi*.

McII (Pl. XLII 1, Tab. 37): The shaft of the McII of V 3191.2 is rather thick, but without particularly widened epiphyses. Proximally, there is only one facet articulating with the trapezoid. On mesial side of the proximal end there are two pairs of facets articulating with both magnum (upper pair) and McIII (lower pair). On distal end the articular trochlea for the PhI is ovoid in anterior half, provided with a median ridge in the posterior half, becoming stronger toward the volar side of the trochlea.

In robustness, V 3191.2 is closer to the McII of *A. prohorovi*, but still shorter and more robust than the latter. The McII of *P. asiaticum* is much longer and slenderer (Tab. 37). The APD of the distal end of V 3191.2 is markedly smaller than in both *A. prohorovi* and *P. asiaticum* (Tab. 37 ratio 5). In the latter two forms, the articular facets for the magnum and the McIII are both strip-like, without further separation into two.

McIII (Pl. XLII 1, Tab. 37): The distal end of the McIII is badly damaged. The shaft becomes thicker from the lower boundary of the upper 1/3 distally. The sagittal ridge of the distal trochlea is rather flat at its posterior end, forming a 20 mm wide flat surface.

The McIII of V 3191.2 is similar to that of *Paraceratherium* in the pattern of widening of the shaft. In *Aralotherium*, as stated by Gromova (1959), the narrowest part of the shaft is always at the mid-length of the shaft.

McIV (Pl. XLII 1, Tab. 18): The distal end is also damaged. It is as long as the McII, but more robust. The bone bends only slightly. The narrowest part of the shaft is below the proximal end. The facet articulating with the unciform is large and flat, but no facet for McV is observed.

Again, it is closer to that of *A. prohorovi*, but shorter and more robust. In the flatness of the proximal facet, it is also close to that of *A. prohorovi*. In *P. asiaticum* this facet is concave in dorsal view, and a facet for McV is still present.

McV (Pl. XXXVIII 4, Tab. 47): It is completely preserved. In volar view, it takes the form of an obliquely oriented comma, volar surface of which is very rugose. Dorsally, there is only one facet articulating with the unciform.

In both size and morphology, the McV of V 3191.2 is very close to that of *A. prohorovi*, differing only in proportion. In *P. asiaticum* this bone is not only much larger, but also has a pronounced volar process extending posterodistally (Borissiak, 1923b, Pl. VII 7c). V 3191.2 is unique in having only one facet articulating with unciform. In *P. asiaticum*, two facets articulating with both unciform and McIV are present, whereas in *A. prohorovi* the McV is articulated with both unciform and McIV by one large facet apparently merged by two smaller facets.

PhI – II of middle finger (Pl. XLI 3 – 4, Tab. 44): Both are dish-formed, width > thickness > height. Seen from above or below, the PhI is more or less oval, while the PhII is more or less rectangular, being lower than the PhI. The proximal facet of the PhII bears weak and blunt sagittal ridge, bordered bilaterally by paired shallow depressions, while the distal facet of PhI – PhII are inversely formed, with sagittal grooves and pairs of convexities.

Both of the two phalanges are more similar to those of *A. prohorovi* than to *P. asiaticum* in general proportion. In *P. asiaticum*, the PhI is higher in proportion, while the PhII, thinner (Tab. 44). Furthermore, the PhI – II in *P. asiaticum* are thicker (APD) at lateral sides than in the medial part (Borissiak, 1923b, Pl. XI 3 – 6). The PhI of V 3191.2 differs from that of *A. prohorovi* in lacking a protruded band at the distal end of the dorsal side, which is well developed in the latter (Gromova, 1959, Fig. 18 A^3), and having more strongly expressed sagittal ridge and groove on proximal and distal surfaces (more similar to *P. asiaticum* than to *A. prohorovi*).

PhIII of middle finger (Pls. XLI 5, XLII 1; Tab. 48): The bone is only partly preserved, with its lateral angle missing. The preserved medial angle shows that the angle is highly reduced. The proximal articular facet bears a median ridge and two lateral depressions.

The PhIII of V 3191.2 differs from all known PhIII's of middle digits of large-sized paraceratheres by its small size and the strongly reduced angles.

PhI – II of lateral fingers (Pl. XLI 6, Tab. 49): The PhI's of lateral fingers are in the form of a trihedral prism, with distal ends strongly slanting. The PhII's of lateral fingers are irregularly cubic in form, with proximal and distal articular facets being basically parallel. "Pseudo-facets" are present at distal ends on dorsal sides in both PhI and PhII.

In the degree of concavity and convexity of the articular facets, the PhI – II of V3191.2 are intermediate between those of *P. asiaticum* and *A. prohorovi*, the latter of which has the most flattened articular facets in large-sized paraceratheres.

PhIII of lateral fingers (Pl. XLI 7 – 8, Tab. 45): In dorsal view, the PhIII of the second finger is generally rectangular in outline (Pl. XLI 8). Each of the mesial and lateral sides is composed of a pair of angles: proximal and distal, but on the mesial side the angles are better separated. The dorsal surface of the PhIII is rather flat and strongly rugose, with a transverse groove at the level slightly above the middle. The proximal facet is weakly saddled. The PhIII of the fourth finger is larger than that of the second one, but alike in morphology (Pl. XLI 7).

They differ from those of *A. prohorovi* and *P. asiaticum* in being smaller and having a flat dorsal side but convex volar side, just opposite to those in the latter two forms. Furthermore, the angles in V 3191.2 are highly reduced than in the latter two forms.

Sesamoids (Pl. XXXVIII 5 – 8): The proximal pair of the middle finger are the largest. Their dorsal articular facets take the form of a Chinese pause mark "、", and their volar sides are strongly convex and rugose. The proximal sesamoids of the second and the proximal mesial sesamoid of the fourth finger are close in form. They are curved and bean-shaped. Those of the second finger are smaller in size (Pl. XXXVIII 6 – 7). However, the proximal lateral sesamoid of the fourth finger is markedly thinner, but longer and more curved (Pl. XXXVIII 8). No comparison with sesamoids of other paraceratheres can be made because of lack of comparable material.

3) Material from Lanzhou Basin (V 3317–3321)

p3 (Pl. XLII 2, Tab. 36): The tooth is moderately worn. Since no contact facet can be detected on the anterior side of the tooth, this tooth should be considered the first tooth in the series. This is in full accordance with the type mandible. Though moderately worn, the tooth remains higher than long. Its crown view is trapezoid in form, strongly narrowed anteriorly. The paralophid is short, but extends to the lingual side of the tooth and slightly bends posteriorly at its lingual end. The protolophid bears a clear vertical groove on buccal side, and the posterobuccal corner of the protoconid is rounded, without tubercles. The ectoflexid is narrow and deep, and the metalophid is very short. The upper border of the hypolophid is concave in lateral view, ascending anteriorly, forming the highest part of the tooth together with the metalophid. The entolophid is very long and narrowed lingually. In lingual view, the paraconid is very high, with its top slightly higher than that of the entoconid. The trigonid basin is narrowed down, becoming a cleft, because of the backward bending of the paraconid toward the base. The entoconid bends anteriorly toward its base, but does not close the talonid basin because of the larger size of the latter. The tooth is surrounded by an almost continuous cingulum. The buccal cingulum is W-shaped, steeply ascending anteriorly and posteriorly. The lingual cingulum is heavier than the buccal one, closing both the trigonid and talonid basins.

p4 (Pl. XLII 2, Tab. 36): It is similar to p3 in general morphology. However, it is rectangular in crown view, with much longer paralophid, but weaker cingulum. The entolophid and the posterior part of the hypolophid are heavily worn, so that the posterior part of the tooth slopes down steeply in lateral view.

m2 (Pl. XLII 3, Tab. 36): The heaviest worn tooth of the described teeth. The trigonid takes the form of an oblique U, with the buccal wall of protolophid weakly rounded. The trigonid basin takes the form of a narrow fissure when heavily worn, but the talonid basin is widely open. The buccal cingulum is well developed only at both ends: the anterior part ascends almost vertically to join the almost horizontal anterior cingulum, and the posterior part ascends less steeply to join the posterior cingulum, which is lower than the anterior one. Tubercles are present at the base of the ectoflexid. The lingual cingulum is developed only at the lingual end of the paralophid, and at the outlet of the talonid basin in the form of tubercles.

m3 (Pl. XLII 4, Tab. 36): It is closely similar to m2, but larger. The anterior part of the lingual cingulum is better developed, closing the trigonid basin.

P4 (Pl. XLII 5): It is rather high crowned, about equally high and long when moderately worn. The buccal wall of the ectoloph is convex, with a faint parastyle fold. The lingual wall of the ectoloph bulges at the place of the metacone. The hypocone is connected with the protoloph, taking the form of a gourd with long stalk turning buccally. The part of the protoloph buccal to the protocone is thin, but links with the ectoloph at higher level. The metaconule takes the form of an elbow, remaining isolated from both ectoloph and hypocone when moderately worn. The tooth is surrounded by a continuous cingulum, with its lingual portion prominent and situated high. Both ends of the buccal cingulum ascend sharply. The tooth is 43.3 mm long, 52.4 mm wide, 44.5 mm high at buccal wall, and 27.2 mm high at the lingual side of the hypocone.

(2) Discussion

The reasons we prefer to associate the manus (V 3191.2) with the anterior part of the mandible (V 3191.1) are threefold. 1) They were found from the same site (IVPP Field no. 64081.3). 2) They are small and comparable in size. The lower cheek teeth of V 3191.1 are generally 0.8–0.9 as long and wide as those of *A. prohorovi* (Tab. 36), while most of the carpal and metacarpal bones are either as large as the smallest of those of *A. prohorovi*, or even smaller (Tabs. 14–18, 35–37, 41–42, 44–49). However, the phalanges of V 3191.2 are certainly the smallest among all the known paraceratheres. 3) In morphology, both V 3191.1 and V 3191.2 possess some mixed features of *A. prohorovi* and *P. asiaticum*, in addition to features uniquely possessed by themselves.

The features of V 3191.1 – 2 similar to those of *A. prohorovi* are the following. 1) The p3 is triangular in crown view; posterobuccal corner of protoconid in p3 – p4 is rounded, without pearl-formed tubercles, but the entolophid is fully formed. 2) Almost all the manus bones are low (carpals) and short (metacarpals) relative to their widths, thus close to those of *A. prohorovi* in proportion. 3) There are "hindering facets" in proximal surfaces of the scaphoid and lunar.

The features of V 3191.1 – 2 similar to those of *Paraceratherium* are the following. 1) The scaphoid bears a small facet articulating with the trapezium. 2) The cuneiform, pisiform, magnum and unciform are more similar to those of *Paraceratherium* in general morphology (*vide supra*). 3) The narrowest part of the metacarpals is around the lower boundary of the proximal 1/3 of the shaft. 4) The paired convex surfaces on the distal side of the PhI of middle finger are more or less confluent rather than clearly separated from each other.

The features possibly uniquely possessed by V 3191.1 – 2 are the following. 1) The symphysis and the paired i1 are very peculiar in morphology: their lower border forms a straight line, the two i1's are widely separated from each other. The i1 is covered by very thin enamel layer, with faint cingulum. 2) The p1 – p2 are completely lost, without even alveoli. 3) The facets articulating the lunar with magnum are rather horizontally positioned. 4) The McIV and its related bones (cuneiform, unciform and phalanges) are wider relative to the McII and its related bones. 5) All the PhIII's are highly reduced, with particularly reduced angles.

It is interesting to note that some of the features of V 3191.1 – 2 are rather close to those of *Benaratherium callistrati* from Benar, Georgia, established by Gabunia (1955, 1964). Both forms are small, comparable in size. The morphology of the lower premolars, the distal facet of the lunar articulating with the magnum, the position of the narrowest part of the metacarpals and the relative robustness of the McIV with its related bones of these two forms are also very close. The two forms differ from each other in a few characters, such as the higher crowned teeth and the presence of "hindering facets" etc. in V 3191.1 – 2. It is a pity that *Benaratherium callistrati* is so far only poorly known, especially concerning its symphysis and i1. A more detailed comparison between these two forms is not possible now. For the time being, we prefer to establish a new genus and species for the material of V 3191.1 – 2: *Turpanotherium elegans*.

The p3 and p4 of the material from the Lanzhou Basin are so close to those of V 3191.1 that we have no hesitation in referring the Lanzhou material to the same taxon as V 3191.1.

Turpanotherium? *yagouense* (Qiu, Wang et Deng, 2004)

Paraceratherium yagouense Qiu, Wang et Deng, 2004

Holotype: V 13820, a juvenile skull with DP1 – DP4, M1 and unerupted M2 and right P2, from Yagou, Dongxiang County, Linxia Prefecture, Gansu Province, Late Oligocene.

Emended diagnosis (according to Qiu *et al.*, 2004a): "Small, close to *P. bugtiense* in size. Length of muzzle anterior to DP1 not surpassing DP1 – DP4. No upper incisors, canines and P1. Cheek teeth high-crowned, with thin layers of cement. M1 possesses crown height equaling the maximum crown length, protocone with lingual groove. DP2 – M1 with large antecrochet, anterior protocone and hypocone constriction grooves, high and ridge-formed anterior and posterior cingula, lacking lingual cingulum, often with pillar-formed tubercles in the middle of anterior cingulum, medisinus, postfossette and posterior to antecrochet."

Comments: Qiu, Wang and Deng (2004a) first attributed this new form to the genus *Paraceratherium*, but did not exclude the possibility that "the Yagou material may represent a new genus" (Qiu *et al.*, 2004a, p. 188, in Chinese text). The small size and the high crowned cheek teeth of this Yagou skull are the features most characteristic of the new genus *Turpanotherium*. This is why we decide to transfer the Yagou skull to the new genus tentatively, with question mark.

***Turpanotherium* sp.**

(Pl. XLIII 1-3; Tabs. 36, 50)

Referred specimens: 1) V 3307 (Geologic Mapping Team of Ningxia Field no. Q127-HB-127), left p4-m1 and trigonid and hypolophid of m2, from grayish and grey-yellow sandstone and conglomerate in the basal part of the Hongliugou Formation, Yuanjiawowo Village, Haiyuan County, Ningxia, Early Miocene?. 2) V 3308 (IVPP Field no. 78018), left MtIV, from the Upper Member of Wulanbulage Formation on west slope of Qianlishan Mountains, 8 km southeast of Taositu Railway Station, late Early Oligocene - Late Oligocene. 3) V 3309 (IVPP Field no. 77046.2), incomplete left astragalus, from upper part of Oligocene deposits near Wulanmannai valley. 4) NMB 4343, a right M3 collected from Bayantaohai, Wuhai, Nei Mongol (IMM collection).

Description and comments: The teeth of V 3307 (Pl. XLIII 1, Tab. 36) are small, but rather high-crowned. The moderately worn p4 is higher than long. The m1 and m2 are also rather high-crowned. Taken as a whole, these teeth are very close to those of V 3191.1 in morphology. The MtIV of V 3308 (Pl. XLIII 2, Tab. 50) is very short and robust, with its narrowest part of the shaft at its upper 1/3. The astragalus of V 3309 is also very small and seems to be rather low relative to its width. The teeth of V 3307 are more or less certain to be referred to *Turpanotherium*, while the referral of the other two specimens to this genus is highly conjectural.

The M3 of NMB 4343 (Pl. XLIII 3) is very small in size, with its lingual L 64.3 mm, Max W 75.5 mm and L of ectometaloph 71.4 mm. However, it is rather high-crowned, with its Max observed H reaching 60 mm. Small antecrochet and crochet can be observed, and the cingula, especially the anterior and lingual ones, are very prominent, rather similar to those in *Dzungariotherium tienshanense*.

Paraceratheriinae gen. et sp. indet.

(Pl. XLIII 4-7; Tabs. 11, 15, 17, 25, 33, 41, 48)

Material: 1) West slope of Qianlishan Mountains: IVPP Loc. 78018: V 3310, heavily damaged right horizontal ramus with part of symphysis, with right i1 and dp3-m1; V 3311, PhI of lateral digit. IVPP Loc. 79013.2: V 3315, left unciform (Tab. 17). 2) Wulanmannai Valley (Saint-Jacques): IVPP Loc. 77046: V 3270, PhI of lateral digit. IVPP Loc. 77046.2: V 3312, PhIII of middle digit (Pl. XLIII 6, Tab. 48). IVPP Loc. 77046.3: V 3313, left trapezoid (Pl. XLIII 4, Tab. 41). IVPP Loc. 77049.4: V 3314, right trapezoid. 3) Haiyuan County, Ningxia, exact locality unknown: V 3316, right MtIII (Pl. XLIII 5, Tab. 33). 4) V 824, right lunar (Pl. XLIII 7), Lingwu, Ningxia, Qingshuiying Formation, Oligocene.

Comments: The above listed specimens were found by the joint team of the IVPP and the 4th Regional Surveying Brigade of Ningxia during 1978 - 1979. Although their stratigraphic position is more or less certain, their systematic position remains unclear because of the paucity of the collected material. Similar case holds true for the material from Lingwu County, Ningxia, about 240 km south of the Wulanmannai (Saint-Jacques), described by Young and Chow in 1956. The material from Lingwu is composed of a cranial part of skull, a P2, a humerus and proximal parts of radius and ulna. Judged from the size of the skull and the morphology of the paroccipital-posttympanic process, the cranial part of the skull is possibly to be attributed to the genus *Paraceratherium*, being probably more advanced than *P. grangeri*, but more primitive than *P. lepidum*. The P2 (originally identified as P3 by Young and Chow) is triangular in outline, protoloph being confluent with the hypocone, thus unlike the P2 of *P. grangeri* and *P. asiaticum* (where P2 is rectangular and the protocone is separated from hypocone, *vide* Granger and Gregory, 1936, Fig. 2). It is more or less similar to that of *P. lepidum*. The humerus is definitely longer and more slender than those in *P. lepidum* and *A. prohorovi* (Tab. 11). In proportion it is closer to that of *P. asiaticum*, but seems to be shorter (Tab. 11). The lunar is small, bearing a small "hindering facet" on its anterior end of the proximal side, and its distal angle is rather symmetrical (Pl. XLIII 7a – c). In size and proportion, it is rather close to that of *T. elegans* (Tab. 15), but differs from the latter species by having a symmetrical distal angle. No lunar has been found in the material of *P. lepidum*, and a comparison with the latter species is impossible. The true affinity of the lunar from Lingwu is so far uncertain. As a whole, the material described by Young and Chow (1956) cannot be safely referred to any of the known paraceratheres at present.

III. GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF PARACERATHERES

In the early stage of study of the paraceratheres, no in-depth stratigraphic investigation of paracerathere-bearing deposits was made. For instance, the 3CAE accumulated rich data of firsthand field observation. However, at the same time large numbers of problems concerning the dating and correlation of these deposits were left unsolved. Similar case holds true also for the other famous paracerathere localities, like Dera Bugti in Pakistan and the Turgai area in Kazakhstan.

Since the ending of the Second World War, especially in the last 20 – 30 years, great progress has been made in the field of stratigraphy. With the application of new techniques (isotopic dating, paleomagnetism, orbital chronology, etc.), the precision of the GTS has been greatly enhanced (Gradstein *et al.*, 2004). Specifically, the boundaries of Oligocene have finally been fixed at 33.9 Ma (lower), 28.45 Ma (Early-Late Oligocene) and 23.03 Ma (upper). The Middle-Late Eocene boundary is fixed at 37.2 Ma, and the Lutetian-Bartonian boundary, at 40.4 Ma. At the same time, considerable amount of field study of the deposits yielding paracerathere fossils was carried out, and numbers of problems concerning stratigraphic correlation and dating of these deposits were cleared up. The following is a briefing of the progresses in light of the current advancement in GTS.

1. Progresses in Stratigraphic Work of the Classical Areas Yielding Rich Paracerathere Fossils

(1) Tsagan Nor Basin, Mongolia

The paracerathere fossils were found from localities near the Loh Camp and in the area of the Grand Canyon (=Tatal Gol, Ulaan Khongil).

The most important paracerathere fossils from the Loh Camp area were those found by the 3CAE. Based on the "Field Records of Fossils" of 3CAE, the first is Field no. 90, including "proximal and distal ends of humerus and fragment of lower jaw. Also left half of skull," found "2 miles southwest of Loh Camp on fourth, August 1922"; while the second is no. 539, including "both fore feet and right hind foot complete, and the distal ends of metacarpals and all phalanges of the left hind foot. Also distal ends of limb bones on three feet," found on June 17th, 1925. "This specimen is on about the same level as the skull of *Baluchitherium* collected in 1922, and about 1/2 mile west of that locality." The locality yielding paracerathere fossils in the Grand Canyon is the valley called Tatal Gol, 8.5 miles west of the Loh Camp. There the paracerathere fossils were chiefly collected by the Mongolian Paleontologic Expedition organized by the USSR Academy of Sciences in 1948 – 1949, composed mainly of skeletal bones of smaller size, including a right pes (Gromova, 1959, p. 38, Tabs. 28, 30 – 33, 35 – 43). Those found by the 3CAE are only a few and unimportant.

Extensive geologic survey with particular emphasis on the paracerathere-yielding localities was done by the Mongolian-American Paleontologic Expeditions (MAE) organized by the AMNH during 1990 – 1998 and by the Austrian-Mongolian Project (AMP) supported by the Austrian Science Foundation and the IGCP project no. 326 conducted in 1995 – 1997. A monographic work containing the main view points on stratigraphy of this area written by McKenna *et al.* on behalf of the MAE is being circulated among vertebrate paleontologists, but not yet published. The results of the AMP geologic survey was already published (Höck *et al.*, 1999).

According to MAE, the redefined Hsanda Gol (replacing Shanda Gol) Formation is composed of 3 members: Tatal Member (Ulaan Khongil Fauna), Khar Khoroo Lava Member, and the Shand Member (Ulaan Khongil and Zavlia Fauna). The total thickness of the formation at the Loh Camp area is 57.5 m. The Tatal Mbr is "dark red color with few color bands," while the Shand Mbr "is represented by reddish-brown claystones and sandstones with abundant paleosols that give the Shand Mbr a subtle striped appearance." Using $^{40}Ar/^{39}Ar$ laser dating method, the Khar Khoroo Lava was dated as 31.2 ± 0.06 Ma. Another important work the MAE made is the tracing of the stratigraphic position of the paracerathere fossils collected by 3CAE in 1922 and 1925. All these paraceratheres fossils, including the type skull (AM 18650), were found from the basal part of the Shand Mbr, containing the Ulaan Khongil Fauna.

The results of the AMP geologic work differ slightly from those of MAE (Daxner-Höck *et al.*, 1997; Höck *et al.*, 1999). They have found two basalt layers in the working areas. The measured ages of 16 samples of Basalt I (= Khar Khoroo lava) show that it erupted around 31.5 Ma, with ages ranging from 30.4 to 32.1 Ma. The Basalt II is already interbedded in sediments of the Loh Formation, and its age is around 28 Ma, ranging from 27 to 29 Ma. Therefore, the transition from the Hsanda Gol Formation to Loh Formation is diachronous, between 29 to 24 Ma.

The recently published GTS 2004 (Gradstein *et al.*, 2004) suggested the age of the boundary between the Early and Late Oligocene is 28.45 Ma. Therefore, all the paracerathere fossils found by the 3CAE, including the holotype skull of *P. grangeri*, should have come from the lower part of the Shand Mbr, above the Khar Khoroo Lava, and their ages should be fixed at about 31 – 28 Ma, i.e., late Early Oligocene.

(2) Eren Region, Nei Mongol, China

1) Localities yielding *Juxia sharamurenensis*

All the material of *J. sharamurenensis* described in this volume is from the type section of the Shara Murun Formation at Ula Usu. The Shara Murun Formation in Eren region is particularly fossiliferous, and its mammal faunas have been extensively studied. In GTS 2004, Sharamurunian has been accepted as one of the Asian Land Mammal Ages (ALMA), representing the upper half of the Middle Eocene, spanning from 40.4 to 37.2 Ma (Gradstein *et al.*, 2004).

Radinsky (1967) mentioned three other specimens of 3CAE kept in the AMNH referred by him to *J. sharamurenensis* (called as *Forstercooperia sharamurenense* by Radinsky): a mandible (AM 20286), a juvenile skull and mandible (AM 20287), and a right pes (AM 20288). The first two specimens are indeed very close to *J. sharamurenensis* in size. However, the pes seems to be too small to be referred to this species, if the scale of the Fig. 10 in Radinsky's paper (× 1/2) is true. Lucas *et al.* (1981) referred some other specimens from Irdin Manha Formation at Irdin Manha, and possibly Shara Murun Formation in localities north of Tukhum to *J. sharamurenensis* as well. However, Lucas *et al.*'s identification is to be further verified.

2) Locality yielding *Juxia shoui*

The creators of *J. shoui* mentioned only that the type specimen came from the Ulan Gochu Formation at Urtyn Obo (Qi and Zhou, 1989, p. 205). Since a lunar bone of *Juxia* size was found from the "Lower White" (Ulan Gochu Formation) at Urtyn Obo (Osborn, 1929a) by Qi and Wang (*vide supra*), the type skull of *J. shoui* may well have been found in the same layer. If this is true, the existence of the genus *Juxia* may extend to the lower part of the Ulangochuian ALMA, i.e., early Late Eocene.

3) Localities yielding *Urtinotherium parvum*

The localities yielding *U. parvum* fossils in Eren region are the "Lower White" beds at Urtyn Obo

(EMM 0146) and the "Baron Sog" beds at Jhama Obo (AM 26190). The presence of *U. parvum* in "Baron Sog" beds at Jhama Obo (metapodials, tarsal bones and phalanges, *vide supra*) renders it highly necessary to reconsider the age assignment of the Jhama Obo's "Baron Sog" beds. At any rate, it should be assigned to the Ulangochuian ALMA, i.e., Late Eocene, rather than to Oligocene.

4) Localities yielding *Urtinotherium intermedium*

The localities yielding *U. intermedium* fossils in Eren region are: the "Middle White" beds at Urtyn Obo, the "Ulan Gochu" beds of Jhama Obo, the "Houldjin gravels" at Camp Margetts and the locality 7 miles W of Camp Margetts.

The type mandible of *U. intermedium* was only loosely reported to be found from Oligocene beds. Judged by the color of the mandible (grayish white) and the adhered matrix (white sandstone and claystone), it is certain that the specimen came from some white beds, but it is hard to decide whether it came from the lower, or middle, or even upper "white beds" in Osborn's profile. However, according to Wood (1939), the radius (AM 26026 [772]), which is referred to *U. intermedium* by the present authors (*vide supra*), was certainly from the "Middle White" in Osborn's 1929 section. This led us to think that the type mandible may also be from the "Middle White." In addition, the maxilla of *Dzungariotherium erdenensis* created by Qi, which is also transferred by us to *U. intermedium* (*vide supra*), probably came from this layer as well (Qi, 1989, p. 301).

A mandible from the "Ulan Gochu beds" of Jhama Obo (AM 26032 [702]) was referred by Radinsky (1967, p. 37) to *Indricotherium parvum*. This specimen is quite large in size, with its m1 – m3 200 mm long. This is roughly comparable with that of *U. intermedium*, which is 209 mm (Tab. 35). There are two layers yielding paracerathere fossils at Jhama Obo: *U. intermedium* from Ulan Gochu beds and *U. parvum* from "Baron Sog beds". *U. intermedium* is certainly more advanced than *U. parvum*. This is in contradiction with the stratigraphic positions of these two layers ("Baron Sog beds" are stratigraphically higher than Ulan Gochu beds), a problem to be clarified in the future.

The McIII from the "Houldjin gravels" at Camp Margetts (AM 26389), originally referred to *Baluchitherium grangeri*, has now been transferred to *U. intermedium* by us (*vide supra*). The other animals reported from the same layer include: *Metatitan relictus*, *Hyotitan thomsoni*, *Hypercoryphodon thomsoni*, *Lophialetes expeditus*, *Entelodon gobiensis* and *E. dirus* (Osborn and Granger, 1932; Granger and Gregory, 1943; Radinsky, 1965; Lucas and Emry, 1996b). This faunal list, especially the presence of the brontotheres and the archaic coryphodonts, tends to show that the "Houldjin gravels" at Camp Margetts are different from the "Baron Sog" at Urtyn Obo, where "no records of titanotheres and embolotheres" were found (Osborn, 1929a, p.3), and considerably different from the typical Houldjin gravels in the suburb areas of Erenhot, where *Aralotherium* sp. was recorded (*vide supra*). It is highly possible that the "Houldjin gravels" at Camp Margetts should be correlated with the middle part of the Ulan Gochu Formation. The same is true of the "Houldjin gravels" at the locality 7 miles west of Camp Margetts, where an axis was first described by Granger and Gregory (1936) as belonging to *Baluchitherium grangeri*, but transferred to *U. intermedium* by us (*vide supra*).

The distribution of the genus *Urtinotherium* in Eren region is restricted to the Ulan Gochu Formation. However, the concept of this formation has not been fully clarified. It was named in 1925, based on the section of the Ulan Gochu escarpment (Osborn, 1929a; Berkey *et al.*, 1929), where the formation is composed of a layer of red clay, only 2 feet thick. The red clay becomes thicker and thicker towards the east: reaching 122 feet at Twin Obo and 195 feet at Urtyn Obo, where the lithology becomes more complicated, consisting of four intercalated white and red beds (Osborn, 1929a, Fig. 2). The fossils of this formation recorded from Twin Obo include *Embolotherium loucksii* and *Brachyhyops neimongolensis* (Wang and Qiu, 2002). The fossils so far known from Urtyn Obo are: *Juxia shoui* and *Urtinotherium parvum* from the "Lower White"; rich embolotheres, including *Embolotherium andrewsi* and *E. grangeri* from the "Middle Red" and *U. intermedium*, *Ardynia praecox* and *Schizotherium avitum* from the "Middle White." Faunistically, the Ulan Gochu Formation is thus better represented at Urtyn Obo, but not the stratotype at Ulan Gochu escarpment.

5) Localities yielding *Paraceratherium grangeri*

Granger and Gregory (1936) indiscriminately lumped all the 3CAE specimens of large-sized paraceratheres from the Eren region into one and the same species, *Paraceratherium grangeri*. After some of them having been transferred to other genera and species (*vide supra*), there remain three major localities yielding *P. grangeri*: the "Baron Sog Formation" at Urtyn Obo and Nom Khong, and the "Houldjin gravels" at Overnight Camp.

The "Baron Sog Formation" at Urtyn Obo and Nom Khong are almost identical. They were characterized by Osborn (1929a) as containing exclusively baluchitheres, but no brontotheres-embolotheres, which became extinct by the end of the underlying Ulan Gochu Formation. Other forms described from there are *Ardynia kazachstanensis* (Radinsky, 1967), *Entelodon gobiensis* (Lucas and Emry, 1996b), *Schizotherium avitum* (Coombs, 1978), and *Tsaganomys altaicus* and *Cyclomylus intermedius* (Wang, 2003). This faunal list is in contradiction with that from the original "Baron Sog beds" proposed by Granger (1925). The faunal list of the latter includes large samples of *Embolotherium ultimum* (Granger and Gregory, 1943), *Zaisanamynodon borisovi* (Lucas *et al.*, 1996), and *Lophiomeryx anagarae* (Granger, 1925). This fauna of the "Baron Sog beds" looks more similar to that of Ulan Gochu Formation rather than to that of "Baron Sog Formation" at Urtyn Obo and Nom Khong. In fact, Jiang (1983) has proposed another name for the so-called "Baron Sog Formation" at Urtyn Obo and Nom Khong: Upper Naogangdai Formation, which we prefer to follow.

The fossils of the large-sized paraceratheres discovered from the "Houldjin gravels" at the Overnight Camp are really similar to those from Urtyn Obo and Nom Khong in size and difficult to be referred to a species other than *P. grangeri*. From the same gravel beds *Metatitan relictus* was reported (Granger and Gregory, 1943). While prospecting the outcrops of this area in 2005, we found a maxilla with P3 – M2 of *Allacerops turgaica* (IVPP Field no. EL 200510), a form often associated with *P. asiaticum* in Kazakhstan. Judged from the mammalian fossils, "Houldjin gravels" at the Overnight Camp may be contemporaneous with the typical Houldjin gravels particularly developed in the suburb areas of Erenhot City. On the other hand, the "Houldjin gravels" on the top of the section at the locality 16 km SW of Camp Margetts are certainly older than the typical Houldjin gravels as evidenced by the presence of mainly Irdin Manha mammals, such as *Eudinoceras mongoliensis*, *Gobiatherium mirificum*, *Lophialetes expeditus*, *Lophialetes* sp., etc. Qi (1987) also found *Andrewsarchus gigas* in the top-most layer of the section.

6) Localities yielding *Aralotherium* sp.

All the materials described in this volume as *Aralotherium* sp. are from the typical Houldjin Formation in the suburb areas of Erenhot City. However, the problems concerning the age of the Houldjin Formation are very perplexing. In addition to *Aralotherium* sp., *Entelodon dirus*, *Cadurcodon* sp., Caenopinae indet., and Brontotheriidae indet. were first reported (Matthew and Granger, 1923a). In recent years some micromammals were also recorded: *Gobiomys neimongolensis*, *G. exiguus*, *Advenimus* cf. *A. bohlini*, *A.* cf. *A. burkei*, *Yuomys* sp. and *Protataromys* sp. (Wang, 2001c). While prospecting these areas, we also found *Aprotodon* and *Hyaenodon* of very large size, in addition to brontotheres and amynodonts. Taken as a whole, the micromammals tend to show a rather older age (probably early Ulangochuian), while the large mammals show a younger age (Ergilian). For example, *Entelodon dirus*, *Hyaenodon* of very large size, *Cadurcodon*, and embolotheres are more or less comparable with those found from the Ergilin Member of Mongolia. *Aralotherium* sp. and *Aprotodon* are commonly found only in Late Oligocene. The presence of the two latter forms in the typical Houldjin Formation is rather enigmatic. At present, the possibility that the Houldjin Formation are heterogeneous, composed of mammals of different ages, can not be fully excluded. However, if *Aralotherium* and *Aprotodon* could occur earlier than presently known, then the age of the typical Houldjin Formation may be correlative with that of Ergilian ALMA, i. e., late Late Eocene in GTS 2004.

(3) Kazakhstan

The localities yielding the large-sized paraceratheres in Kazakhstan are mainly in two regions: the region along the Turgai River and the Lake of Chelkar-Teniz (type locality of *P. asiaticum*), and the Northern Priaral area (Kumbulak, type locality of *A. prohorovi*). In addition, some paracerathere fossils were also found from the lower reach of Ili River and southwest slope of Alatau Mountains in southeastern part of Kazakhstan.

As early as 1915, Borissiak dated the deposits yielding the large-sized paraceratheres around the Lake of Chelkar-Teniz as Oligocene, based mainly on the evolutionary level of *Allacerops turgaica*. In 1948 Borissiak already correlated these paracerathere deposits with those of Loh in Mongolia in age. Borissiak's opinion has been followed up to now. Recent study shows that the facies of the deposits yielding *P. asiaticum* in the Turgai area changes from west to east. In western part the deposits are called Saryin Formation, consisting of light-colored sandstone intercalated with clay of deltaic facies. Near the Lake of Chelkar-Teniz they are called Chelkarnura Formation, consisting of lagoonal green clay. In eastern part of the area they are called Betpakdala Formation, turning into brown or red clay of continental origin. All these three formations are rich of paracerathere fossils. However, they may not be strictly contemporaneous. The Saryin Formation may be slightly older than the Chelkarnura Formation, which may be in turn slightly older than the Betpakdala Formation.

According to Lucas *et al*. (1998), the Oligocene deposits are continental intercalated with marine and brackish layers. The base of the Oligocene deposits is Kutanbulak Formation of marginal marine facies, unconformably overlying the Eocene marine Chegan Formation. Next is the Chilikta Formation, which is mixed marine-freshwater in facies, yielding *Paraceratherium* fossils. Chagray Formation of marginal marine facies overlies unconformably the Chilikta Formation. The top of the Oligocene deposits is Aral Formation, which is mixed marine-freshwater in facies, yielding rich bivalve *Corbicula* and the rich samples of *Aralotherium prohorovi*. The unconformity between Chilikta and Chagray formations is considered the Early-Late Oligocene boundary. Therefore, *Paraceratherium asiaticum* occurred in the later half of Early Oligocene; while *Aralotherium prohorovi*, late Late Oligocene.

(4) Baluchistan, Pakistan

Dera Bugti, where the first large-sized paraceratheres were found, had long been assigned to Miocene, mainly because of the presence of the proboscidean fossils allegedly in association with the paraceratheres. In recent years since the end of 1990's, a joint expedition organized by French and Pakistan scholars has pursued an extensive geologic survey in this area, and succeeded in clarifying a number of long standing perplexities. Among them the most important is the alleged coexistence of the proboscideans with the paraceratheres. According to Welcomme *et al*. (2001), in Dera Bugti area the Oligocene deposits are represented by the Chitarwata Formation. Its basal part, Nal Member, is composed of typical marine deposits with rich Early

Oligocene nummulites. The majority of the Chitarwata Formation is called Bugti Member, which is totally continental. Thirty meters above the Nal Member, in Layer C2, not only fossils of *Paraceratherium bugtiense*, but also rich micromammals were found. Among the latter, *Pseudocricetodon nawabi* was recorded (Marivaux *et al.*, 1999), which might belong to the earliest Oligocene forms of the Pseudocricetodontinae in Europe. Above the Layer C2 are three fossiliferous layers containing *Paraceratherium*, *Aprotodon*, *Paraentelodon*, *Palaeohypsodontus*, etc. Only at the top, 25 – 40 m above the above mentioned fossiliferous layers, typical Miocene forms, such as *Prodeinotherium*, *Gomphotherium*, *Bunolistriodon*, *Eotragus*, start to occur.

(5) Turpan Basin, Xinjiang, China

The localities yielding large-sized paraceratheres are centered in three gullies north of the railway station of Feiyue (IVPP Loc. 64080, 64081 and 64082), with Loc. 64081 being the richest. According to Zhai (1978), all these localities were situated within the top-most 100 m of the more than 700 m thick Taoshuyuanzi Group.

The paraceratheres of this area now include four forms: *Paraceratherium lepidum*, *Dzungariotherium turfanense*, *D.? tienshanense* and *Turpanotherium elegans*. Judged from their evolutionary levels, especially that of *T. elegans*, it is perhaps safe to say that these fossiliferous layers should be Late Oligocene in age. Zhai (1978) described eight other forms from these same localities: *Amphechinus* cf. *A. rectus*, *Amphechinus*? sp., *Hyaenodon*? sp., *Sinolagomys kansuensis*, *Yindirtemys* sp. (originally *Tataromys* cf. *A. sigmodon*), *Aceratherium*? sp., *Schizotherium* sp., and *Didymoconus berkeyi*. Among them, *A.* cf. *A. rectus*, *S. kansuensis*, *Yindirtemys* sp. and *D. berkeyi* are the commonly occurred species in the Oligocene paracerathere beds. Having checked the limb-bones referred by Zhai to *Schizotherium* sp., we found that they are much larger and more advanced than those of *S. turgaicum*, which was found in association with *P. asiaticum*. This is in good accordance with the conclusion drawn from the evolutionary levels of the paraceratheres.

Fig. 29 depicts the major formations yielding Paraceratheriinae fossils in Asia.

2. Localities Yielding Sparse Paracerathere Fossils in China

(1) Ordos

Wulanmannai Valley, Nei Mongol: Having visited this valley three times (1977, 1978 and 2006), we are fully convinced that this valley is the same valley where Teilhard de Chardin collected his Oligocene mammals in 1923. So far two forms of paraceratheres have been recorded by us: *Dzungariotherium turfanense* and *Paraceratherium* sp. (*vide supra*). These deposits have never been formally named. While describing the newly found carnivores from this valley, Wang and Qiu (2003) gave a revised list of the Saint-Jacques fauna, including about 35 forms, mainly of small mammals. On the basis of the investigation of the team of IVPP and the Fourth Geologic Mapping Brigade (1978 – 1979), the lithology of these fossiliferous deposits (mainly Teilhard de Chardin's first and second layers of sands with *Baluchitherium*) can be compared with the Wulanbulage Formation established on the western slope of the Qianlishan Mountains. Their age assignment differed considerably, from Early Oligocene (Wang and Qiu, 2003), Middle Oligocene (Wang, 1987a – b), Late Oligocene (Teilhard de Chardin and Licent, 1924c; Teilhard de Chardin, 1926), to Aquitainian (Teilhard de Chardin and Leroy, 1942). Judged from the evolutionary level of the paraceratheres, these fossiliferous deposits are more likely to be later than those of the Loh and Turgai localities, i.e., early Late Oligocene.

West slope of Qianlishan Mountains, Nei Mongol: This is one of the best exposed Oligocene deposits with rather rich mammalian fossils in China, containing the stratotypes of both Wulanbulage and Yikebulage formations (Wang *et al*., 1981). The large-sized paraceratheres were discovered only in the Upper Member of the Wulanbulage Formation. Our identification revealed three forms: *P. lepidum*, *D. turfanense* and *Turpanotherium* sp. But the identification of the latter form is highly conjectural (*vide supra*). The age of the Upper Member of the Wulanbulage Formation is better to be assigned to early Late Oligocene.

Qinshuiying, Lingwu, Ningxia: The only paracerathere fossils from this locality were those first described by Young and Chow (1956) as *Baluchitherium grangeri*. Our observation of these specimens tends to show that they have nothing to do with *P. grangeri*, but their true nature is hard to determine at present. The accompanied mammals, *Cyclomylus lohensis* and *Archaeotherium ordosius*, are comparable to those commonly occurred in Hsanda Gol Formation. Therefore, the fossiliferous beds of the locality Qingshuiying may be Early Oligocene in age.

(2) Lanzhou and Linxia Basins, Gansu

Lanzhou Basin: Preliminary geological investigation was conducted by Young and Bien (1937), who established the Xianshuihe Formation for the most fossiliferous part of the section along the Xianshuihe River. The age of the Xianshuihe Formation was first assigned to Miocene based on the mammalian fossils of Tunggurian character found from the top of the formation. A detailed study of the Xianshuihe Formation by Qiu *et al*. (1997, 2001) resulted in subdividing the formation into three members characterized by different faunal assemblages: lower (Oligocene), middle (Early Miocene) and upper (Middle Miocene) members. The large-sized paracerathere fossils were found from both lower (*Paraceratherium* sp.) and middle (*Turpanotherium elegans*) members (*vide supra*).

Linxia Basin: The first paracerathere fossils of the Linxia Basin were reported by Qiu *et al*. (1990). They were from the basal part of the Cenozoic deposits, called Jiaozigou Formation, and identified as belonging to *D. orgosense*. Base on the wrong information that a part of proboscidean tusk had been collected together with the paraceratheres, Qiu *et al*. first assigned the formation to Early Miocene. Later, more careful investigation of the area proved that the alleged association of the paraceratheres with the proboscideans was certainly wrong. Another form of paracerathere found from Linxia Basin is *Turpanotherium*? *yagouense* (originally described as *Paraceratherium yagouense*). The latter is rather advanced in character, being rather high-crowned, provided with multiple accessary column-like tubercles in upper cheek teeth, etc. Thus, the age of the Jiaozigou Formation is better to be considered Late Oligocene.

(3) Xinjiang

Junggar Basin: The type skull of *Dzungariotherium orgosense* was excavated from the brown beds of Shawan Formation in south border area of the Junggar Basin. An advanced form of *Lophiomeryx* was reported from the same site (Chiu, 1965). The progressive characters of both forms suggested strongly that the Shawan Formation should be late Late Oligocene in age.

Another paracerathere is *Aralotherium suni* (Ye *et al*., 2003), found from the newly established Tieersihabahe Formation along the north bank of Ulungur River in north Junggar Basin. Rich micromammal fossils, including more than 20 species, were collected together with the paracerathere specimen. The age of this new formation is considered Late Oligocene.

(4) Eastern Yunnan

Lunan Basin: The type specimen of *Urtinotherium parvum* was found from the upper part of the Lunan

Group (Chow, 1958; Pei *et al*., 1963). Xu and Chiu (1962) separated the upper part of the Lunan Group containing *Urtinotherium parvum* from the underlying deposits and established a new formation, Anrencun Formation. Zheng *et al*. (1978) subdivided the Lunan Group into a lower Lumeiyi and an upper Xiaotun formations. Meanwhile, *Forstercooperia shiwopuensis* and some other specimens referred to this genus without determination at species level were later added to the faunal list of the Lunan Group (Chow *et al*., 1974; Zheng *et al*., 1978; Zhang *et al*., 1978). However, their stratigraphic positions have never been clearly settled.

Based on the paraceratheres and in light of the currently used GTS 2004, the Xiaotun (or Anrencun) Formation could only be assigned to early Late Eocene because of the presence of *U. parvum*, which was recorded in Nei Mongol only in lower Ulan Gochu Formation. If *Juxia* is present in Lunan Basin as Zheng *et al*. suggested, it should occur only in the Lumeiyi Formation.

Qujing Area: The fossiliferous deposits in this area are the Caijiachong Formation. Since the only paracerathere fossils found from this formation have now been transferred to *Urtinotherium parvum*, the age of Caijiachong Formation is accordingly to be assigned to Late Eocene.

Shizong Area: The only known mammalian fossils found from this area are the paraceratheres. Now these fossils have been identified as *Urtinotherium intermedium* (*vide supra*). This would mean that the fossiliferous beds of Shizong Area are late Late Eocene in age, since otherwise this species has only been found in the upper half of Ulan Gochu Formation in Nei Mongol.

(5) Other Areas

Wucheng Basin, Henan: Having revised the paracerathere fossils from the Wulidun Formation described by Wang (1976), we recognized three paracerathere forms: *Juxia micracis*, *Forstercooperia mazhuangensis*, and possibly *Pappaceras* sp. The first form is more advanced than *J. sharamurenensis*. Taken as a whole, the Wulidun Formation may still be late Middle Eocene in age.

Yuanqu Basin: According to Huang *et al*. (1998), a tooth of *Juxia sharamurenensis* was found from the Heti Formation in this basin. A large amount of mammalian fossils were described from this formatiom. There is no doubt that the Heti Formation belongs to Middle Eocene.

The stratigraphic positions of the above discussed Chinese localities are illustrated in Fig. 30.

IV. REMARKS ON SYSTEMATIC POSITION AND EVOLUTION OF PARACERATHERES

1. Origin of Paraceratheres and Their Position in Rhinocerotoidea

(1) *Juxia sharamurenensis*, the Earliest Known Ancestor of Paraceratheres

Before the discovery of *Juxia*, there had been two major suggestions as to the ancestor of the paraceratheres. Borissiak (1918) proposed that *Allacerops* (originally as *Epiaceratherium*) *turgaica* be their ancestor, an opinion supported by Granger and Gregory (1936). Having discussed the systematic position of the genus *Forstercooperia* in great details, Wood (1938) argued strongly that *Forstercooperia* would be the best candidate for the ancestor of the paraceratheres. This opinion had been held until 1963 by Wood himself. The discovery of the genus *Juxia* has finally settled this problem. Now it is generally accepted that the diagnostic morphology of *Juxia sharamurenensis* is convincing enough to show that this form is best fitted to be the ancestor of the large-sized paraceratheres, especially *Paraceratherium* group.

The characters exclusively shared by all the large-sized paraceratheres and *Juxia sharamurenensis* have been summarized in the diagnosis of the Paraceratheriinae (*vide supra*).

(2) Relationships of *Juxia* with Other Mid-Eocene Asian Rhinocerotoids

With the exception of the amynodonts, there are altogether eight early rhinocerotoid genera living more or less contemporaneously with *Juxia*: *Rhodopagus*, *Pataecops*, *Yimengia*, *Triplopus*, *Prohyracodon*, *Ilianodon*, *Forstercooperia* and *Pappaceras*. Three other genera, *Ulania*, *Ardynia* (= *Parahyracodon*) and *Guixia*, occurred later than *Juxia*, in Late Eocene.

The affinities of *Rhodopagus* and *Pataecops* are still debatable. Lucas *et al*. (1981), Dashzeveg (1991) and McKenna and Bell (1997) referred them to Rhinocerotoidea, but Gabunia and Kukhaleishvili (1992) still supported Radinsky's early opinion (1965) that they belonged to Tapiroidea. *Yimengia* of Wang (1988) resembles closely to *Rhodopagus*. Irrespective of what they might be, these three forms are morphologically so different from *Juxia* that they have nothing to do with any of the paraceratheres.

Triplopus was considered by Radinsky (1967) a large and wide-spread genus existing in Eurasia and North America in Middle Eocene. In Asia four species were described: *T. proficiens*, *T. progressus*, *T. ckhikvadzei* and *T. mergenensis*. They are all of small size. In the largest one, *T. mergenensis*, the L of m1 - m3 is 70 mm, much smaller than that of *Juxia* (> 110 mm). They are very primitive in tooth morphology, particularly their trapezoid M3 (triangular in *Juxia*) with long metaloph separated from ectoloph, and posteriorly convex border of m3 (with a few exceptions). No postcranial bones of this genus were reported from Asia, but those of North America show clearly that they are extremely long and thin in proportion. This Asian group of rhinocerotoids seems to be a branch evolving independently from the paraceratheres.

Whether *Prohyracodon* and *Ilianodon* belonged to the true Rhinocerotidae is still an open question. The main obstacles to make a judgment about their true systematic position are our poor knowledge of their front teeth. Furthermore, they are likely small in general size.

Radinsky (1967) was apparently right when he pointed out that *Parahyracodon* should be a preoccupied synonymy of *Ardynia*. He also provided us with a good diagnosis of *Ardynia*: "Medium-sized hyracodontids; length of M1 – M3, approximately 60 mm. Teeth relatively high crowned: crown height index higher than 1.1. Incisors spatulate, increasing in size anteriorly; canines slightly smaller than I3 and i3. Relatively long postcanine diastema. Premolar series shortened: P1 and p1 lost, P2 and p2 reduced in size. p3 – 4 molariform; P3 – 4 non-molariform, with protoloph-metaloph loop. M1 – 2 relatively long and narrow, with oblique cross crests; M3 with or without a trace of the metacone. Manus tridactyl." This clearly shows that *Ardynia* is a specialized group of hyracodontids developed in Asia, evolving separately from the paraceratheres.

Ulania wilsoni was erected by Qi (1990b), based on both jaws and postcranial bones from the lower part of the Ulan Gochu Formation. A rough examination of Qi's pictures inclined us to believe that the sample described by Qi might be heterogeneous. The upper M1 – 3 are closer to those of some amynodontids, while the lower teeth are closer to *Ardynia*, but distinct from the latter in certain features. This new genus may be a valid one if it is based on the lower teeth only. At any rate, the material described by Qi (1990b) cannot be directly linked with *Juxia* in systematic relationships.

All the above discussed eight genera (*Rhodopagus*, *Pataecops*, *Yimengia*, *Triplopus*, *Prohyracodon*, *Ilianodon*, *Ulania* and *Ardynia*) are easily separated from *Juxia* by their small size and primitiveness in tooth morphology.

As far as the size is concerned, only three forms, *Guixia*, *Pappaceras* and *Forstercooperia*, are comparable with *Juxia*.

Guixia was erected by You (1977), based on isolated teeth from Gongkang Formation in Bose Basin, Guangxi. It is almost certain that these teeth belong to Rhinocerotidae. The molarization of the premolars in this form is high: in the uppers the protoloph and metaloph are fully separated; in the lowers the entolophid is fully formed. Its M3 is typically rhinocerotid in pattern: triangular in form, with little expressed crested metacone. Furthermore, the posterolingual part of cingulum in upper premolars is high and ridge-like, and the upper molars possess crochets and cristae, etc.

The morphological differences between *Juxia* and *Pappaceras* and *Forstercooperia* have been described in great length in the "comments" of the systematic description of the genus *Juxia* (*vide supra*). As to their systematic relationships, opinions differ widely. Radinsky (1967) lumped all these three genera into one genus, *Forstercooperia*, containing multiple species including the North American *Forstercooperia grandis* (formerly *Hyrachyus grandis*). Chow *et al*. (1974) resurrected the generic status of *Juxia*. Lucas *et al*. (1981) supported Chow *et al*.'s opinion and subdivided *Forstercooperia* into three species: *F. minuta* sp. nov., *F. grandis* (= *Pappaceras confluens*) and *F. totadentata* (= *F. shiwopuensis*).

The most important progress in the study of North American "*Forstercooperia*" can be found in the paper of Holbrook and Lucas (1997). Possessing good skull material and postcranial bones, Holbrook and Lucas picked out all the North American specimens ever referred to *Forstercooperia* (mainly *F. grandis*) from that genus, and erected a new form of uncertain family: *Uintaceras radinskyi*. According to Holbrook and Lucas (1997), the North American *Uintaceras* differs from the Asian *Forstercooperia* and *Pappaceras* in a number of characters. *Uintaceras* is brevicephalic, posterior border of nasal notch above P1, anterior border of orbit above M1 – M2, upper molars with very prominent paracones and deep parastyle folds, M3 with rudimentary crested metacone, all limb bones short and thick, manus tetradactyl; while in *Forstercooperia* and/or *Pappaceras*, posterior border of nasal notch shifted more anteriorly, and anterior border of orbit shifted more posteriorly, making the distance between the nasal notch and the orbit particularly long, upper molars with little expressed paracones and parastyle folds, M3 more triangular in shape (*Pappaceras*), and tridactyl manus (*Forstercooperia*). In doing so, Holbrook and Lucas finally denied the existence of *Forstercooperia* in

North America.

The above discussion led to the following conclusions. *Juxia* should be considered a valid genus. It is widely different from all the small and primitive early rhinocerotoids. *Guixia* evidently belongs to the true rhinoceroses (Rhinocerotidae), apparently separated from *Juxia* earlier in time. *Pappaceras* and *Forstercooperia* existed only in Asia in Middle Eocene. They are the only forms approximating *Juxia* in size and evolutionary level in tooth morphology. Nevertheless, they are readily distinguished from *Juxia*.

(3) Relationships Between Asian *J*.-*F*.-*P*. and North American Hyracodonts

Radinsky (1966) first used the enlargement of I1 and i2 as the unique criterion to separate the true rhinocerotids from all the other primitive rhinocerotoids, which were lumped into a separate family Hyracodontidae. In so doing, the Rhinocerotidae had really become more compact, with clear-cut boundaries; however, the Hyracodontidae then inevitably had become a new "waste-basket," replacing the Rhinocerotidae based singularly on the triangular M3. Radinsky's arguments were partly based on the North American hyracodont and rhinocerotid fossils and partly on the possible presence of *Forstercooperia* (= *Juxia*) in North America (*F. grandis*), thought to be a linkage between hyracodonts and paraceratheres. However, it has turned out that no *Forstercooperia* has ever existed in North America. Without this linkage, the hyracodontids became readily distinguished from the rhinocerotids in North America, while the Asian hyracodontids of small size, represented by a number of specialized forms like *Ardynia* etc., and the ancestral forms of paraceratheres as represented by *Juxia* are even more sharply distinguished from each other than the North American counterparts.

According to Radinsky's revision (1967), the North American hyracodontids include mainly four genera: *Triplopus*, *Epitriplopus*, *Triplopides* and *Hyracodon*.

Triplopus cubitalis is the earliest form of the whole hyracodontid group, from middle Middle Eocene, Early Uintan. It is already extremely long-limbed, with tridactyl manus. However, in tooth morphology it remains very primitive, with the paracones particularly protruded and the M3 trapezoid in form with long and crested posterior end of ectoloph. All the other three forms (*Epitriplopus*, *Triplopides* and *Hyracodon*) are derivative from this earliest form. None of them are morphologically referable to any of the Asian *J*.-*F*.-*P*. group.

(4) Systematic Position of Paraceratheres in Rhinocerotoidea

What a systematic position the paraceratheres occupy within the Superfamily Rhinocerotoidea is a long debated problem. At first, the paraceratheres were considered worthy of a subfamily rank, and the subfamily name Indricotheriinae was proposed by Borissiak (1923b). A few years later (1928), Weber raised it to a family rank, using the family name Baluchitheriidae. In 1939 Borissiak himself adopted also the family rank, using however, the family name Indricotheriidae. Kretzoi (1940, 1943) even separated this family into two subfamilies: Baluchitheriinae and Forstercooperiinae. While summarizing all the paracerathere materials, Gromova (1959) supported Borissiak's later suggestion to group all the paraceratheres under the family Indricotheriidae.

Since 1966, Radinsky started to advocate a radically new point of view, i.e., to lump all the primitive rhinocerotoids without particularly enlarged and rhinoceros-formed I1/i2, including *Forstercooperia* (including *Eotrigonias borissiaki*), *Pappaceras*, *Juxia* and all the large-sized paraceratheres into the single family Hyracodontidae. This point of view has gained wide acceptance from majority of paleontologists (Lucas, Prothero, Schoch, Sobus, Holbrook, McKenna, Emry, Heissig, Dashzeveg, Gabunia, Wang, Qi, etc.). Only a few scholars remain in disagreement with this point of view (for instance, Spassov, 1989).

While comparing *Juxia* with other more closely related forms of primitive rhinocerotoids, some doubts as to the rationality of Radinsky's argumentation have arisen. They are the following:

i. Whether is it rational to accept *Triplopus* as the best candidate of ancestor of paraceratheres? It is parsimonious to conceive that all the specialized characters in skull and teeth of *Juxia* can be derived from those of *Triplopus*, which possesses only plesiomorphic features of the archaic rhinocerotoids. However, this does not hold true in the case of the postcranial bones. It is difficult to believe that the long, but rather sturdy limb bones and the tetradactyl manus of *Juxia* can be derived from such a specialized, extremely slender limb bones and already tridactyl manus of *Triplopus*. Furthermore, the earliest *Triplopus* (*T. cubitalis*) so far known from North America is from Uintan NALMA, about 46 Ma. The earliest *Juxia* (*J. sharamurenensis*) known in Asia is from the Sharamurunian ALMA, about 40 Ma. This means that the highly specialized *Triplopus* occurred 6 my earlier than the less specialized *Juxia* in limb bones. It would be much more parsimonious to consider them as two separately evolving branches derived from a more primitive stock of some early rhinocerotoids.

ii. Whether is it reasonable to expel the genus *Hyrachyus* completely from the Superfamily Rhinocerotoidea as Radinsky once proposed? One of the corollaries of such a point of view would leave the whole superfamily rootless, and one would have to seek the ancestor of the superfamily in other perissodactyl groups. In fact, few paleontologists followed Radinsky in this respect. For example, Prothero and Schoch (1989), Janis *et al.* (1998) and McKenna and Bell (1997) all placed *Hyrachyus* in Rhinocerotoidea as a stem form of the latter groups. In fact, the cheek teeth of *Hyrachyus* are already essentially rhinocerotoid in basic pattern. This is clearly shown in the development of the crested metacone and the stronger reduction of the parastyles relative to paracones in upper molars. *Hyrachyus* could well serve as the best candidate of a possible ancestor of the whole superfamily of Rhinocerotoidea.

iii. Whether is it an appropriate procedure to simplify the problem of Rhinocerotidae at the expense of the Hyracodontidae, creating another "waste-basket" for all the other early rhinocerotoids? Spassov (1989) has dwelt on this problem already, and pointed out its irrationality (*vide supra*).

From a cladistic point of view, the first appearance of any apomorphic features is critical in phylogenetic analysis. If it can be firmly proved that a given apomorphic feature has occurred in different taxa and in different times (parallel or convergent evolution), this feature can safely be used as evidence to separate these taxa taxonomically. The "sabre tooth" developed independently in Marsupialia, Creodonta and Carnivora is such an example. Radinsky discarded the triangular M3 (without a crested posterior end of ectoloph) as a useful criterion in phylogenetic analysis in rhinocerotoids, mainly because of its multiple occurrences in rhinocerotoids. Our current knowledge of the rhinocerotoid evolution renders it possible to trace the first occurrences of this character in different groups of rhinocerotoids. In North America, the first appearance of a triangular M3 was recorded from *Epitriplopus*, one of the earliest hyracodonts from Uinta C beds (46 Ma). The M3 of *Teletaceras* from Duchesnean, the earliest representative of the true rhinoceros, bears still rudimentary crested posterior end of ectoloph in M3. This would mean that this apomorphic feature appeared in Rhinocerotidae no earlier than 40 Ma. In Asia, this apomorphic feature appeared first in *Pappaceras* from Irdin Manha Formation (45 – 41 Ma), still with highly rudimentary posterior end of ectoloph in M3. Later in *Juxia* (ancestor of large-sized paraceratheres, Sharamurunian, 40 – 38 Ma) and *Prohyracodon* (true rhinoceros, of the same age) the M3 became typically triangular in form. Then this feature occurred in the specialized Asian hyracodont, *Ardynia*, and a particular form of rhinocerotoids, *Allacerops*, from Ulangochuian and Ergilian ALMA (37 – 34 Ma).

Another argument of Radinsky's concerns the quality of a given taxon of higher rank. According to Radinsky, Rhinocerotidae is the most successful family among the rhinocerotoids, in terms of time duration, morphologic diversity and number of included taxa. All the other rhinocerotoid groups are to be considered unsuccessful, and none of them is comparable with Rhinocerotidae in this regards. However, the paraceratheres can be considered very successful too. In fact, the morphologic diversity in paraceratheres is not inferior to that of hyracodonts at all. The paraceratheres as studied in this volume contain at least seven genera (five genera in hyracodonts) lasting from 45 – 41 to 23 Ma, i. e., more than 18 myr (18 myr for hyracodonts).

As a result of the above analysis, we think that the inclusion of the paraceratheres into the family Hyracodontidae is inappropriate. The primitive *Hyrachyus* is a good candidate of ancestor for all the rhinocerotoids, and its status as a stem member of the rhinocerotoids should be restored. From the beginning of Middle Eocene (46 Ma) in North America the hyracodonts appeared, while slightly later (45 – 41 Ma) in Asia appeared the paraceratheres, represented by the *J.-F.-P.* complex, and possibly the true rhinoceros. The North American true rhinoceros appeared no earlier than 40 Ma and then greatly flourished. There are two particularly flourishing periods in the evolutionary history of the rhinocerotoids: The Late Eocene – Oligocene period of the Asian paraceratheres and Oligocene – Recent period of the true rhinoceroses of the world. A new proposal for subdivision of the rhinocerotoids at family rank is given as follows:

- Family Hyrachyidae Osborn, 1892
    - Subfamily Hyrachyinae Osborn, 1892
    - Subfamily Amynodontinae Scott et Osborn, 1883
    - Subfamily Hyracodontinae Cope, 1879
- ? Family Eggysodontiidae Breuning, 1923
- Family Paraceratheriidae Osborn, 1923
    - Subfamily Forstercooperiinae Kretzoi, 1941
    - Subfamily Paraceratheriinae Osborn, 1923
- Family Rhinocerotidae Gray, 1821

2. Evolutionary History of Paraceratheriinae

Under our current understanding, Paraceratheriinae include seven genera: *Juxia*, *Urtinotherium*, *Paraceratherium*, *Dzungariotherium*, *Aralotherium*, *Turpanotherium* and *Benaratherium*. Except the last one, all the other six genera are easily distinguishable in the structure of their muzzles, representing different stages of different evolutionary directions as illustrated in Fig. 31. *Juxia* has the most primitive muzzle, with full number of incisors and canines of subequal size. *Urtinotherium* possesses still full number of incisors and canines, with the I1/i1 pair much enlarged over the other front teeth. *Paraceratherium* has much elongated premaxilla with only downturned I1 of enormous size and anteriorly extended symphysis with only i1. *Dzungariotherium* has both maxialla-premaxilla and symphysis highly reduced, and their I1/i1 pair strongly atrophied. *Aralotherium* is characterized by strongly reduced and upturned maxilla-premaxilla part and atrophied I1, and strongly downturned symphysis and i1. *Turpanotherium* is known as having anteriorly stretching symphysis and i1, lower borders of which forming a straight line.

It seems probable that the first three genera form a continuous evolutionary trend from *Juxia* to *Urtinotherium* and then to *Paraceratherium*. The changes include: rapid increase in size, more dolichocephaly, enlargement of condyles, widening of sagittal crest, deepening of nasal notch, lengthening of premaxilla, anteriorly extension of symphysis, reduction of incisors and canines to one pair of I1/i1 in skull and mandible; elongation of cervical vertebrae, with capita and vertebral fossae being much wider than high, but less convex-concave; backward slanting of spinous processes of all thoracic vertebrae, with deeply excavated posterior sides of the processes; reduction of numbers of lumbar vertebrae to four, with less imbricated pre- and postzygapophyses; graviportal tendency in limb bones (becoming thicker relative to length, more erected in position, flattened articular facets, short phalanges, etc.).

Dzungariotherium could possibly be derivative from *Pacaceratherium*, given the reverse tendency leading to reduction of maxilla-premaxilla and the I1 already shown in the evolutionary trend from *P. grangeri* to *P. lepidum*. However, *Aralotherium* is to be considered a genus uniquely specialized in having downturned symphysis. The origin of *Turpanotherium* is still unclear. It is even more so in the case of *Benaratherium* (Fig. 32).

V. SOME BIOLOGIC ASPECTS OF *JUXIA SHARAMURENENSIS* AND *PARACERATHERIUM LEPIDUM*

1. Reconstruction of Muscles and Ligaments, and Functional Analysis of *J. sharamurenensis*

(1) Reconstruction of Muscles and Ligaments

A number of difficulties were encountered during the reconstruction of the muscles and ligaments. 1) The skeleton of *J. sharamurenensis* is not complete, with about 3/10 missing. 2) Not all the muscles can be clearly traced by their impressions left on the skeleton. 3) There are little anatomical study of muscles and ligaments of the living rhinoceroses in literature, let alone fossil species. As a result, only part of the muscles and ligaments can be more or less reliably reconstructed and described in the Chinese text. In English summary we choose only a small fraction of the described muscles and ligaments worthy of special attention. Even so, we would admit that the following reconstruction is highly conjective in nature.

1) Head

M. levator nasolabialis and levator labii superior proprius (Fig. 33 1-2): Compared with *Coelodonta antiquitatis* (Borsuk-Bialynicka, 1973, Fig. 5 A c), *Chilotherium cornutum* (Qiu and Yan, 1982) and *Rhinoceros unicornis* (IVPP O 1383), the facial surface anterior to the orbit in *J. sharamurenensis* is considerably large, but without clear impression of muscle attachment. The m. levator nasolabialis in *J. sharamurenensis* may be comparable to that of living horses in volume and strength, and the m. levator labii superior proprius would be rather large in surface, but probably thin in thickness.

M. masseter (Fig. 33 6): In *J. sharamurenensis* there are two areas for attachment of the masseters on mandible: the masseteric fossa and the lower part of the ascending ramus. The former is small, but very deep, bordered inferiorly by a horizontal flange at the level slightly above the alveolar border, while the latter is a rather smooth and large surface bordered inferoposteriorly by weakly developed crested margins of the mandibular angle. Thus, the masseters must at least be separated into two layers: a deeper one attaching to the masseteric fossa and the superficial one, to the surface lower to the above mentioned fossa. The deeper layer must be small but thick in cross section, with its fibres chiefly vertical in direction, while the superfacial layer, large but thin, with fibres stretching in anterosuperior-posteroinferior direction. In living rhinoceroses the deeper layer of masseter is weakened, while the superfacial one is usually much more strengthened.

M. pterigoideus: This muscle could be more developed than in the living rhinoceroses, judged by the presence of considerably large concave surface on the lingual side of the ascending ramus and the roughened mesial edges of the mandibular angle in *J. sharamurenensis*.

The other muscles of head are illustrated in Fig. 33.

2) Neck

Lig. nuchae: In livng horses the nuchal ligament is very strong and attached to the external occipital protuberance immediately below the central part of the occipital crest and the large nuchal fossa immediately below the protuberance (Klimov, 1955, p. 108, Fig. 67). In living Indian rhinos (IVPP O 1383) and *Coelodonta antiquitatis* (Borsuk-Bialynicka, 1973, p. 45) the external occipital protuberance is situated in the middle part of the occipital crest and confluent with the crest, forming a wide band of rough surface. The protuberance extends downwards, forming a very narrow sagittal crest (unnamed) of varying lenghts. Therefore, the main part of the nuchal ligament is attached to the external occipital protuberance in the middle part of the occipital crest, and only a samll part of the nuchal ligament is attached to the thin and weak sagittal crest below the protuberance. In *J. sharamurenensis* the external occipital protuberance is not particularly large, but the sagittal crest below the protuberance is better developed. Therefore, the part of the nuchal ligament attached to the sagittal crest is stronger and the part attached directly to the external occipital crest is relatively weak. Taken as a whole, the nuchal ligament is comparatively weaker in rhinoceros than in living horses.

M. rectus capitis dorsalis major et minor: In Indian rhinos (IVPP O 1383) and *Coelodonta antiquitatis* (Borsuk-Bialynicka, 1973, Fig. 5 B c), these muscles are attached to the depressed areas situated bilaterally to the sagittal crest on the nuchal surface. In *J. sharamurenensis* these areas are so deeply concave that they form a "pseudo-nuchal fossa" with a sagittal crest. However, this fossa should be the place of attachment of the m. rectus capitis dorsalis, but not for the nuchal ligament as in living horses. At any rate, the muscles in question must be very strong, and may be more tendinous.

M. sterno-cephalicus (Fig. 33 9): According to Windle and Parsons (1901), in majority of hoofed animals this muscle is composed of two branches: one from sternum to mastoid process, called m. sterno-mastoideus; the other from sternum to the posterior border of mandible, called m. sterno-mandibularis or m. sterno-masseterícus. However, in living horses the m. sterno-mastoideus is absent. One of the highly distinctive characters in the skull of *J. sharamurenensis* is the particularly enlarged and plate-formed paroccipito-posttympanic process. This would mean that the m. sterno-mastoideus is particularly developed in *J. sharamurenensis*. On the other hand, the posterior border of the mandible in *J. sharamurenensis* bears a particularly widened and rough area under the condyle, implying a considerable development of the m. sterno-mandibularis.

M. brachiocephalicus (Fig. 33 10): This muscle is also attached to the mastoid process. The large paroccipito-posttympanic process means that the m. brachiocephalicus is also well developed here.

3) Back and Waist

Lig. supraspinale: In *J. sharamurenensis* the apexes of the spinous processes of T1 – T5 are moderately developed, forming isosceles triangles in dorsal view. In Indian rhinos (IVPP O 1383) the apexes of the spinous processes of the anterior thoracic vertebrae are much more broadened, but thin anteroposteriorly. Thus, the supraspinal ligament would be only moderately developed in *J. sharamurenensis*.

M. longissimus dorsi (Fig. 34): The structure of this group of muscles is very complicated. Slijper (1946, p. 48 – 51) described this group of muscles in great details, noting that "in connection with the special movements of mammalian body-axis in the sagittal plane, the m. logissimus dorsi shows a marked tendency to developing long fascicles with long tendons that originate at the prae- and are inserted into the post-diaphragmatic vertebrae." Slijper also noted that in most ungulates "longissimus inserted into ilium, metapophyses and spinous processes, chiefly of postdiaphragmatic region, as illustrated in living horse." However, "in rhinoceroses the fascicles of the longissimus are only inserted into the spinous processes." It is interesting to note that *J. sharamurenensis* is similar to living horses in having a diaphragmatic vertebra in T16, rather than to living rhinoceroses where no diaphragmatic vertebra is formed. The ilium in *J. sharamurenensis* has a more or less straight iliac crest like in horses (strongly convex in rhinoceroses). This led us to think that the m. longissimus dorsi in *J. sharamurenensis* may be similar to that of living horses in having a side branch attached to ilium called m. lilio-lumbalis.

M. spinalis et semispinalis dorsi (Fig. 35 1) **and M. multifidus dorsi** (Fig. 35 2): These muscles are composed of a large number of short fascicles lying between vertebrae, often fused together so that their separation is difficult, especially in the postdiaphragmatic region. According to Slijper (1946), the fascicles of m. semispinalis is "originating at the spinous processes and inserted into the metapophyses belonging to a vertebra, four or usually more vertebrae caudal of the vertebra at which they originate." The fascicles of m. spinalis lie only "between the spinous processes." The fascicles of m. multifundus dorsi "inserted into the third vertebra caudal of the vertebra at which they originate." According to Sisson (1956), in living horses anterior to T12 the fascicles of the m. multifundus dorsi become more horizontal, inserted into the spinous processes in lower part. In *J. sharamurenensis* the posterior surfaces of the anterior thoracic vertebrae are clearly excavated, forming two pairs of depressions: the upper one is larger and apparently for the m. spinalis et semispinalis dorsi, while the lower, smaller and for the m. multifundus dorsi.

4) Forelimb

Ligaments of fetlock joint of the third digit (Figs. 36–37): The collateral ligaments are subdivided into two layers: deep and superfacial. The former originates from the cavity on lateral side of McIII, above the distal articular trochlea; and ends at the prominent rugosity of proximal end of volar side of PhI respectively. The superfacial layer originates from the prominent ridge above the just mentioned cavity in McIII, and ends at the place below the rugosity where the deep layer attaches in PhI. In *J. sharamurenensis* the cavity in McIII is especially deep and the rugosity above the cavity is very prominent, horizontal and ridge-like (based on examination of MtIII). The proximal rugositiy in PhI is short, ridge-like, but restricted to the posterior part of the lateral side. Above and below this rugosity the surface is roughened. The above described structures made us to believe that in *J. sharamurenensis* the collateral ligaments are strong, especially the deep one.

Sesamoidean ligaments (Fig. 37): According to Camp and Smith, in living horses the most important sesamoidean ligaments are the following four groups: straight, oblique, cruciate sesamoidean ligaments and the proximal annular ligament. In *J. sharamurenensis* only scars of two groups can be located. The scars for the cruciate sesamoidean ligaments form a V-shaped ridge (Fig. 37 5). Bilateral to this ridge is a pair of prominent tuberosities, corresponding to the proximal prominences of Camp and Smith (Fig. 37 9), apparently for the annular ligament. On the distal end, a small tubercle (Fig. 37 8) can be observed immediately above the pit for the attachment of the tendon of the superficial digital flexor. This may be the scar for the lateral volar ligament, which is highly variable in Equidae (Camp and Smith, Fig. 12). The scars for the attachment of the oblique sesamoidean ligaments cannot be located at all in *J. sharamurenensis*.

Ligaments of pastern joint (Figs. 36–37): The collateral ligaments of pastern joint originate from the pits on distal ends of lateral sides in PhI, and are inserted to the rough areas on proximal ends of lateral sides of PhII. In *J. sharamurenensis* the pits of PhI take the form of semilunar grooves, and the rough areas of PhII are not particularly bulged laterally. Therefore, these collateral ligaments in *J. sharamurenensis* must be weaker than those of the fetlock joint.

In living horses the straight sesamoidean ligament originates from the proximal sesamoids and is inserted into the fibrocartilaginous plate, which is located below the proximal end on the volar side of PhII. Accordingly, the posterior side of the proximal end of PhII forms an oval flat area (Fig. 37 3). A smaller flat area of similar kind can also be found in the PhII of *J. sharamurenensis*. This prompted us to suggest that *J. sharamurenensis* may have already had a weakly developed straight sesamoidean ligament.

Ligaments of coffin joint (Fig. 36): The collateral ligaments of the coffin joint originate from the pits on the distal ends of lateral sides of PhII, and are inserted to the depressions on the dorsal sides of the proximal angles of the PhIII. In living horses, these pits are considerably large, therefore, the collateral ligaments are strong. In *J. sharamurenensis* the pits of PhII are also very large, extending to the dorsal side of the PhII, but the pits on the PhIII seem to be smaller. At any rate, these collateral ligaments are considered well developed.

The suspensory ligaments (or sesamoidean collateral ligaments) originate from the rough areas anterior to the distal pits of PhI (Fig. 36 4), and are inserted to the distal sesamoid (Os sesamoideum phalangis tertiae) and angles of PhIII. In *J. sharamurenensis* the rough areas above the distal pits in PhI are rather large, extending anterior to and above the pits, indicating that the suspensory ligaments may well be rather large in *J. sharamurenensis*.

The reconstructed insertion points of the forelimb muscles of *J. sharamurenensis* are schematically shown in Fig. 38, and some muscles of superfacial layers are illustrated in Fig. 40. The reconstructions are based primarily on comparative study of myology of living horses, tapirs, living and fossil rhinoceroses taken from literature. Most of the reconstructed muscles conform to those of perissodactyls in general, only a few of them show some differences merit to be mentioned separately in a few words.

The deltoid muscle (Figs. 38 1, 40 26) may be smaller than that in living rhinoceroses, since the deltoid tuberosity of the humerus in *J. sharamurenensis* is considerably smaller than in most living rhinoceroses. The supraspinous muscle originates from the supraspinous fossa of the scapula, and is inserted to the lateral and medial proximal tuberosities of the humerus. In *J. sharamurenensis* the supraspinous fossa of the scapula is very large and the lateral proximal tuberosity of the humerus is larger than the medial one. In living horses the supraspinous fossa of the scapula is very narrow and the medial proximal tuberosity of the humerus is larger than the lateral one. These differences tend to show that in *J. sharamurenensis* the supraspinous muscle is large and more laterally situated than in the living horses. Furthermore, the intertuberal groove of the humerus in *J. sharamurenensis* is situated more or less in the middle of the anterior side of the shaft, but without clear middle ridge, while this ridge is strongly developed in living horses. On the other hand this intertuberal groove in living rhinoceroses is shifted more laterally. This would mean that the m. biceps branchii in *J. sharamurenensis* may be similar to that of living horses in position, but not clearly separated into two heads as in living horses.

Judged from the slender proportion of the forearm bones, the metacarpals and the phalanges, and the deep pits for the attachment of the extensors and flexors, the tendinous parts of the extensors and flexors must be comparatively long, probably as in living horses. The scars for the attachment of the m. flexor carpi radialis (Figs. 39 9, 40 28), m. flexor carpi ulnaris (Figs. 39 10, 40 30), and m. flexor digitalis superficialis (Figs. 37 11, 39 11, 40 36), are all very deep, implying that they may be rather tendinous and strong.

5) Hindlimb

Some of the muscles of hindlimb of *J. sharamurenensis* are illustrated in Fig. 40. Detailed description of them is omitted because of the fact that most of these muscles in perissodactyls are highly homologous in structure and disposition, differing mainly in proportion in different groups of the order. A few points to be noted are the following. The ilium in *J. sharamurenensis* is comparatively long and slender, with its crista iliaca more or less straight. The third trochater of the femur is rather small and comparatively higher situated. Taken as a whole, the ilium and femur of *J. sharamurenensis* are morphologically closer to those of living horses rather than of living rhinoceroses, where the ilium is very short and wide, with its crista iliaca strongly convex, and the third trochanter of femur is especially developed and situated lower. Therefore, the m. iliacus and m. gluteus (Fig. 40 13-14) in *J. sharamurenensis* might be like those in living horses, but much weaker than in living rhinoceroses. The supracondyloid fossa in the femur of *J. sharamurenensis* is rather deep (Pl. XVI 1a f), indicating that the m. flexor digitalis pedis superficialis (Fig. 40 53, 56), and probably the m. gastrocnemius (Fig. 40 54), are also strong. Again, this is similar to living horses than to living rhinoceroses where the supracondyloid fossa is weakly developed.

(2) Functional Analysis

1) Standing pose

Head and neck (Figs. 41 – 42; Tab. 52): The condyles in *J. sharamurenensis* are proportionally large, especially relative to the nuchal surface. It is well known in mechanics that the force supporting the head will increase with elongation of the neck. Being the fulcrum of the head, the condyles play a critical role in transmitting the force coming from the neck. Therefore, enlargement of the condyles may be one of the characteristic features of the animals with a long neck. The position of the head relative to the neck in standing pose can be inferred by the form of the condyles. According to Flerow (1957, p. 49), the angle formed by the long axis of the skull and the linea divisa condyli would roughly be the angle between the neck and the skull. The possible position of the head of *J. sharamurenensis* in standing pose is illustrated in Fig. 42.

The cervical vertebrae are among the most characteristic elements in *J. sharamurenensis*. First of all, they are very long, with their total length reaching 624 mm, slightly surpassing the skull length, which is 595 mm. Among the primitive rhinocerotoids only *Hyracodon nebraskensis* has a similarly long neck (Tab. 52). Furthermore, morphologically the cervical vertebrae of *J. sharamurenensis* are very distinctive. The capita and the vertebral fossae of the vertebrae are subparallel. They form acute angles with the long axis of the vertebral body (Fig. 15A). The pre- and postzygapophyses are large and roughly parallel, but the prezygapophyses are much higher than the postzygapophyses in position. The transverse processes are considerably large. If the capita and /or vertebral fossae are placed vertically, the whole neck will certainly incline up and forward, with only the C3 being transitional in direction turning more horizontally (Figs. 41 – 42). All these morphological characters can readily be explained mechanically. The weight of the head will be transmitted to the body of the animal by the neck partly through the bodies of the cervical vertebrae and partly through the enlarged pre- and postzygapophyses.

Forelimb (Fig. 42)

In ungulates the forelimb supports approximately 3/4 of the body weight (head, neck, chest and part of stomach) when standing at ease (Hildebrand, 1982, Fig. 22 – 9). The angles between the segments of the forelimb are apparently governed by this particular factor. This led to the effect that the radius-ulna and the metacarpals being basically upright in position.

Angles of shoulder and elbow joints: Osborn (1929b, p. 731 – 732) noticed that in ungulates, when standing, the hemispherical articular surface of the caput of the humerus faces always directly upward, and the angle formed by the baseline of the hemisphere and the long axis of the shaft of the humerus is always larger in graviportal animals (for instance, 75° in indian elephant) than in cursorial or non-graviportal animals. This latter angle estimated for the *J. sharamurenensis* skeleton is roughly only 45° and the angle between the long axes of the scapula and humerus is roughly 90° (Fig. 42).

As to the angle of the elbow joint, Osborn pointed out that, while in graviportal animals this angle tends to be very close to 180°, it is less in non-graviportal animals. This angle is estimated about 135° in the skeleton of *J. sharamurenensis*, when the radius-ulna are placed vertically (Fig. 42).

Angles of fetlock joint and between the phalanges: Hildebrand (1982) stresses that in ungulates the fetlock joint is always bent when standing. The mechanism is explained in the following manner. Firstly, he considers this as "a sling mechanism that prevents collapse of the fetlock joint" and "an important shock absorber. Because it is bent, it must be supported. This is accomplished by a remarkable ligamentous sling ..." (Hildebrand, 1982, p. 425). Under the ligamentous sling concept, Hildebrand implies the sesamoidean ligaments and the tendons of flexors. Hildebrand explains further: "As the foot is heavily loaded by shifting weight when at ease, the ligament (and tendon) stretches, thus allowing the joint to flex sharply.

In doing so, the ligament stores potential energy that is released by returning the joint to a neutral angulation when the load is diminished," and "giving an initial upward impetus to the entire body" (Hildebrand, 1982, p. 453, Fig. 23-18).

In *J. sharamurenensis* the sesamoidean ligaments has not been fully developed as in living horses. For instance, there is no V-scar on volar side of the PhI, indicating the oblique sesamoidean ligaments have not been developed yet. This primitive state of development of sesamoidean ligaments in *J. sharamurenensis* appears not strong enough to support its body (estimated as around 800 kg, *vide infra*). *Juxia sharamurenensis* apparently needs the help of lateral digits to support its heavy body. Taken into consideration of the fact that the length of the lateral digits is shorter than McIII (about 110 mm), to receive the lateral digits' help, the distal end of McIII must be lowered down at least to a level 90 mm above the ground. Our calculation shows that this can be achieved only when the phalanges are bent at angles of 135° – 140°. This is also in good accordance with the morphology of the articular surfaces between the phalanges (Fig. 42).

Hindlimb (Fig. 42): In non-graviportal, especially cursorial ungulates, the hindlimb supports only about 1/4 of the body weight when standing at ease. It plays mainly the role of propelling the animal forward. This led to the effect that none of the segments of the hindlimb is really erect in position in standing pose. Taken as a whole, the segments of the hindlimb of *J. sharamurenensis* is generally similar to that of living horses in direction. This also holds true for the possession of the particular "locking device" in the patella-femur joint.

2) Adaptation to running

Vertebral column: According to Slijper (1946), in ungulates capable of making leap-gallop runs "a great mobility of the vertebral column" is required; in ungulates capable of making horse-gallop runs, especially in heavy ungulates, "a very immovable vertebral column" is required. With decreasing mobility of their body-axis "the spinous processes of the postdiaphragmatic region change their cranial inclination into an upright position or even into a caudal inclination" (Slijper, 1946, p. 103). Slijper pointed out also that with increasing rigidity of the lumbar region some particular feature may occur. Two of the four points mentioned by Slijper are directly relevant to the lumbar vertebrae of *J. sharamurenensis*: the accessory articulations between the transverse process of the last two lumbar vertebrae and with the sacrum, and the embracing type of zygapophyses of the postdiaphragmatic region (Slijper, 1946, p. 38).

The posterior thoracic and lumbar vertebrae of *J. sharamurenensis* have the following characters. There is no true diaphragmatic vertebra. The spinous processes of the T's posterior to T16 and the Lm's are all vertical in direction. The spinous processes are broad (APD), with enlarged top tuberosities. The lumbar region is rather large, composed of 5 or 6 vertebrae. Their transverse processes are broad and the zygapophyses are of embracing type. All this suggests that the posterior part of the thoracic and the lumbar regions in *J. sharamurenensis* is half-rigid, allowing the animal a horse-gallop running.

Innominate bone: According to Osborn (1929b), the innominate bones differ widely in different groups of ungulates. In cursorial type the pedicle of the ilium is slender and long, the anterior wing of the ilium is triangular in form, with the iliac crest concave; while in graviportal type the pedicle of the ilium is thick, the wing is very wide and fan-shaped, with the iliac crest strongly convex. The innominate bone of *J. sharamurenensis* is more similar to that of living horses than to living rhinoceroses in general proportion and form, thus closer to that of cursorial type.

Limb bones: According to Gregory (1912) and Osborn (1929b), as two extremes in locomotion adaptations, the graviportal and cursorial ungulates have two different types of limb bones: the former has all segments of limb bones thick and proportionally short, with stylopodia (humerus and femur) long, upright in position, but the others short, often rectigrade; while in the latter, all the segments slender, bent at angles, stylopodia comparatively short, but the others long, often unguligrade, lateral digits reduced. The limb bones of *J. sharamurenensis* have all the features listed above for the cursorial type. Therefore, it is safe to conclude that *J. sharamurenensis* is an animal of cursorial type. These features are described more specifically in the following lines.

The limb bones of *J. sharamurenensis* are light and not compact. This is clearly shown when compared with those of *Rhinotitan mongoliensis* excavated from the same layer of the same locality (Wang, 1982). The long bones of the latter are mostly preserved intact, while those of the former, almost all somehow compressed. Observation of cross sections of these bones revealed that the compact substance of the bone of *Rhinotitan mongoliensis* is about twice thicker than that of *J. sharamurenensis*. The L/W indices of the long bones of *J. sharamurenensis* as compared with those of some other mammals are shown in Tab. 53.

Hildebrand (1982, p. 427) proposed an empirical criterion to define the heavy animals, i.e., when the body weight equals or exceeds 900 kg, the animal is to be called heavy. Our estimation shows that the body weight of *J. sharamurenensis* (about 800 kg, *vide infra*) is below the number set in this criterion.

The relative lengths of the segments of the limb bones of *J. sharamurenensis* compared with those of some other ungulates are given in Tabs. 54 – 55. Four major conclusions can be drawn from the Tabs. 54 – 55. 1) In the total length of the three main long bones (stylopodium, zeygopodium and metapodium), *J. sharamurenensis* is closer to living giraffes. 2) In the length ratios of the three main long bones of the forelimb relative to hindlimb, *J. sharamurenensis* is higher (forelimb slightly shorter than hindlimb) than in living horses and tapirs, but lower than in living giraffes. 3) In *J. sharamurenensis* the zeygopodium of the forelimb is especially long, but the metapodium is relatively short. 4) The PhI of middle digit in *J. sharamurenensis* is very close to that of *Triplops cubitalis* in L/W ratio, proportionally much longer than in any known forms of Rhinocerotidae. Taken as a whole, the relative lengths of the limb bones show clearly that *J. sharamurenensis* is a cursorial animal, approximating the Miocene equids in mobility.

3) Adaptation to unidirectional (longitudinal) movement

As Hildebrand (1982, p. 450) has correctly pointed out, in order to run well, the "large cursors reduce or eliminate many oscillating motions" and "the legs must swing back and forth."

This kind of adaptation can well be found in shoulder, elbow and fetlock joints in *J. sharamurenensis*. The caput of humerus is ovoid in shape, with its upper border nearly straight transversely, but strongly convex longitudinally (Fig. 43). This is a peculiar specialization of this form to limit the motion of the shoulder joint in largely anteroposterior direction. The elbow joint takes the form of a trochlea. The distal articular trochlea of the humerus not only has a longitudinal intermediate groove, but also a longitudinal crest on lateral condyle, while the proximal articular surface of the radius is inversely formed. The sagittal ridge of the distal articular trochlea of the McIII reaches almost the anterior border of the facet, and the corresponding groove on proximal surface of the PhI is almost visible in dorsal view. This shows clearly that the fetlock joint is much better adapted to sagittal movement than any other rhinocerotoids.

4) Monodactylism

Borissiak (1923b) pointed out that the tendency to monodactylism is already clearly shown in *Paraceratherium asiaticum*. In fact, this tendency is also clear in *J. sharamurenensis*, expressed in the reduction of the lateral metapodia and phalanges in length and thickness.

5) Reduction of pronation-supination function of ulna

In *J. sharamurenensis*, although still complete and weakly coalesced with the radius, the ulna is considerably reduced in thickness relative to the radius. A similar case can be found in *Triplopus cubitalis* (Cope, 1884), while in living rhinoceroses the ulna remains thick and robust, playing an important role in supporting the body weight.

6) Character hinting at graviportal direction of evolution

While discussing the differences shown in ulnae between the cursorial and graviportal ungulates, Osborn pointed out that in graviportal ungulates the olecranon process of ulna tends to be horizontally oriented and downwardly shifted (Osborn, 1929b, p. 752). The olecranon process in *J. sharamurenensis* is formed as in graviportal ungulates. This is the most clear sign evolving in the direction of becoming heavy in the skeleton of *J. sharamurenensis* so far known.

7) Some special feeding adaptation of skull and neck

Fig. 44 shows basically two patterns of skull and mandible representing carnivorous and herbivorous mammals respectively. In the first pattern the skull has well developed sagittal crest, the skull and mandible are associated by a hinge-formed articulartion, the ascending ramus of the mandible is low, but with a very large masseteric fossa; while in the second pattern these characters are inversely developed. Together with musculature and dentition, these two patterns of skull and mandible afford good explanations of the different feeding habits of the carnivorous and herbivorous mammals (Smith and Savage, 1959).

There is no doubt that the skull and mandible of *J. sharamurenensis* are basically of the second pattern. However, they differ from this pattern in having a prominent and long sagittal crest, low ascending ramus of mandible and deep masseteric fossa. This tends to show that the action of the mandible relative to skull in *J. sharamurenensis* may be mainly vertical bitting, not necessarily as quick as in carnivorous animals, and incapable of making circular movements of the lower teeth against the upper ones as in advanced grinders.

The cheek teeth of *J. sharamurenensis* are functionally rather weak, incompatible with its "gigantic" body size. They are brachydont and simple in structure of enamel bands, producing transverse grinding grooves and ridges after wearing. This tends to show that *J. sharamurenensis* is strictly herbivorous, probably mainly folivorous, eating only leaves or stems, or occasionally fruits.

The front teeth of *J. sharamurenensis* are unique in form and arrangement among rhinocerotoids. They are full in number, subequal in size, with the first pair being the largest, and arranged loosely in two converging lines. The uppers are vertically planted, while the lowers, procumbent, in particular the i1, interlocking when occluded. The two I1's are separated, leaving a vacant space between them. This prompted us to think that *J. sharamurenensis* may have a special habit in gathering food. The animal may first bite on the stem with leaves, then either turn its head sideways, or pull its head backward to "comb" the leaves into its mouth. The particularly developed paroccipito-posttympanic processes in *J. sharamurenensis* may well be accounted for by this kind of combing action.

8) Plesiomorphic characters preserved in skeleton

Osborn (1929b) divides the scapulae of ungulates into four types. The scapula of the primitive ungulates, as exemplified by *Phenacodus*, is usually oval in form, with its vertebral margin convex and almost centrally situated spine, with a small acromion. The scapula of graviportal type ususally takes the form of a broad triangle; while that of the cursorial type, narrow and long triangular in form, with its vertebral border straight, weak spine and the supraspinous fossa reduced in size. The scapula of *J. sharamurenensis* is like that of the primitive ungulates, without characters of graviportal and cursorial types.

The number of lumbar vertebrae in *J. sharamurenensis* is five or six. As Scott (1941) pointed out, the numbers of the lumbar vertebrae in primitive rhinocerotoids are usually 5 – 7, while in living rhinoceroses the number is diminished to three. Furthermore, the zygapophyses of lumbar and posterior thoracic vertebrae are embracing in pattern. The ribs in *J. sharamurenensis* are generally thick and rod-like, with their cross sections being roughly rectangular in form. In advanced ungulates the ribs often become plate-like. All this shows that *J. sharamurenensis* is primitive in posterior part of the vertebral column and the ribs.

(3) Skeleton Mounting and Appearance Restoration

The skeleton of *J. sharamurenensis* (V 2891) was mounted in 1964 (Pl. XLIV), with the missing parts restored (white parts are restored in plaster). The mounting is not fully accordant with the ideas expressed in this volume. Originally the skeleton was designed to show the posture of the animal imagined to gather the leaves from a tall tree, with its head and neck maximally stretched. However, the forelimbs were arranged in a walking posture. This may not be the real case. It is more reasonable to suggest that the forelimbs stand more or less upright on the ground. In doing so, another error may also be corrected, i. e., the lumbar region is higher than the withers.

The measurements of the skeleton are: the body length (without tail) is slightly longer than 3 m; the withers height is 1.9 m; the height of head in standing pose is 2.2 – 2.3 m, about 2.5 m when maximally stretching to gather food.

There are two restorations of the external appearance of *J. sharamurenensis*: a pencil drawing made in 1965 (Pl. XLV) and a clay sculpture made during the preparation of the present volume (Pl. XLVI). The difference of the two restorations lies mainly in the proportion of the head and neck relative to the body. In the sculpture the head is proportionally larger and the neck is proportionally thicker and shorter. The sculpture may more exactly reflect the imagination of the present authors than the drawing does.

The appearance of *J. sharamurenensis* may be summarized as follows. Head comparatively small, with eyes situated midway, but the ears more anteriorly located than in other ungulates. Nostriles large, lips not particularly movable and nimble. Neck powerful, long and thick, ascending anteriorly. Stomach comparatively small, much smaller than in living rhinoceroses. Limbs slender, angles between long segments similar to those in living horses. Functionally tridactyl. McV shortened, with phalanges, lying well above ground. Lateral metapodia markedly reduced in thickness, deviated from middle metapodia at distal ends. Angle of coffin joint 135°. If a bold guess is allowed, the skin might be thin and soft, brown or grey in color, with fine and sparse hair.

2. Restoration of Head and Neck of *P. lepidum*

(1) Restoration of Muscles and Ligaments

The most remarkable distinctions in skulls of *P. lepidum* from *J. sharamurenensis* are the shortening of the nasal bone, the backward shifting of the nasal notch and the appearance of depression on the frontal surface above the orbit (Pl. XXIV 1 – 2). These changes seem to parallel with those in evolutionary trends occurred in tapirids. By analogy we may infer that *P. lepidum* has a particularly developed m. levator nasolabialis, extending posteriorly onto the depression above the orbit (Fig. 45 1).

Judged from the rough areas developed on the posterior part of the horizontal ramus and the mandibular angle, the superfacial layer of the masseter muscles might be more developed than in *J. sharamurenensis* as well (Fig. 45 5). The deep notch on the lower border anterior to the mandibular angle seems to be analogous with the incisura vasorum in living horses, the place where the facial blood vessels transit. Therefore, in *P. lepidum* the facial blood vessels may intersect the middle part of the superfacial layer of the masseter muscles.

The appearance of a deep "pseudo-nuchal fossa" below the middle part of the occipital crest in TP 9401 made the restoration of the nuchal ligament and the m. capitis dorsalis rather difficult to decide. Similar kind of fossa is present in living horses, but it is called "nuchal fossa," where the nuchal ligament is attached

(Klimov, 1955, p. 108). No such a fossa is present in living rhinoceroses. Instead, this place is occupied by a pair of slightly depressed surfaces where the m. capitis dorsalis is attached. In the latter case, the m. capitis dorsalis must be more tendinous in nature, playing more important role in supporting the head than the muscle does in living rhinoceroses.

With the enlargement of the paroccipito-posttympanic process and the posterior border of the mandible in TP 9401, the m. sterno-cephalicus and m. brachiocephalicus must be enormously strong in *P. lepidum* (Fig. 45 9-10, 46 3-4).

The spinous processes in anterior thoracic vertebrae, at least in T1 – T8, are particularly broad, with strongly excavated posterior sides and enlarged, rough top tubercles. This indicates that the supraspinous ligament and the m. spinalis and m. multifidus must be particularly strong in *P. lepidum* (Fig. 46 1).

(2) Functional Analysis

Paraceratherium lepidum has a number of characters distinctive from *J. sharamurenensis* in skull, vertebral column and in musculature, as discussed above. Functional implications of these characters can be briefly summarized as follows.

i. *Paraceratherium lepidum* may have possessed a longer snout, with half prehensile nose (Fig. 45). The way to gather food (leaves, stems and occasionally fruits) may be concentrated in the anterior-most part of the snout. It is accomplished by coordinated action of the prehensile nose, the first pairs of enlarged incisors, and probably a dexterous tongue. The first pairs of incisors apparently do not play a part in chewing the food, since only very weak wear facets can be seen on the tops of i1, although the specimen of TP 9401 is very old in age. The special way of gathering food (combing leaves from stems) often needs to move the skull sideways and/or backward, hence is the enormous size of the paroccipito-posttympanic processes, where the powerful muscles pulling the skull (m. sterno-cephalicus and m. brachiocephalicus) are attached.

ii. The relatively larger size of the masseters and probably the digastric muscles, in combination with the reduced temporal ones, tend to show that, in *P. lepidum*, when the jaws occlude, the cutting and pressing forces between the upper and lower cheek teeth are intensified, while the rapidity of contraction of the jaws may play less important role in feeding.

iii. In *P. lepidum*, the cervical vertebrae are enormously elongated and enlarged. The elongation is especially noticeable in C2 – C5, body lengths of which are four times as long as those in *J. sharamurenensis*, while the lengths of skull and thoracic vertebrae increase only twice (Tabs. 6 – 8). All the cervical vertebrae are hollowed, with their spinous processes almost wanting. All these characters can be fairly well accounted for in terms of mechanics. In the evolutionary process to get food from higher and higher trees in paraceratheres, the neck had to become longer and longer. With lengthening of the neck, the force needed to support the head and the neck itself has to be tremendously increased. This will be accomplished in two ways: to make the head and neck lighter, and to strengthen the supporting forces. Thus the anterior part of the skull has been reduced in size and the cervical vertebrae become greatly hollowed. On the other hand, the m. capitis dorsalis (or nuchal ligament?), the supraspinous ligament, and the m. spinalis and m. multifidus, become enormously strong in order to reinforce the strength to hold the skull and the elongated neck.

iv. Based on the length of the thoracic and lumbar region of the vertebral column and the lengths of ribs preserved in TP 9401, the volume of the chest and stomach in *P. lepidum* (L: 3 m; H: 1.2 m; W: 1 m) is estimated as 3.6 m^3. This is about nine times as large as that of *J. sharamurenensis*, which is estimated as slightly larger than 0.4 m^3 (L: 1.5 m; H: 0.55 m; W: 0.5 m). The distal ends of most of the ribs are flattened and plate-like. The plate-like ribs are beneficial in supporting the chest and stomach by making the ribs lighter and increasing the supporting surface. This is the strategy adopted by the majority of ungulates with large chest and stomach.

(3) Restoration of Head and Withers (Fig. 46)

The head and neck are very long relative to the body in *P. lepidum*. In TP 9401 the body length (from tip of skull to posterior end of innominate bone) is 7215 mm, while the length of head + neck is 3495 mm, i. e., the latter is about 1/2 of the former. In cervical vertebrae (C2 – C7) the planes of the zygapophyses and the axes of bodies are subparallel with each other. This is different from those in *J. sharamurenensis*, where the above mentioned planes and the axes are convergent anteriorly. This would mean that the planes of the zygapophyses are not closely relevant to the direction of the neck as in *J. sharamurenensis*. Furthermore, the enormously enlarged attachment areas on the posterior borders of the mandible in TP 9401 imply strongly that in *P. lepidum* the m. sterno-mandibularis must be very strong. At the same time, the spinous processes of anterior thoracic vertebrae, especially T1 – T5, are all subequally high. All these characters tend to show that in *P. lepidum* 1) the neck would not necessarily be strongly ascending anteriorly as in *J. sharamurenensis*, 2) the withers could be rather high relative to the head, and 3) the neck could be very thick and hardly separable from the head by a notch on the lower border behind the mandible. These features are demonstrated in Fig. 46.

3. Estimation of Body Mass and Ontogenetic Ages

(1) Estimated Body Mass of *J. sharamurenensis* and *P. lepidum*

The paraceratheres have long been considered the largest land mammals. However, the problem of exactly how large and heavy they are is still unclear. In recently appeared popular science movie "Walking with beasts," these animals were described as 4.5 m high at shoulder and 15 – 20 tons heavy (Haines, 2001). Their maximum weight was once estimated as much as 34 tons (Alexander, 1989). Another question is how large and heavy was *J. sharamurenensis*. In recent years special attention has increasingly been paid to the problem of body weight. It has been considered as one of the most important properties in biology in general (Peters, 1983; Schmidt-Nielsen, 1984; Damuth and MacFadden, 1990; Silva and Downing, 1995, etc.).

Since in principle any part of skeleton is variously correlated to body weight of an animal, a great variety of measurements have been used to estimate body weight in vertebrate paleontology. However, it is generally agreed that the head-body length (HBL), which is highly correlated to body weight in extant mammals, is probably the best one. Of the paracerathere fossils so far known, only in two forms, i. e., *J. sharamurenensis* and *P. lepidum*, the head-body lengths can be obtained. According to the methods of measurements proposed by MacFadden and Hulbert (1990), the HBL in the former measures 3015 mm (head, 595; neck, 640 and body, 1780), and that in the latter, 7215 mm (head, 1325; neck, 2170 and body, 3720).

Based on HBL, using the commonly accepted regression equation ($\lg W = a + b \lg L$), estimated body weight can be calculated against certain reference groups of extant animals, as is shown in Tab. 56. The body weights of *J. sharamurenensis* calculated against the whole Mammalia is 463 kg, against ungulates is 749 kg, and against Perissodactyla is 888 kg. The above figures clearly show that, with the lowering of the ranks of the taxa (from Class to Order) the calculated body weights become larger and larger. This is understandable because the higher the taxon rank is, the more the animals smaller than average size are included. On the other hand, the closer the rank of taxa to the animal to be studied is, the closer the calculation would be to the actual body weight of the given animal. The result calculated against the

Perissodactyla for the body weight of *J. sharamurenensis* (888 kg) may be overestimated because of the fact that the living perissodactyls are exclusively composed of middle-sized (horses and tapirs) and graviportal (rhinos) forms. Taken as a whole, it would be more reasonable to estimate the body weight of *J. sharamurenensis* somewhere between 749 kg (based on ungulates) and 888 kg (based on perissodactyls), say around 800 kg. Using the same method, the body weight of *P. lepidum* can be estimated as around 15 tons (Tab. 56).

(2) Estimated Life Span

As convincingly stated by Peters, the majority of biological phenomena are somehow correlated to body mass. Among these phenomena is the life span, which can be calculated by the generalized equation $Y = aW^b$ (Peters, 1983, p. 1). However, the methods proposed by Peters and others are still far from satisfactory when applied to paleontology. Tab. 57 shows the results of some preliminary attempts. The results show that the average life span of *J. sharamurenensis* calculated against Artiodactyla is about 25 years, while that of *P. lepidum* is about 45 years.

These results can be tested by comparing the sequence of tooth eruption in paraceratheres with living rhinoceroses whose tooth eruptions are linked with known ages. Garutt (1992) attempted to compare the sequences of tooth eruption between wooly rhinoceros and the living African rhinoceroses, and found that (Garutt, 1992, p. 102): "the development and eruption of P4 and M3 in the wooly rhinoceros are identical to those in recent *D. bicornis* and *C. simum*." The sequence of tooth eruption in these three forms can be summed up as follows: the eruption of P2 at 2.5 – 3 years, P3, 3 – 4 years, P4, about 10 years, M1, 1.5 – 3 years, M2, 6 – 8 years, and M3 8 – 15 years. The average life span of the African rhinoceroses is suggested to be around 45 years, reaching maximum of 50 years (Kingdon, 1979). Peters noted (1983, p. 119 – 124) that: "the average mammal still has 90% of its maximum life span ahead when sexual maturity is achieved." This would mean that when the African rhinoceroses reach their sexual maturity, the P3 has erupted, but the P4 is still embedded in its alveolus. On the other hand, the M3 would erupt at the age of 1/3 of the maximum life span.

In SS 4103.1, the degrees of wearing of the P4 and P2 – P3 differ only slightly, but the M3 has already erupted, hardly worn (Pl. IV 1). This seems to indicate that the P4 and M3 apparently erupt earlier than in living rhinoceroses. Assuming that in *J. sharamurenensis* the P4 erupted at age seven (three years earlier than in living African rhinos), then the maturity of *J. sharamurenensis* will be reached at an age of about 3, or 3.5, and the maximum life span will be 30 or 35 years. This assumption is 5 – 10 years longer than the calculated years in Tab. 57, but seems to be more realistic. Based on this, SS 4103.1 would be about 12 – 15 years old, and V 2891, about 22 – 25 years old.

The sequence of tooth eruption in *P. lepidum* is more similar to that of *J. sharamurenensis* than of living rhinoceroses. The degrees of wearing of P2 – P4 are close to those of Class XVI (33.5 years) in *Diceros bicornis*, the degree of wearing of M1 is close to that of Class XVII (37 years), but the degree of wearing of M3, Class XIV (21 years) in Hitchins classification (1978). It would be acceptable if 40 – 45 years are supposed for the rough estimation of the maximum life span of *P. lepidum*. Then TP 9401 would be roughly 35 years old.

VI. ENVIRONMENTAL CHANGES OF ASIAN CONTINENT WHEN PARACERATHERES EXISTED

1. Asian Continent During Late Eocene – Oligocene

(1) Configuration and Geomorphology of Ancient Asian Continent

Nowadays Eurasia is a supercontinent in northern hemisphere stretching over more than 180° longitudes. However, in Paleocene and Eocene time the European and Asian parts were separated by the "West Siberian Sea." The Paleoasian continent was much smaller, called by Wang (2004) the "slim" Asia (Fig. 47). During the Oligocene the part once occupied by the "West Siberian Sea" gradually and diachronically emerged from the bottom of the sea. For example, in the area north of the Aral Sea, the Oligocene deposits of this area are very complicated in lithology, represented by marginal marine facies (Kutanbulak Fm. of early Early Oligocene and Chagray Fm. of early Late Oligocene) and mixed marine and freshwater facies (Chilikta Fm. of late Early Oligocene and Aral Fm. of late Late Oligocene, *vide* Lucas *et al.*, 1998). The southwestern part of Paleoasia may have turned into land during the Oligocene as well (Kummel, 1970, Fig. 13-4), with a few remnants of sea water as evidenced by some marine fish-bearing deposits of possibly Oligocene age in Tarim Basin, Xinjiang (Li, 1997). The eastern border of the Paleoasian continent also changed during that time. In its north part the sea shoreline retreated westward compared to that of the Eocene (Figs. 47 – 48), while the south part of the sea shoreline advanced eastward, according the recent investigation of the shelf deposits in East China Sea (Research Party of Marine Geology, 1989) and the deposits of South China Sea (Wang *et al.*, 2003a, b).

(2) Paleolatitudes of Asia

The earliest restoration of the paleolatitudes of the Paleoasian continent was done by Vinogradov (1967) for the Eocene time. Later, Szalay and McKenna (1971) and McElhinny (1973a), and Seyfert and Sirkin (1973) made similar attempts to locate the North Pole of Paleogene age as well. Recently, applying more elaborated methods to handle with the paleomagnetic data, Besse and Courtillot (1991) proposed a new apparent polar wandering curve and located the North Pole at the cross point of 145.4°E, 80.2°N for 40 Ma, and that of 132.8°E, 81°N for 30 Ma.

Of the five sets of data, the earliest one by Vinogradov (135°W, 67°N for North Pole around 40 Ma) seems rather deviated from the others, which are more or less closely clustered. The latest data provided by Besse and Courtillot are accepted in the present volume (Fig. 48). Accordingly, the North Pole drifted southeastwards during 40 – 30 Ma, compared to that of present day. As a result, the latitude lines turn clockwise, forming an angle of about 20° at the crossing points, which lie at the longitude of 50°E, around the Caspian Sea. This has the effect of southward shifting of the paleolatitudes lying east to the crossing, but northward shifting of the paleolatitutes west to the crossing. As a rule, the more distant from the crossing a given area is located, the greater the extent of shifting this given area has. The shifting of the paleolatitudes of the localities with paracerathere fossils in terms of angles are presented in Tab. 58. Taken as a whole, the extent of shifting varies 3° – 7° (Fig. 48, Tab. 58).

2. Climate of Asian Continent During Late Eocene – Oligocene

(1) General Tendency of Global Climatic Changes

Now it is generally accepted that the earth's climate gradually changed from an essentially uniformly warm Late Cretaceous to the cooler, more heterogeneous Neogene (Berggren and Prothero, 1992, p. 5). The late Mesozoic is often euphemistically called "hothouse" period, the Neogene, "icehouse," while the Paleogene, particularly Eocene, "doubthouse" period. However, the cooling process is by no means rectilinear. According to Berggren and Prothero (1992), during the early Eocene the global climate reached its optimum warmth, followed by a gradual, stepwise cooling during the remainder of the Paleogene. A severe cooling occurred around 40 – 41 Ma, while the other one occurred around the Eocene-Oligocene boundary. The latter was called by Wolfe (1978) the "Terminal Eocene Event." This general cooling trend has been widely documented in paleoclimatic and fossil researches, especially those conducted in North America and Europe as illustrated in the book "Eocene-Oligocene Climatic and Biotic Evolution" (Prothero and Berggren, 1992).

(2) Paleoclimate of Asian Continent

According to Makulbekov (1987), by the end of Eocene a subtropical flora of Poltava type dominated almost the whole Kazakhstan (except for eastern part) and the Middle Asia, while a moderately warm, deciduous flora of Turgay type became dominant since Oligocene in these areas.

Based on sedimentation characters and floristic analysis, Li and Zheng (1995) subdivided the territory of China into three climatic regions. 1) The warm and humid region in Northeast China, characterized by dark colored deposits including oil-shales and coal-seams, as typified by the Fushun coalfield. 2) The hot and/or semiarid region of Northwest and Central China, characterized by red-beds with gypsum and other rock salts. 3) The tropical humid region of Southeast China, characterized by alluvial and lacustrine deposits with coal and oil shales. The hot and/or semiarid region is the largest of the three and is the main area with rich Eocene and Oligocene paracerathere fossils. The most common plant fossils in this region during the Eocene and Oligocene are the leaves of *Palibinia*, small in size and coracious in texture, indicating the arid and hot climatic conditions. Wang defined this arid zone and demonstrated its north and south boundaries in Fig. 6 of his paper (Wang, 2004). The tropical humid region of Southeast China bears only a few Eocene paracerathere fossils.

While keeping to the general tendency of cooling, the climate of the Chinese part of the Asian continent during the Late Eocene – Oligocene possessed the following three particular features.

i. The eastern coastal region north of 31°N formed a narrow warm-temperate and subtropical zone with considerable moisture. This can be accounted for partly by the warmer climate and lower gradient of temperature against latitudes prior to the formation of the monsoonal system in East Asia, and partly by the influence of the western boundary currents of the Pacific Ocean on the coastal areas of the Paleoasian continent.

ii. As stated above, during the Paleogene there existed an arid zone, stretching in southeastern-northwestern direction. At the east end this arid zone is situated in 25° – 40°N of present day, while at west end, 35° – 50°N. At present day, deserts and semideserts occur "in belts of dry climate from 30° to 40° N and S latitudes" (Brown and Gibson, 1983, p. 105). Compared with the latitudinal distribution of the arid zones of the present day, the distribution of above stated Paleogene arid zone seems too low in latitude (close to the Tropic of Cancer) at eastern end, on the one hand, and tilted at an angle with the latitudes of present day, on the other. However, if the distribution of this arid zone is viewed against the latitudes restored by us for the Late Eocene and Oligocene time (Fig. 48), both incongruities disappear. It is significant to note that most of the paracerathere fossils were found in this arid zone.

iii. The climatic changes between Eocene and Oligocene in East Asia were apparently more or less gradual, not so abrupt as in North America, where a severe cooling, often called the Terminal Eocene Event, was well recognized (Retallack, 1992; Wolfe, 1992).

3. Evolution of Paraceratheres and Environmental Changes

(1) Stage of Development of *Juxia*

So far is known, *Juxia* lived only in late Early to early Late Eocene (45 – 38 Ma) in middle latitudes of East Asia (32° – 44°N, 108° – 114°E). In southern part of the distribution area where the Wucheng Basin is situated would be low mountainous landscape with hot and arid climate, based on the sedimentology of the Wulidun Formation where *Juxia micracis* was found (with gypsum and leaves of *Palibinia*). In Eren region, where *Juxia sharamurenensis* and *J. shoui* were found, the climate may be slightly colder and more mesic as evidenced by the presence of conifer pollen (Li, 1984, p. 102). At any rate, the vegetation type would be woodland with fairly dense undergrowth, providing plentiful foodstuff for various plant-eating ungulates. *Juxia* apparently stood on a particularly favorable position in competition with the other rhinocerotoid animals owing to its superiority in height of stature and swift running away from the possible predators.

(2) Stage of Development of *Urtinotherium*

Urtinotherium contains two species: a smaller *U. parvum* and a larger *U. intermedium*. The former was recorded in the lower part of the Ulan Gochu Formation (around 40 Ma), while the latter, probably from the upper part of that formation (around 37 Ma). If the length of the cheek teeth is taken as the representative measurement of the size of the animal, the rate of size increase from *Juxia* to *Urtinotherium* would be much higher than that from *Urtinotherium* to *Paraceratherium*. The lengths of the upper cheek teeth of the four forms [*J. sharamurenensis*, *U. parvum*, *U. intermedium* (estimated based on lower teeth), and *P. grangeri*] are 210 mm, 285 mm, 360 mm, and 403 mm respectively. The increment from *Juxia* to *U. parvum* (42 – 40 Ma) is 37.5 mm/Ma, that from *U. parvum* to *U. intermedium* (40 – 37 Ma) is 25 mm/Ma, while that from *U. intermedium* to *P. grangeri* (37 – 33 Ma) is only 11 mm/Ma. It is clear from the above figures that the most rapid increase in size in paraceratheres occurred around the boundary between Middle and Late Eocene (around 40 Ma). Then the rate of size increase gradually decreased, but at the beginning of the Oligocene the paraceratheres attained their largest size. By implication, during Late Eocene in middle part of East Asian continent, the living condition, i.e., the landscape, climate, vegetation, etc., must have been highly favorable for the paraceratheres.

(3) Stage of Development of Oligocene Paraceratheres

With gradual cooling since the Late Eocene, the vast territory of the middle part of the present-day China, especially its northwestern parts, might have become mostly woodland with sparse undergrowth. The size differences between the genera of the Oligocene paraceratheres are not very marked, a fact implying some kind of dynamic equilibrium between the food supply of high trees and intake of the paraceratheres has been reached during Oligocene. The trend of evolution has changed from size increase to improvement in gathering food. For this purpose, different types of muzzles evolved. However, the main trend in this direction was the development of movable lips or some kind of "proboscis," as illustrated for *P. lepidum* (Fig. 45). The living condition of latest Oligocene or earliest Miocene in this area for the paraceratheres might be further deteriorated in view of the fact that *Turpanotherium* became somewhat "dwarfed" with higher crownd cheek teeth and anteriorly stretching lower tusks, probably capable of barking the trees.

(4) Cause of Development of Paraceratheres in Asia

The development of the paraceratheres, almost exclusively in Asia, is apparently closely related to the presence of a wide arid and hot climatic zone in the middle part of the present day China. It is well known that during Middle and Late Eocene and Oligocene the climate (more humid and warm) and vegetation in the same latitudes in Europe were quite different (Collinson, 1992). One of the possible reasons to account for such a phenomenon may be the shifting of the paleolatitudes relative to the recent ones. It is clearly seen in Fig. 48 that the paleolatitudes around 40 – 30 Ma shifted about 10° northwards. Similar shifting of paleolatitudes would occur in North America.

Leopold *et al*. (1992, p. 412) characterized the vegetation of Late Eocene in Northwest China as "subtropical woody savanna type or open deciduous forest with a lot of shrubby areas dominated by cf. *Nitraria* and *Ephedra*." Such kind of vegetation cover would have been favorable for two diverging adaptations among plant-eating ungulates: one adapted to feeding on leaves, fruits and probably tender twigs from high trees; the other, mainly on bushes and shrubs. Paraceratheres quickly won the battle in competition to gather food from high trees and became the unique group living purely on the high trees. While the other plant-eating animals were forced mainly to live on the undergrowth. They were small in size, and often with rather high crowned cheek teeth, probably an adaptation to xerophilous undergrowth. The Asian hyracodont *Ardynia* may serve as a good example of these kinds of ungulates, while the numerous forms of the tsaganomyids may well be the examples from the rodents.

图 版 说 明

图 版 I

沙拉木伦始巨犀头骨,正模 (skull of *Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 背面 (dorsal view)
2. 左侧面 (left lateral view), f. 副枕-鼓后突间孔 (foramen between paroccipital and posttympanic processes)

图 版 II

沙拉木伦始巨犀头骨,正模 (skull of *Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 右侧面 (right lateral view), c. 副枕突的外后嵴 (posterolateral ridge of paroccipital process)
2. 腹面 (ventral view)

图 版 III

沙拉木伦始巨犀,正模 (*Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 头骨 (skull): 1a. 颅部腹面 (cranium, ventral view), t. 副枕突内侧小突起 (tubercle at medial side on ventral surface of paroccipital process); 1b. 枕面 (nuchal surface)
2. 下颌 (mandible): 2a. 冠面 (crown view), 2b. 右侧面 (right lateral view)

图 版 IV

沙拉木伦始巨犀 (*Juxia sharamurenensis*), SS 4103.1 – 2, 比例尺 (scale bar) = 10 cm

1. 头骨前半部,腭面,模型 (anterior part of skull, palatal view, cast), SS 4103.1
2. 下颌,模型 (mandible, cast): 2a. 冠面 (crown view), 2b. 左侧面 (left lateral view), SS 4103.2

图 版 V

沙拉木伦始巨犀颈椎,正模 (cervical vertebrae of *Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 寰椎 (atlas): 1a. 背面 (dorsal view), 1b. 前面 (anterior view), 1c. 腹面 (ventral view), 1d. 后面 (posterior view)
2. 第三颈椎 (C3): 2a. 右侧面 (right lateral view), 2b. 背面 (dorsal view)
3. 第五颈椎 (C5): 3a. 右侧面 (right lateral view), 3b. 背面 (dorsal view), 3c. 前面 (anterior view)

图 版 VI

沙拉木伦始巨犀颈椎和胸椎,正模 (cervical and thoracic vertebrae of *Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 第六颈椎 (C6): 1a. 右侧面 (right lateral view), 1b. 背面 (dorsal view), 1c. 腹面 (ventral view), 1d. 前面 (anterior view), 1e. 后面 (posterior view)
2. 第七颈椎 (C7): 2a. 左侧面 (left lateral view), 2b. 背面 (dorsal view), 2c. 前面 (anterior view), 2d. 后面 (posterior view)
3. 第一胸椎 (T1): 3a. 右侧面 (right lateral view), 3b. 前面 (anterior view)

图 版 VII

沙拉木伦始巨犀胸椎和腰椎,正模 (thoracic and lumbar vertebrae of *Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 第三胸椎 (T3): 1a. 后面 (posterior view), 1b. 左侧面 (left lateral view)

2. 第五胸椎 (T5)：2a. 后面 (posterior view)，2b. 前面 (anterior view)，2c. 左侧面 (left lateral view)
3. 倒数第二胸椎 (penultimate T)：3a. 前面 (anterior view)，3b. 左侧面 (left lateral view)，3c. 后面 (posterior view)
4. 最后胸椎，左侧面 (last T，left lateral view)
5. 第二腰椎，前面 (Lm2，anterior view)
6. 第四腰椎，前面 (Lm4，anterior view)

图 版 VIII

沙拉木伦始巨犀腰椎和肋骨，正模 (lumbar vertebrae and rib of *Juxia sharamurenensis*，holotype)，V 2891，比例尺 (scale bar) = 10 cm

1. 第二腰椎，后面 (Lm2，posterior view)
2. 第四腰椎，后面 (Lm4，posterior view)
3. 最后腰椎 (last Lm)：3a. 后面 (posterior view)，3b. 背面 (dorsal view)
4. 右第一肋骨 (1st right rib)：4a. 前面 (anterior view)，4b. 内面 (medial view)

图 版 IX

沙拉木伦始巨犀肩胛骨和肱骨，正模 (scapula and humerus of *Juxia sharamurenensis*，holotype)，V 2891，比例尺 (scale bar) = 20 cm

1. 右肩胛骨 (right scapula)：1a. 外面 (lateral view)，1b. 内面 (medial view)
2. 左肱骨，外面 (left humerus，lateral view)

图 版 X

沙拉木伦始巨犀肱骨和尺骨，正模 (humerus and ulna of *Juxia sharamurenensis*，holotype)，V 2891，比例尺 (scale bar) = 10 cm

1. 右肱骨 (right humerus)：1a. 前面 (anterior view)，1b. 后面 (posterior view)，1c. 内面 (medial view)，1d. 外面 (lateral view)；肌肉附着区 (muscle attachment scars)：i. 冈下肌 (m. infraspinatus)，s. 旋后长肌 (pronator longus)，t. 大圆肌 (m. teres major)，tr. 肱三头肌 (m. triceps)
2. 右尺骨，外面 (right ulna，external view)

图 版 XI

沙拉木伦始巨犀桡骨、尺骨和腕舟骨，正模 (radius，ulna and scaphoid of *Juxia sharamurenensis*，holotype)，V 2891；1－2：比例尺 (scale bar) = 10 cm，3：比例尺 (scale bar) = 2 cm

1. 右桡骨 (right radius)：1a. 前面 (anterior view)，1b. 后面 (posterior view)，1c. 外面 (lateral view)；肌肉附着区 (muscle attachment scars)：b. 臂肌 (m. brachialis)，i. 桡-尺骨间韧带 (lig. interosseum)
2. 右尺骨 (right ulna)：2a. 前面 (anterior view)，2b. 内面 (medial view)
3. 右腕舟骨 (right scaphoid)：3a. 近端面 (proximal view)，3b. 远端面 (distal view)，3c. 内面 (medial view)，3d. 外面 (lateral view)，3e. 背面 (dorsal view)；m. 与巨骨关节之面 (articular facet for magnum)，td. 与小多角骨关节之面 (articular facet for trapezoid)，tm. 与大多角骨关节之面 (articular facet for trapezium)

图 版 XII

沙拉木伦始巨犀腕骨 (carpals of *Juxia sharamurenensis*)，比例尺 (scale bar) = 2 cm

1. 右月骨，正模 (right lunar，holotype)，V 2891：1a. 前面 (anterior view)，1b. 近端面 (proximal view)，1c. 远端面 (distal view)，1d. 内面 (medial view)，1e. 外面 (lateral view)
2. 左楔骨 (left cuneiform)，V 2891.1：2a. 外面 (lateral view)，2b. 近端面 (proximal view)，2c. 远端面 (distal view)，2d. 内面 (medial view)；r. 与桡骨关节之面 (articular facet for radius)，u. 与尺骨关节之面 (articular facet for ulna)，p. 与豌豆骨关节之面 (articular facet for pisiform)
3. 右钩骨缺后结节，正模 (right unciform without posterior tubercle，holotype)，V 2891：3a. 前外面 (laterodorsal view)，3b. 近端面 (proximal view)，3c. 远端面 (distal view)；mg. 与巨骨关节之面 (articular facet for magnum)，mcIII. 与 McIII 关节之面 (articular facet for McIII)，mcIV. 与 McIV 关节之面 (articular facet for McIV)

4. 左钩骨,远端面 (left unciform, distal view), V 2891.7, mg. 与巨骨关节之面 (articular facet for magnum), mcIII. 与McIII 关节之面 (articular facet for McIII), mcIV. 与McIV 关节之面 (articular facet for McIV), mcV. 与McV 关节之面 (articular facet for McV)

图 版 XIII

沙拉木伦始巨犀腕、掌骨 (carpals and metacarpals of *Juxia sharamurenensis*)

1. 右第四掌骨,正模 (right McIV, holotype), V 2891: 1a. 远中面 (lateral view), mcV. 与 McV 关节的面 (articular facet for McV), x 为前隆起的消失处(place where the ridge disappears); 1b. 近中面 (mesial view); 比例尺 (scale bar) = 5 cm; 1c. 近端面 (proximal view), 1d. 远端面 (distal view); 比例尺 (scale bar) = 2 cm
2. 左第三、四掌骨近端 (proximal ends of left McIII – IV), V 2891.2: 2a. 背面 (dorsal view), 比例尺 (scale bar) = 5 cm; 2b. McIII 近端面 (proximal end of McIII), 比例尺 (scale bar) = 2 cm
3. 左腕、掌骨背面视,x 为复原部分 (left carpals and metacarpals, dorsal view, reconstructed parts designated by x), 比例尺 (scale bar) = 5 cm

图 版 XIV

沙拉木伦始巨犀指 (趾) 节骨 (phalanges of *Juxia sharamurenensis*), 正模 (holotype), V 2891; 1 – 2, 3a, 4 – 5: 比例尺 (scale bar) = 5 cm; 其余 (all others): 比例尺 (scale bar) = 2 cm

1. 右中第一至第三趾节骨 (right PhI – III of middle toe): 1a. 蹠面 (plantar view), c. X 状籽骨韧带附着区 (attachment area of X-shaped sesamoidean ligaments), t. 近端粗隆 (proximal prominence); x. 远籽骨关节面? (articular facets for distal sesamoids ?), 1. 趾浅屈肌腱下附着疤印 (lower scar for flexor digitalis pedis superficialis), 2. 趾浅屈肌腱上附着疤印 (upper scar for flexor digitalis pedis superficialis); 1b. 背面 (dorsal view), d. 凹陷面 (depression), e. 伸腱突下方凹坑 (depression under extensor process), f. 假关节面 (false articular facet), v. V 形粗糙隆起 (V-shaped prominence)
2. 右中第一趾节骨 (right PhI of middle toe): 2a. 内侧面 (medial view), 2b. 近端面 (proximal view), 2c. 远端面 (distal view)
3. 右中第二趾节骨 (right PhII of middle toe): 3a. 内侧面 (medial view), 3b. 近端面 (proximal view), 3c. 远端面 (distal view)
4. 右中第三蹄骨,近端面 (right PhIII of middle toe, proximal view): y. 与远籽骨相关节的窄面 (narrow facet articulating with distal sesamoid)
5. 侧第一至三指(或趾)节骨 (PhI – III of lateral digit): 5a. 背面 (dorsal view), f. 假关节面 (false articular facet); 5b. 掌或蹠面 (volar or plantar view)
6. 侧第一指(或趾)节骨 (PhI of lateral digit): 6a. 近端面 (proximal view), 6b. 近中面 (mesial view), 6c. 远中面 (lateral view), 6d. 远端面 (distal view)
7. 侧第二指(或趾)节骨 (PhII of lateral digit): 7a. 近端面 (proximal view), 7b. 远端面 (distal view), 7c. 远中面 (lateral view)
8. 侧蹄骨,近端面 (PhIII of lateral digit, proximal view)
9. 侧第二至三指(或趾)节骨,背面 (PhII – III of lateral digit, dorsal view)

图 版 XV

沙拉木伦始巨犀的盆骨、股骨和髌骨,正模 (pelvis, femur and patella of *Juxia sharamurenensis*, holotype), V 2891, 1 – 2: 比例尺 (scale bar) = 10 cm; 3: 比例尺 (scale bar) = 2 cm

1. 盆骨,背面 (pelvis, dorsal view), g. 臀肌线 (gluteal line), x. 坐骨嵴后圆沟 (groove behind ischiatic spine)
2. 右股骨 (right femur): 2a. 前面 (anterior view), 2b. 内面 (medial view); c. 头窝 (fovea capitis), lt. 大转子前外部 (anterolateral part of greater trochanter), m. 内上髁 (medial epicondyle), v. 股内肌附着线 (attachment of m. vastus medialis)
3. 右髌骨 (right patella): 3a. 前面 (anterior view), 3b. 后面 (posterior view)

图 版 XVI

沙拉木伦始巨犀的股骨和胫、腓骨,正模 (femur, tibia and fibula of *Juxia sharamurenensis*, holotype), V 2891, 比例尺 (scale bar) = 10 cm

1. 右股骨 (right femur): 1a. 后面 (posterior view), c. 头窝 (fovea capitis), f. 髁上窝 (supracondyloid fossa), g. 腓肠肌附着部 (attachment of m. gastrocnemius), n. 滋养孔 (nutrient foramen), pt. 大转子内后部 (posteromedial part of greater trochanter); 1b. 外侧面 (lateral view), e. 伸肌窝 (fossa extensoria), l. 外髁上嵴 (lateral supracondyloid crest), p. 腘肌窝 (m. popliteus fossa)
2. 左胫骨 (left tibia): 2a. 前面 (anterior view); 2b. 外侧面 (lateral view), f. 与腓骨关节的粗糙面 (rough area articulating with fibula), l. 与腓骨接触的粗糙面 (rough area contacting with fibula); 2c. 后面 (posterior view)
3. 右胫骨,前面 (right tibia, anterior view)
4. 左腓骨,外面 (left fibula, lateral view)

图版 XVII

沙拉木伦始巨犀的跗骨 (tarsals of *Juxia sharamurenensis*), 1－3: 比例尺 (scale bar) = 5 cm, 4－5: 比例尺 (scale bar) = 2 cm

1. 左距骨 (left astragalus), V 2891.3: 1a. 背面 (dorsal view); 1b. 蹠面 (plantar view), 1. 蜗突关节面 (facet for processus cochlearis), 2. 舌状面 (tongue-shaped facet), 3. 载距关节面 (sustentacular facet), 4. 与跟骨关节的第三面 (3rd facet articulating with calcaneum), 5. 内上结节 (medioproximal tubercle); 1c. 近端面 (proximal view); 1d. 远端面 (distal view)
2. 右距骨,外面 (right astragalus, lateral view), V 2891.3
3. 左跟骨缺近端 (left calcaneum without proximal end), V 2891.4: 3a. 内面 (medial view), 3b. 蹠面 (plantar view), 3c. 外面 (lateral view), f. 与腓骨关节之面 (facet articulating with fibula)
4. 右跗舟骨 (right navicular), V 2891.7: 4a. 近端面 (proximal view); 4b. 远端面 (distasl view), i. 与内楔骨关节的面 (articular facet for entocuneiform), m. 与中楔骨关节的面 (articular facet for mesocuneiform), e. 与外楔骨关节的面 (articular facet for ectocuneiform); 4c. 外面 (lateral view)
5. 右外楔骨 (right ectocuneiform), V 2891.7: 5a. 近端面 (proximal view); 5b. 内面 (medial view), mcII. 与第二蹠骨关节的面 (articular facet for MtII); 5c. 外面 (lateral view); 5d. 远端面 (distal view)

图版 XVIII

沙拉木伦始巨犀后足 (pes of *Juxia sharamurenensis*), 2a－b, 3a－d: 比例尺 (scale bar) = 5 cm; 5: 比例尺 (scale bar) = 10 cm; 其余 (all others): 比例尺 (scale bar) = 2 cm

1. 左内楔骨 + 第一蹠骨,正模 (left entocuneiform + MtI, holotype), V 2891, 1a. 背面 (dorsal view), 1b. 蹠面 (plantar view)
2. 左第二蹠骨,正模 (left MtII, holotype), V 2891: 2a. 近中面 (mesial view), 2b. 远中面 (lateral view), 2c. 近端 (proximal view); i. 与内楔骨 + 第一蹠骨关节之面 (articular facet for entocuneiform + MtI), e. 与外楔骨关节之面 (articular facet for ectocuneiform), mtIII. 与 MtIII 关节之面 (articular facet for MtIII)
3. 右第三蹠骨,正模 (right MtIII, holotype), V 2891: 3a. 背面 (dorsal view), 3b. 蹠面 (plantar view), 3c. 内面 (medial view), 3d. 外面 (lateral view), 3e. 近端 (proximal view), 3f. 远端 (distal view); r. 蹠面上的纵嵴 (ridges on plantar side of MtIII), mtII. 与第二蹠骨关节之面 (articular facets for MtII), mtIV. 与第四蹠骨关节之面 (articular facets for MtIV), c. 与骰骨关节之面(articular facet for cuboid)
4. 右第四蹠骨近端 (proximal part of right MtIV), V 2891.5: 4a. 近端面 (proximal view), 4b. 近中面 (mesial view); c. 与骰骨关节之面 (articular facet for cuboid), mtIII. 与 MtIII 关节之面 (articular facets for MtIII)
5. 左后足,背面,局部复原 (left pes, dorsal view, partly reconstructed): x. 为修复的部分 (reconstructed parts designated by x)

图版 XIX

小刺始巨犀 (*Juxia micracis*), 1－3, 6: 比例尺 (scale bar) = 1 cm; 4, 5 , 7: 比例尺 (scale bar) = 2 cm

1. 右上第一、二门齿 (right I1 - I2), V 5072: 1a. 唇面 (labial view), 1b. 舌面 (lingual view)
2. 右上第二、三门齿,舌面 (right I2－I3, lingual view), V 5073
3. 左下第一、二门齿 (left i1－i2), V 5072: 3a. 舌面 (lingual view), 3b. 唇面 (labial view)

4. 左上第二－四前臼齿，冠面 (left P2－P4，crown view)，V 5073
5. 左月骨 (left lunar)，V 5074.8：5a. 外面 (lateral view)，5b. 背面 (dorsal view)，5c. 内面 (medial view)
6. 左小多角骨 (left trapezoid)，V 5074.5：6a. 近端面 (proximal view)，6b. 内面 (medial view)，6c. 外面 (lateral view)
7. 左钩骨 (left unciform)，V 5074.4：7a. 背面 (dorsal view)；7b. 远端面 (distal view)，mcV. 与第五掌骨关节之面 (articular facet for McV)

马庄柯氏犀 (*Forstercooperia mazhuangensis*)，比例尺 (scale bar) ＝ 5 cm

8. 右腕骨和掌骨近端，前外面 (right carpal bones and proximal ends of metacarpals，dorsolateral view)，unc. 钩骨 (unciform)，McIV. 第四掌骨近端 (proximal end of McIV)

图版 XX

小额尔登巨犀 (*Urtinotherium parvum*)，比例尺 (scale bar) ＝ 10 cm

EMM 0146

1. 右上颊齿列 (right P2－M3)，冠面 (crown view)

AM 26190

2. 左第三掌骨 (left McIII)：2a. 近端面 (proximal view)，2b. 背面 (dorsal view)，2c. 掌面 (volar view)
3. 左跟骨 (left calcaneum)：3a. 内面 (medial view)，3b. 背面 (dorsal view)，3c. 远端面 (distal view)
4. 右第三蹠骨 (right MtIII)：4a. 近端面 (proximal view)，4b. 背面 (dorsal view)，4c. 蹠面 (plantar view)
5. 第二中指(蹠)节骨 (PhII of middle digit)：5a. 近端面 (proximal view)，5b. 远端面 (distal view)
6－7. 中蹄骨 (PhIII of middle digit)：6a，7a. 背面 (dorsal view)；6b，7b. 后面 (posterior view)

图版 XXI

葛氏巨犀 (*Paraceratherium grangeri*)，AM 21618，比例尺 (scale bar) ＝ 5 cm

1. 右腕舟骨 (right scaphoid)：1a. 内面 (medial view)，1b. 近端面 (proximal view)，1c. 远端面 (distal view)，1d. 外面 (lateral view)，1e. 掌面 (volar view)；m. 与巨骨关节的面 (articular facet for magnum)，td. 与小多角骨关节的面 (articular facet for trapezoid)，tm. 与大多角骨关节的面 (articular facet for trapezium)
2. 右月骨 (right lunar)：2a. 背面偏内 (dorsomedial view)，2b. 近端面 (proximal view)，2c. 远端面 (distal view)，2d. 内面 (medial view)，2e. 外面 (lateral view)；m. 与巨骨关节的面 (articular facet for magnum)，un. 与钩骨关节的面 (articular facet for unciform)
3. 右楔骨 (right cuneiform)：3a. 背面偏外 (dorsolateral view)，3b. 内面 (medial view)，3c. 远端面 (distal view)，3d. 近端面 (proximal view)；p. 与豌豆骨关节的面 (articular facet for pisiform)，r. 与桡骨关节的面 (articular facet for radius)，l. 与月骨关节的面 (articular facet for lunar)
4. 右小多角骨 (right trapezoid)：4a. 近端面 (proximal view)，4b. 内面 (medial view)，4c. 远端面 (distal view)，4d. 外面 (lateral view)

图版 XXII

葛氏巨犀 (*Paraceratherium grangeri*)，比例尺 (scale bar) ＝ 5 cm

1. AM 26166，下颌前部，冠面视 (anterior part of mandible，crown view)
2. AM 21618，右巨骨 (right magnum)：2a. 近端面 (proximal view)，2b. 背面 (dorsal view)，2c. 外面 (lateral view)，2d. 内面 (medial view)，2e. 远端面 (distal view)；sc. 与腕舟骨关节的面 (articular facet for scaphoid)，l. 与月骨关节的面 (articular facet for lunar)
3. AM 21618，右钩骨 (right unciform)：3a. 背面，稍偏内 (dorsomedial view)，3b. 近端面 (proximal view)，3c. 远端面 (distal view)；cu. 与楔骨关节的面 (articular facet for cuneiform)，l. 与月骨关节的面 (articular facet for lunar)

图版 XXIII

中间额尔登巨犀 (*Urtinotherium intermedium*)，1a－b：比例尺 (scale bar) ＝ 5 cm；1c－e：比例尺 (scale bar) ＝ 10 cm

1. AM 26389，左第三掌骨 (left McIII)：1a. 近端面 (proximal view)，1b. 远端面 (distal view)，1c. 背面 (dorsal

view)，1d. 掌面 (volar view)，1e. 外面 (lateral view)；un. 与钩骨关节的面 (articular facet for unciform)

葛氏巨犀 (*Paraceratherium grangeri*)，2－3：比例尺 (scale bar) = 10 cm；4－6：比例尺 (scale bar) = 5 cm

2. AM 26179,左跟骨 (left calcaneum)：2a. 外面 (lateral view)，2b. 蹠面 (plantar view)，2c. 背面 (dorsal view)，2d. 近端面 (proximal view)，2e. 远端面 (distal view)
3. AM 26387,右距骨 (right astragalus)：3a. 背面 (dorsal view)，3b. 近端面 (proximal view)，3c. 内面 (medial view)，3d. 蹠面 (plantar view)，3e. 外面 (lateral view)，3f. 远端面 (distal view)；a. 蜗突面下的舌状面 (tongue-shaped facet under cochlear facet)，b. 载距关节面 (sustentacular facet)，c1. 蜗突关节面 (cochlear facet)，c2. 外下关节面 (inferolateral facet)
4. AM 26387,右骰骨 (right cuboid)：4a. 背面 (dorsal view)，4b. 近端面 (proximal view)，4c. 远端面 (distal view)，4d. 外面 (lateral view)
5. AM 26387,右第一中趾骨 (PhI of right middle toe)：5a. 近端面 (proximal view)，5b. 远端面 (distal view)，5c. 背面 (dorsal view)
6. AM 26387,侧蹄骨,背面 (PhIII of lateral digit，dorsal view)

图版 XXIV

美丽巨犀 (*Paraceratherium lepidum*)，TP 9401,头骨 (skull)，1－2：比例尺 (scale bar) = 10 cm，3：比例尺 (scale bar) = 1 cm

1. 左侧面,黑线以前的部分系复原 (left lateral view，part anterior to black line is reconstructed)
2. 顶面,黑线以前的部分系复原 (dorsal view，part anterior to black line is reconstructed)
3. 鼻骨断处断面 (anterior view of nasal bones where broken)

图版 XXV

美丽巨犀 (*Paraceratherium lepidum*)，1－2：比例尺 (scale bar) = 5 cm；3－5：比例尺 (scale bar) = 10 cm

1. V 3194，左上颌带 P4－M2 (left maxilla with P4－M2)，冠面 (crown view)
2. V 3305，右 (right) p3－m1，冠面 (crown view)

TP 9401，头骨 (skull)

3. 枕面 (occipital view)
4. 吻部,顶面 (dorsal view of muzzle part)，pm. 前颌骨 (premaxilla)
5. 右上颊齿列,冠面视 (right P2－M3，crown view)

图版 XXVI

美丽巨犀 (*Paraceratherium lepidum*)，TP 9401，下颌 (mandible)，1－2：比例尺 (scale bar) = 10 cm；3－6：比例尺 (scale bar) = 5 cm；7：比例尺 (scale bar) = 1 cm

1. 左侧面 (left lateral view)
2. 后面 (posterior view)，c. 杯后突 (postcotyloid process)
3. 联合部,顶面 (symphysis，top view)
4. 联合部,前面 (symphysis，anterior view)
5. 左 (left) p2－m3，冠面 (crown view)
6. 右 (right) m2－m3，冠面 (crown view)
7. 左 (left) p2，冠面 (crown view)

图版 XXVII

美丽巨犀 (*Paraceratherium lepidum*)，TP 9401，比例尺 (scale bar) = 10 cm

1. 寰椎 (atlas)：1a. 背面 (dorsal view)，1b. 腹面 (ventral view)，1c. 右侧面 (right lateral view)
2. 枢椎 (axis)：2a. 背面 (dorsal view)，2b. 左侧面 (left lateral view)，2c. 腹面 (ventral view)，2d. 前面 (anterior view)，2e. 后面 (posterior view)，2f. 齿突背面视 (dorsal view of odontoid process)

图 版 XXVIII

美丽巨犀（*Paraceratherium lepidum*），TP 9401，比例尺（scale bar）= 10 cm

1. 第三－四颈椎（C3－C4）：1a. 右侧面（right lateral view），1b. 背面（dorsal view）
2. 第五－六颈椎（C5－C6）：2a. 右侧面（right lateral view），2b. 背面（dorsal view）
3. 第七颈椎（C7）：3a. 右侧面（right lateral view），3b. 前面（anterior view），3c. 腹面（ventral view）

图 版 XXIX

美丽巨犀（*Paraceratherium lepidum*），1－3：比例尺（scale bar）= 20 cm；4－5：比例尺（scale bar）= 10 cm

TP 9401

1. 颈椎，右侧面（cervical vertebrae，right lateral view）
2. 胸椎和右肋骨，复原肩胛，右侧面（thoracic vertebrae，ribs and reconstructed scapula，right lateral view）
3. 第一右肋，外面（1^{st} right rib，lateral view）
4. 右胫骨，腓骨为复原（right tibia，with reconstructed fibula），TP 9402：4a. 前面（anterior view），4b. 近端面（proximal view），4c. 远端面（distal view）
5. 右第三掌骨（right McIII），TP 9403：5a. 背面（dorsal view），5b. 掌面（volar view），5c. 近端面（proximal view），5d. 远端面（distal view）

图 版 XXX

美丽巨犀（*Paraceratherium lepidum*），比例尺（scale bar）= 10 cm

1. V 3195.2，右肱骨（right humerus）：1a. 前面（anterior view），1b. 外面（lateral view），1c. 后面（posterior view）
2. V 3196，左第四蹠骨远端及趾节骨（distal end of left MtIV and PhI－III）：2a. 左第四蹠骨远端背面（dorsal view of left MtIV），2b. 左第四蹠骨远端近中面（mesial view of left MtIV），2c. 左 PhI－III 背面（dorsal view of left PhI－III）
3. V 3300，侧指（或趾）节骨（PhI－III of lateral digit），背面（dorsal view）

巨犀？（未定种）（*Paraceratherium*？sp.），比例尺（scale bar）= 5 cm

4. V 3306，左（left）m2－m3：4a. 冠面（crown view），4b. 颊面（buccal view），4c. 舌面（lingual view）

图 版 XXXI

巨犀（未定种）（*Paraceratherium* sp.），比例尺（scale bar）= 10 cm

1. V 3322，下颌（mandibles）：1a. 右侧面（right lateral view），1b. 冠面（crown view）
2. V 3269，左第二蹠骨（left MtII）：2a. 近中面（mesial view），2b. 远中面（lateral view），2c. 近端面（proximal view）

霍尔果斯准噶尔巨犀（*Dzungariotherium orgosense*），比例尺（scale bar）= 10 cm

3. V 3323，左下颌，左侧面（left lateral view of mandible）

图 版 XXXII

吐鲁番准噶尔巨犀（*Dzungariotherium turfanense*），IMM-1995-IMBLG-1，1c－d，3b：比例尺（scale bar）= 5 cm；其他（others）：比例尺（scale bar）= 10 cm

1. 残破头骨和下颌（crushed skull，associated with mandible）：1a. 右侧面（right lateral view），1b. 下颌联合部，外面（symphysis，lateral view），1c. M3 冠面（crown view），1d. M3 颊面（buccal view），1e. 下颊齿，冠面（lower cheek teeth，crown view）
2. 发掘时位于第二的胸椎（2^{nd} T when excavated，T11 or T12）：2a. 前面（anterior view），2b. 后面（posterior view）；r. 与肋骨头关节的面（articular facet for caput of rib），m. 乳突（metapophysis）
3. 发掘时位于第三的胸椎（3^{rd} T when excavated，T13?）：3a. 前面（anterior view），3b. 椎体部分，前面（lower part of T13?，anterior view），3c. 左侧面（left lateral view），3d. 后面（posterior view）；pr. 前关节面（prezygapophysis），m & r. 与 2 者同（as in 2）

图 版 XXXIII

吐鲁番准噶尔巨犀（*Dzungariotherium turfanense*），IMM-1995-IMBLG-1，3a：比例尺（scale bar）= 5 cm，其余（others）：

比例尺（scale bar）= 10 cm

1. 发掘时位于第四的胸椎（4th T when excavated, T14?）：1a. 前面（anterior view），1b. 椎体部分，前侧面（lower part of T14?, anterolateral view），1c. 右侧面（right lateral view），1d. 后面（posterior view）；d. 深凹（depression），r. 与肋骨头关节的面（articular facet for caput of rib）
2. 发掘时位于第五的胸椎（5th T when excavated, T15?）：2a. 前面（anterior view），2b. 左侧面（left lateral view），2c. 后面（posterior view）；po. 后关节面（postzygapophysis）
3. 发掘时位于第六的胸椎（6th T when excavated, T17?）：3a. 椎体部分，前面（lower part of T17?, anterior view），3b. 右侧面（right lateral view），3c. 后面（posterior view）；pr, r & d. 见前（vide supra）
4. 最后胸椎和第一腰椎（last thoracic, T18?, and Lm1）：4a. 前面（anterior view），4b. 左侧面（left lateral view），4c. 背面（dorsal view）；m. 乳突（metapophysis），tr. 横突（transverse process）

图 版 XXXIV

吐鲁番准噶尔巨犀（*Dzungariotherium turfanense*），IMM-1995-IMBLG-1，比例尺（scale bar）= 10 cm

1. 第二腰椎（Lm2）：1a. 前面（anterior view），1b. 后面（posterior view），1c. 右侧面（right lateral view）
2. 第三腰椎（Lm3）：2a. 前面（anterior view），2b. 后面（posterior view），2c. 背面（dorsal view）；f. 与第四腰椎关节的面（facet articulating with Lm4）
3. 第四腰椎（Lm4）：3a. 前面（anterior view），3b. 后面（posterior view），3c. 背面（dorsal view）；sf. 与荐椎关节的面（facet articulating with sacrum）
4. 盆骨（pelvis）：背面（dorsal view）；ac. 髋臼（acetabulum），ct. 髋结节（coxial tuberosity），gsn. 坐骨大切迹（greater ischiatic notch），ic. 髂骨嵴（iliac crest），st. 荐结节（sacral tuber），ti. 坐骨结节（tuber ischii）
5. 左距骨（left astragalus）：5a. 前面（anterior view），5b. 后面（posterior view），5c. 远端面（disatal view）

图 版 XXXV

咸海巨犀（未定种）（*Aralotherium* sp.），EMM 0016，比例尺（scale bar）= 10 cm

1. 下颌前部（anterior part of lower jaw）：1a. 冠面（crown view），1b. 左侧面（left lateral view），1c. 前面（anterior view）

吐鲁番准噶尔巨犀（*Dzungariotherium turfanense*），2：比例尺（scale bar）= 5 cm；3：比例尺（scale bar）= 10 cm

2. V 3301，左距骨（left astragalus）：2a. 背面（dorsal view），2b. 蹠面（plantar view），2c. 远端面（distal view）
3. V 3304，右下颌缺联合部，带 p3 后半部至 m3（right ramus with posterior half of p3, p4 – m3）：3a. 冠面（crown view），3b. 右侧面（right lateral view）

图 版 XXXVI

咸海巨犀（未定种）（*Aralotherium* sp.），1 – 3：比例尺（scale bar）= 5 cm；4 – 7：比例尺（scale bar）= 2 cm

1. EMM 0012，右上颌带 M2 – M3（right maxilla with M2 – M3）：1a. 颊面（buccal view），1b. 冠面（crown view），1c. 舌面（lingual view）
2. EMM 0013，右（right）M2：2a. 颊面（buccal view），2b. 冠面（crown view），2c. 舌面（lingual view）
3. EMM 0058，右（right）M3：3a. 后面（posterior view），3b. 冠面（crown view）
4. EMM 0071，左 p3 外壁（buccal wall of left p3）
5. EMM 0077，右（right）m2：5a. 颊面（buccal view），5b. 冠面（crown view）
6. EMM 0087，左（left）m1 or m2：6a. 舌面（lingual view），6b. 冠面（crown view），6c. 颊面（buccal view），
7. EMM 0076，左（left）m3：7a. 冠面（crown view），7b. 颊面（buccal view），

图 版 XXXVII

咸海巨犀（未定种）（*Aralotherium* sp.），5 – 6：比例尺（scale bar）= 5 cm；其他（others）：比例尺（scale bar）= 10 cm

1. EMM 0032，枢椎前半部（anterior half of axis）：1a. 前面（anterior view），1b. 背面（dorsal view），1c. 后面（posterior view），1d. 腹面（ventral view）
2. EMM 0135，枢椎背棘后半部，背面（posterior half of spinous process of axis, dorsal view）

3. EMM 0136,左肩胛骨远端和肱骨头 (distal end of scapula and humeral caput, left side): 3a. 外面 (lateral view), 3b. 肩胛骨远端面 (distal view of scapula), 3c. 肱骨头后面 (humeral caput, posterior view)
4. EMM 0022,右肱骨远端 (distal end of right humerus): 4a. 前面 (anterior view), 4b. 远端面 (distal view)
5. EMM 0145,左巨骨 (left magnum): 5a. 背面 (dorsal view), 5b. 近端面 (proximal view), 5c. 远端面 (distal view), 5d. 外面 (lateral view), 5e. 内面 (medial view)
6. EMM 0054,左第三掌骨近端,前面 (proximal end of left McIII, anterior view)

图版 XXXVIII

咸海巨犀 (未定种) (*Aralotherium* sp.), 1: 比例尺 (scale bar) = 5 cm; 2: 比例尺 (scale bar) = 10 cm

1. EMM 0143,左髌骨 (left patella): 1a. 前面 (anterior view), 1b. 后面 (posterior view), 1c. 外面 (lateral view)
2. EMM 0009,右胫骨 (right tibia): 2a. 近端面 (proximal view), 2b. 前面 (anterior view), 2c. 内面 (medial view), 2d. 外面 (lateral view), 2e. 远端面 (distal view)

秀丽吐鲁番巨犀 (新属、新种) (*Turpanotherium elegans* gen. et sp. nov.), 3: 比例尺 (scale bar) = 10 cm; 4: 比例尺 (scale bar) = 5 cm; 5－8: 比例尺 (scale bar) = 2 cm

3. V 3191.1, 下颌前部 (anterior part of mandible): 3a. 左侧面 (left lateral view), 3b. 冠面 (crown view)

V 3191.2

4. 左第五掌骨 (left McV): 4a. 掌面 (volar view), 4b. 背面 (dorsal view)
5. 中指近端籽骨 (proximal sesamoid of middle finger): 5a. 掌面 (volar view), 5b. 背面 (dorsal view)
6. 第二指远中侧近端籽骨,外面 (lateral proximal sesamoid of 2nd finger, lateral view)
7. 第四指近中侧近端籽骨,外面 (mesial proximal sesamoid of 4th finger, lateral view)
8. 第四指远中侧近端籽骨 (lateral proximal sesamoid of 4th finger): 8a. 外面 (lateral view), 8b. 背面 (dorsal view)

图版 XXXIX

秀丽吐鲁番巨犀 (新属、新种) (*Turpanotherium elegans* gen. et sp. nov.), 左腕骨 (left carpals), V 3191.2, 比例尺 (scale bar) = 5 cm

1. 腕舟骨,前外角破失 (scaphoid, dorsolateral process broken): 1a. 内面 (medial view), 1b. 外面 (lateral view), 1c. 近端面 (proximal view), 1d. 远端面 (distal view); p."抑止面" ("hindering facet"), l1, l2. 与月骨关节的近、远端面 (proximal and distal facets articulating with lunar), m. 与巨骨关节的面 (articular facet for magnum), td. 与小多角骨关节的面 (articular facet for trapezoid), tm. 与大多角骨关节的面 (articular facet for trapezium)
2. 月骨 (lunar): 2a. 近端面 (proximal view), 2b. 内面 (medial view), 2c. 外面 (lateral view), 2d. 远端面 (distal view); s. 与腕舟骨关节的面 (articular facet for scaphoid), c. 与楔骨关节的面 (articular facet for cuneiform), m. 与巨骨关节的面 (articular facet for magnum), u. 与钩骨关节的面 (articular facet for unciform), p. "抑止面" ("hindering facet")

图版 XL

秀丽吐鲁番巨犀 (新属、新种) (*Turpanotherium elegans* gen. et sp. nov.), 左腕骨 (left carpals), V 3191.2, 比例尺 (scale bar) = 5 cm

1. 楔骨 (cuneiform): 1a. 近端面 (proximal view), 1b. 外面 (lateral view), 1c. 内面 (medial view), 1d. 远端面 (distal view); r. 与桡骨关节的面 (articular facet for radius), p. 与豌豆骨关节的面 (articular facet for pisiform), u. 与尺骨关节的面 (articular facet for ulna), l1, l2. 与月骨关节的近端和远端面 (proximal and distal articular facets for lunar)
2. 小多角骨 (trapezoid): 2a. 内面 (medial view), 2b. 外面 (lateral view), 2c. 近端面 (proximal view), 2d. 远端面 (distal view)
3. 巨骨 (magnum): 3a. 近端面 (proximal view), 3b. 外面 (lateral view); s. 与腕舟骨关节的面 (articular facet for scaphoid), l. 与月骨关节的面 (articular facet for lunar), u. 与钩骨关节的面 (articular facet for unciform)

图版 XLI

秀丽吐鲁番巨犀 (新属、新种) (*Turpanotherium elegans* gen. et sp. nov.), 左腕骨 (left carpals), V 3191.2, 比例尺 (scale bar) = 5 cm

1. 钩骨 (unciform)：1a. 近端面 (proximal view)，1b. 掌面 (volar view)，1c. 远端面 (distal view)；l. 与月骨关节的面 (articular facet for lunar)，c. 与楔骨关节的面 (articular facet for cuneiform)，m. 与巨骨关节的面 (articular facet for magnum)，mcIII－V. 与第三至五掌骨关节的面 (articular facets with McIII－V)
2. 豌豆骨 (pisiform)：2a. 内面 (medial view)，2b. 背面 (dorsal view)；u. 与尺骨关节的面 (articular facet for ulna)，c. 与楔骨关节的面 (articular facet for cuneiform)
3. 第一中指节骨 (PhI of middle finger)：3a. 近端面 (proximal view)，3b. 远端面 (distal view)，3c. 外面 (lateral view)
4. 第二中指节骨 (PhII of middle finger)：4a. 近端面 (proximal view)，4b. 远端面 (distal view)
5. 中指蹄骨，近端面 (PhIII of middle finger, proximal view)
6. 第四指第一指节骨 (PhI of 4th finger)：6a. 近端面 (proximal view)，6b. 远端面 (distal view)，6c. 远中面 (lateral view)；p.“假关节面”(“pseudo-facet”)，g. 肌腱沟 (groove for tendo)
7. 第四指蹄骨，近端面 (PhIII of 4th finger, proximal view)
8. 第二指蹄骨 (PhIII of 2nd finger)：8a. 近端面 (proximal view)，8b. 背面 (dorsal view)；g. 背沟 (dorsal sulcus)，1, 2. 内蹄角的近、远支 (proximal and distal parts of medial angle)，3. 外蹄角近支 (proximal part of lateral angle)

图版 XLII

秀丽吐鲁番巨犀（新属、新种）(*Turpanotherium elegans* gen. et sp. nov.)，1：比例尺 (scale bar) = 10 cm；2－5：比例尺 (scale bar) = 5 cm

1. V 3191.2，左前足 (left manus)，背面 (dorsal view)
2. V 3317，右 (right) p3－p4：2a. 冠面 (crown view)，2b. 颊面 (buccal view)，2c. 舌面 (lingual view)
3. V 3320，右(right) m2：3a. 冠面 (crown view)，3b. 颊面 (buccal view)，3c. 舌面 (lingual view)
4. V 3321，左 (left) m3：4a. 冠面 (crown view)，4b. 颊面 (buccal view)，4c. 舌面 (lingual view)
5. V 3319，左 (left) P4：5a. 冠面 (crown view)，5b. 颊面 (buccal view)

图版 XLIII

吐鲁番巨犀（未定种）(*Turpanotherium* sp.)，1，3：比例尺 (scale bar) = 5 cm，2：比例尺 (scale bar) = 10 cm

1. V 3307，左 (left) p4－m2：1a. 冠面 (crown view)，1b. 颊面 (buccal view)，1c. 舌面 (lingual view)
2. V 3308，左第四蹠骨 (left MtIV)：2a. 背面 (dorsal view)，2b. 外面 (lateral view)
3. NMB 4343，右 (right) M3：3a. 冠面 (crown view)，3b. 外后面 (posterolateral view)

巨犀亚科（属、种未定）(Paraceratheriinae gen. et sp. indet.)，4，7：比例尺 (scale bar) = 5 cm；5－6：比例尺 (scale bar) = 10 cm

4. V 3313，左小多角骨 (left trapezoid)：4a. 近端面 (proximal view)，4b. 外面 (lateral view)
5. V 3316，右第三蹠骨 (right MtIII)：5a. 近端面 (proximal view)，5b. 背面 (dorsal view)，5c. 蹠面 (plantar view)
6. V 3312，中蹄骨 (PhIII of middle digit)：6a. 背面 (dorsal view)，6b. 掌或蹠面 (valar or plantar view)，6c. 近端面 (proximal view)
7. V 824，右月骨 (right lunar)：7a. 远端面 (distal view)，7b. 背面 (dorsal view)，7c. 近端面 (proximal view)

图版 XLIV

始巨犀装架，部分系复原 (mounted skeleton of *Juxia sharamurenensis*, partly reconstructed)，V 2891，比例尺 (scale bar) ≈ 100 cm

图版 XLV

沙拉木伦始巨犀摄食时外形复原，沈文龙绘 (reconstructed life appearance of *Juxia sharamurenensis* while browsing, drawn by Shen Wenlong)，比例尺 (scale bar) ≈ 100 cm

图版 XLVI

沙拉木伦始巨犀伫立时外形复原，赵忠义雕刻 (reconstructed life appearance of *Juxia sharamurenensis* in standing pose, sculptured by Zhao Zhongyi)，比例尺 (scale bar) ≈ 100 cm