



## **TAXONOMIC COMPOSITION AND SYSTEMATICS OF LATE CRETACEOUS LIZARD ASSEMBLAGES FROM UKHAA TOLGOD AND ADJACENT LOCALITIES, MONGOLIAN GOBI DESERT**

Authors: KEQIN, GAO, and NORELL, MARK A.

Source: Bulletin of the American Museum of Natural History, 2000(249) : 1-118

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0090\(2000\)249<0001:TCASOL>2.0.CO;2](https://doi.org/10.1206/0003-0090(2000)249<0001:TCASOL>2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

TAXONOMIC COMPOSITION AND  
SYSTEMATICS OF LATE CRETACEOUS  
LIZARD ASSEMBLAGES FROM UKHAA  
TOLGOD AND ADJACENT LOCALITIES,  
MONGOLIAN GOBI DESERT

GAO KEQIN

*Frick Research Fellow, Division of Paleontology  
American Museum of Natural History*

MARK A. NORELL

*Chairman and Associate Curator, Division of Paleontology  
American Museum of Natural History*

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 249, 118 pages, 37 figures, 1 table, 1 appendix

Issued March 24, 2000

Price: \$11.30 a copy

Copyright © American Museum of Natural History 2000

ISSN 0003-0090

# CONTENTS

Abstract .....	4
Introduction .....	4
Geological Setting .....	5
Systematic Paleontology .....	11
Squamata Oppel, 1811 .....	11
Iguania Cope, 1864 .....	11
Iguanidae (sensu lato: nonacrodontan iguanians) .....	11
<i>Ctenomastax parva</i> , new genus and species .....	11
<i>Temujinia ellisoni</i> , new genus and species .....	18
<i>Zapsosaurus sceliphros</i> , new genus and species .....	25
<i>Polrussia mongoliensis</i> Borsuk-Bialynicka and Alifanov, 1991 .....	31
Acrodonta Cope, 1864 .....	32
<i>Mimeosaurus crassus</i> Gilmore, 1943 .....	32
<i>Priscagama gobiensis</i> Borsuk-Bialynicka and Moody, 1984 .....	34
<i>Phrynosomimus asper</i> Alifanov, 1996 .....	36
Iguania Incertae sedis .....	40
<i>Isodontosaurus gracilis</i> Gilmore, 1943 .....	40
Gekkota Cuvier, 1817 .....	46
Family Incertae sedis .....	47
<i>Myrmecodaptria microphagosa</i> , new genus and species .....	47
Scincomorpha Camp, 1923 .....	52
Teiidae Gray, 1827 .....	52
<i>Adamisaurus magnidentatus</i> Sulimski, 1972 .....	53
<i>Gobinatus arenosus</i> Alifanov, 1993 .....	55
<i>Tchingisaurus multivagus</i> Alifanov, 1993 .....	62
<i>Pyramicephalosaurus cherminicus</i> Alifanov, 1988 .....	66
<i>Macrocephalosaurus</i> Gilmore, 1943 .....	70
<i>Macrocephalosaurus</i> sp. ....	70
<i>Macrocephalosaurus chulsanensis</i> Sulimski, 1975 .....	70
<i>Erdnetesaurus robinsonae</i> Sulimski, 1975 .....	72
<i>Cherminisaurus kozlowskii</i> Sulimski, 1975 .....	73
?Scincoidea Oppel, 1811 .....	74
<i>Parmeosaurus scutatus</i> , new genus and species .....	74
<i>Hymenosaurus clarki</i> , new genus and species .....	79
Scincomorpha Incertae sedis .....	82
New genus and species (unnamed) .....	82
<i>Slavoia darevskii</i> Sulimski, 1984 .....	86
<i>Globaura venusta</i> Borsuk-Bialynicka, 1988 .....	86
<i>Eoxanta lacertifrons</i> Borsuk-Bialynicka, 1988 .....	89
Anguimorpha Fürbringer, 1900 .....	90
Carusioidae Gao and Norell, 1998 .....	90
Carusiidae Borsuk-Bialynicka, 1987 .....	90
<i>Carusia intermedia</i> Borsuk-Bialynicka, 1985 .....	90
Platynota Camp, 1923 .....	92
Monstersauria Norell and Gao, 1997 .....	92
<i>Gobiderma pulchrum</i> Borsuk-Bialynicka, 1984 .....	93
<i>Estesia mongoliensis</i> Norell et al., 1992 .....	94
Varanoidea Camp, 1923 .....	95
<i>Cherminotus longifrons</i> Borsuk-Bialynicka, 1984 .....	95
<i>Aiolosaurus oriens</i> , new genus and species .....	97
Varanoidea, genus and species undetermined .....	100

Taxonomic Diversity, Phylogenetic Significance, and Stratigraphic Distribution of the Lizard Assemblage .....	100
Paleoecology and Mode of Specimen Preservation .....	105
Conclusions .....	107
Acknowledgments .....	108
References .....	108
Appendix 1 .....	115



## ABSTRACT

Upper Cretaceous deposits at Ukhaa Tolgod and adjacent localities in the Mongolian Gobi Desert have yielded a large number of superbly preserved lizard specimens, including representatives of several new taxa (described in this paper) and important supplementary material of several previously poorly known taxa. Study of these specimens gives important insight into the taxonomic diversity and systematics of the Late Cretaceous lizard fauna of the Gobi Desert. A preliminary survey indicates that the lizard assemblage from Ukhaa Tolgod and adjacent localities consists of some 30 species in four higher groups (Iguania, Gekkota, Scincomorpha, and Anguimorpha). The iguanians are documented by eight species, including three species newly recognized in this paper. The Scincomorpha are the most diverse group, represented by as many as 14 species including three new and 11 previously known species. The Anguimorpha are nearly as diverse as the Iguania, while the Gekkota is the least diverse group with a single species documented in the assemblage. The scincomorphs include forms that are highly specialized for burrowing life-styles, interpreted from their cranial morphology as possibly analogous to extant species. The anguimorphs include phylogenetically important basal members of several major anguimorph clades.

The paleoecological significance of these lizards cannot be overlooked. According to tooth morphology, most lizards are predatory in terms of habit, while true herbivorous species are rare. Most specimens are preserved as skulls articulated with mandibles, but virtually complete skeletons *in situ* are quite common. Delicate parts of the skull, such as the braincase and ear ossicles, are undistorted and the surfaces of the bones show no sign of sand abrasion. These observations indicate not only relatively quick burial but also burial under relatively mesic climatic conditions with low-energy water involved during the taphonomic process.

## INTRODUCTION

During the past few years, the Mongolian Academy of Science–American Museum of Natural History Expeditions made extraordinary fossil collections from a remarkably productive locality named Ukhaa Tolgod in the Nemegt Basin, southwestern Gobi Desert (fig. 1), Mongolia. Ukhaa Tolgod is part of a suite of localities throughout the Gobi Desert that display a characteristic fauna (Dashzeveg et al., 1995). Most of these are in the Djadokhta and Barun Goyot formations. The Djadokhta Formation has been considered mid-Campanian, and the Barun Goyot late Campanian in age (Fox, 1978; Lillegraven and McKenna, 1986; Jerzykiewicz et al., 1993). However, recent work in Kazakhstan suggests an early Campanian age for the Djadokhta Formation (Averianov, 1997). Besides significant mammal and dinosaur fossils, Ukhaa Tolgod has yielded some 1000 lizard specimens. This is the largest collection of fossil lizards ever collected from a single locality within the Gobi Desert. Correlation of Ukhaa Tolgod with Djadokhta and Barun Goyot sections is not unambiguous (see e.g., Dashzeveg et al., 1995), but Loope et al. (1998) hinted that the Ukhaa Tolgod

beds are Djadokhta equivalents. The dinosaur and mammal assemblages show both Djadokhta and Barun Goyot affinities (Norell, 1997b; Dashzeveg et al., 1995).

Most of the specimens are superbly preserved skulls with mandibles. Some have articulated postcranial skeletons. The majority of lizard specimens were collected in structureless or vaguely cross-bedded, fine to coarse sandstones. These sediments are interpreted as originating from alluvial fans that were built from dune sands at the margins of stabilized bedforms during mesic climatic episodes (Loope et al., 1998). The surfaces of the bones show no sand abrasion as is common in elements preserved in typical eolian deposits. This exquisite preservation and extraordinary concentration of vertebrate specimens is characteristic of Ukhaa Tolgod when compared to other localities within the Cretaceous series of the Gobi Desert.

The purposes of this paper are to describe and diagnose several new lizard taxa, to provide an overview of the taxonomic diversity of lizards from Ukhaa Tolgod, and to compare this with the fauna of other Djadokhta and Barun Goyot localities. As lizards are

sensitive environmental indicators (Greene, 1982; Pianka, 1986), these specimens allow preliminary comment to be made regarding the environment in which they lived. Most of the specimens described in this paper are from the Ukhaa Tolgod locality. In addition, specimens from other localities such as Tugrugen Shireh, Khulsan, and Zos are included, because they provide material for recognition of new lizard taxa, supplementary data for a better understanding of previously known taxa, and additions to faunal lists compiled for these localities. These localities are briefly described below.

Throughout this paper the general taxonomic framework follows that proposed by Estes (1983), Estes et al. (1988), and Frost and Etheridge (1989) with modifications as explained in the text. The intent of this paper is to describe these lizard specimens and, in cases where new taxa are discussed, to provide diagnoses. It is outside the scope of this paper to provide an explicit phylogenetic hypothesis for all of the taxa included here. This work is ongoing (Norell and Gao, 1997; Gao and Norell, 1998), and it is hoped that this paper will inspire work on this collection.

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York; **AMNH-DVP-CA**, American Museum of Natural History, Department of Vertebrate Paleontology comparative anatomy collec-

tion; **IGM**, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MAE**, Mongolian Academy of Sciences–American Museum of Natural History Expeditions, field numbers; **PIN**, Paleontological Institute, Academia Nauk, Moscow, Russia; **ZPAL**, Palaeobiological Institute, Polish Academy of Sciences, Warsaw, Poland.

Abbreviations used in the figures: **an**, angular; **an proc**, angular process; **ant cor emarg**, anterior coracoid emargination; **asaf**, anterior surangular foramen; **bo**, basioccipital; **bs**, basisphenoid; **cap**, capitellum; **cl**, clavicle; **cor**, coronoid; **cora**, coracoid; **cora for**, coracoid foramen; **den**, dentary; **ect**, ectopterygoid; **ecte**, ectepicondyle; **ente**, entepicondyle; **ept**, epipterygoid; **fr**, frontal; **hu**, humerus; **ju**, jugal; **la**, lacrimal; **liaf**, lateral inferior alveolar foramina; **lsaf**, lateral superior alveolar foramina; **max**, maxilla; **m sc proc**, mesoscapular process; **na**, nasal; **oc cond**, occipital condyle; **pa**, parietal; **paf**, parietal foramen; **pal**, palatine; **palp**, palpebral; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pof**, postorbitofrontal; **prart**, prearticular; **prcor proc**, procoracoid process; **prf**, prefrontal; **psaf**, posterior surangular foramen; **ptg**, pterygoid; **qu**, quadrate; **sa**, surangular; **sc**, scapula; **spl**, splenial; **sq**, squamosal; **supoc**, supraoccipital; **supt**, supratemporal; **supt fene**, supratemporal fenestra; **troch**, trochlea; **vom**, vomer.

## GEOLOGICAL SETTING

The fossiliferous Late Cretaceous red and white sandstones of Mongolia and northern China have been known for over 75 years (Andrews, 1932). However, even though several international expeditions have made important collections in these deposits (see Lavas, 1993; Dong, 1993; Novacek, 1996; Kielan-Jaworowska, 1969), relatively little is known concerning their age, origin, and interrelationships.

The best known of these localities are Bayn Dzak (the Flaming Cliffs), Udan Sayr, Bayan Mandahu, Khermeen Tsav, Khulsan, Alag Teg, the Monadonocks, Tugrugen Shireh, and the focus of most of this report,

Ukhaa Tolgod (fig. 1). Collectively, these are called the Djadokhta-like or protoceratopsian beds (Norell et al., 1996). On the basis of fauna and lithology, two separate formations are recognized (see Gradzinski et al., 1977): the Djadokhta (the localities of Bayn Dzak, Tugrugen Shireh, Bayan Mandahu, and Udan Sayr), and the Barun Goyot (the localities of Khulsan and Khermeen Tsav). The two geological formations are regarded as mid- and late Campanian in age, respectively (see above).

Ukhaa Tolgod is from an undefined unit; however, it has been suggested that it has strong Djadokhta similarities (Loope et al.,

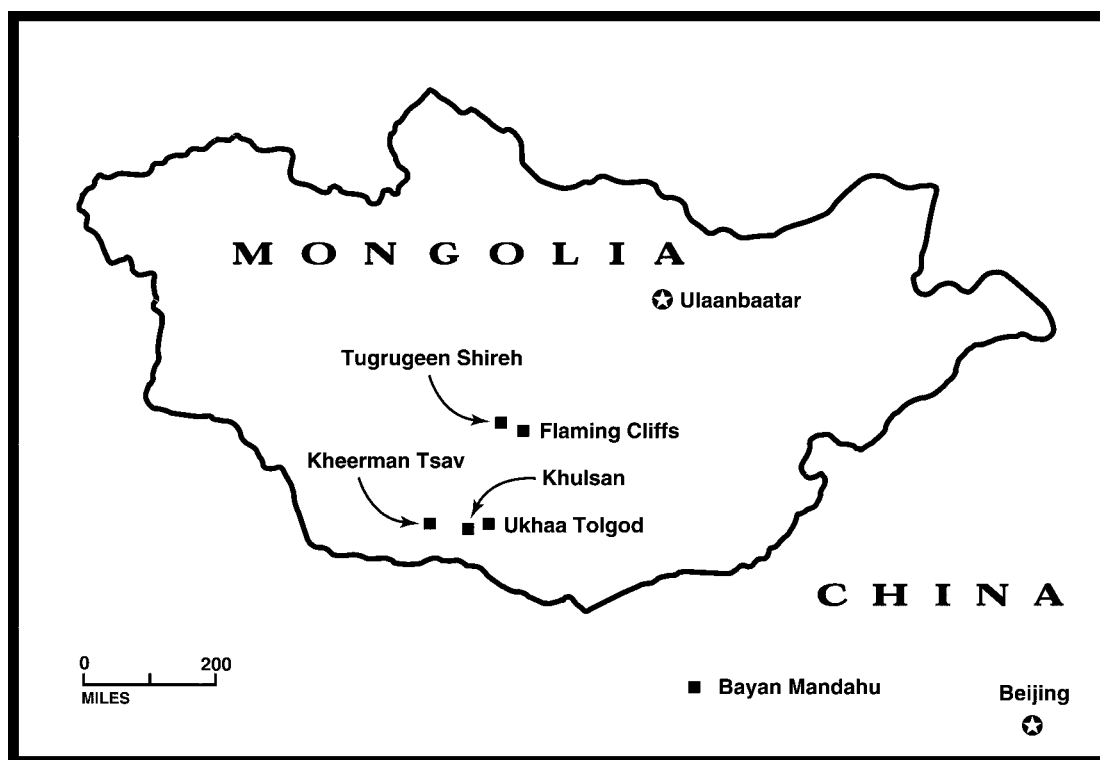


Fig. 1. Map of Mongolian Gobi Desert showing major fossil localities.

1998). Detailed reviews of many of these localities (some with conflicting interpretations of sedimentary history) can be found in Berkey and Morris (1927); Gradzinski et al. (1968), Gradzinski et al. (1977); Jerzykiewicz et al. (1993); Lefeld (1971); Eberth (1993); Gradzinski and Jerzykiewicz (1972, 1974a, 1974b). Faunal lists for many of the localities are given in these papers as well as notably in several other papers (Jerzykiewicz and Russell, 1991; Dashzeveg et al., 1995; Kielan-Jaworowska, 1974; Osmólska, 1980; Borsuk-Bialynicka, 1991b). These lists are badly in need of revision to reflect discoveries over the last decade. Fossil lizard occurrences at these localities are discussed in a later section (stratigraphic distribution). A brief description of each of the localities referred to in this paper is given below.

#### DJADOKHTA LOCALITIES

##### Bayn Dzak

Commonly called the "Flaming Cliffs," Bayn Dzak (Shabarakh Usu) was the first

Djadokhta locality to be discovered and is the type locality of the Djadokhta Formation (Berkey and Morris, 1927). It was found during the final day of the 1922 segment of the American Museum of Natural History's Central Asiatic Expeditions (Andrews, 1932; Norell, 1997a). Parties returned there on subsequent years and made large collections. The locality (fig. 2) consists of an extensive cliff face with small badlands and outlying outcrops at its base. The name "Flaming Cliffs" was inspired by the color of the sediments which at sunset glow with a brilliant red-orange color (see Novacek et al., 1994).

Remains of *Protoceratops andrewsi* are extremely common. Eggs and nests are also regularly encountered. Other dinosaurs are found with less frequency, and these include the typical "Djadokhta fauna" of *Pinacosaurus grangeri*, and rare theropods like velociraptorine dromaeosaurs, oviraptorids, and troodontids (Jerzykiewicz and Russell, 1991). Remains of mononykine alvarezsaurids (Norell et al., 1993), and a variety of tur-

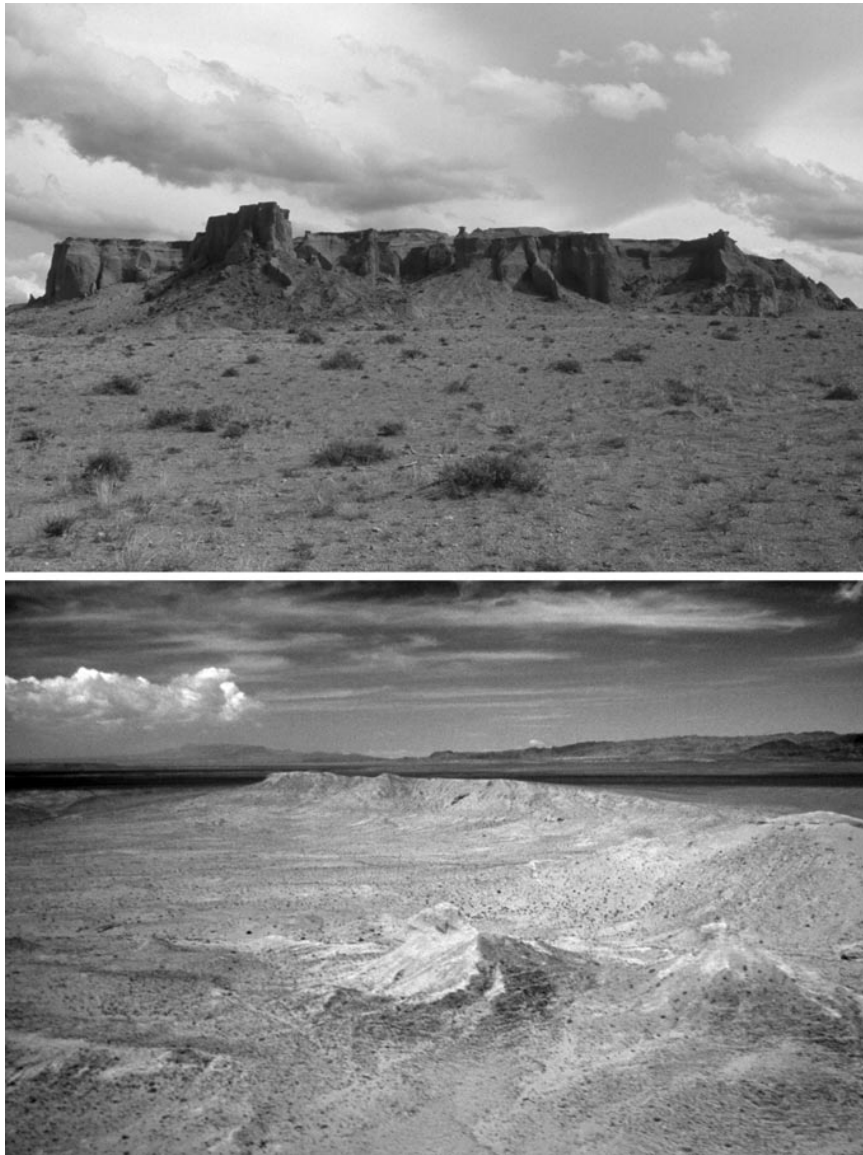


Fig. 2. Landscape of the Gobi localities. Top photo: view of the Flaming Cliffs (the classic locality Bayn Dzak); bottom photo: the new fossil bonanza, Ukhaa Tolgod.

tles (Gilmore, 1931) and crocodiles (Osmólska, 1972) have also been collected. Occasionally, extremely fragmentary specimens of large dinosaurs are also encountered. Large collections of mammal (both therians and nontherians) and lizard specimens have also been made here by American, Polish, Mongolian, Russian, and Mongolian-American expeditions (Lavas, 1993).

A total of 11 lizard taxa are recorded from

this locality. These include five taxa described by Gilmore (1943): *Macrocephalosaurus ferrugineus*, *Conicodontosaurus djadochtaensis*, *Mimeosaurus crassus*, *Isodontosaurus gracilis*, and *Telmasaurus grangeri*. Later discoveries added six more taxa: *Priscagama gobiensis*, *Bainguis parvus*, *Adamsaurus magnidentatus*, *Globaura venusta*, *Carusia intermedia*, and *Estesia mongoliensis* (see later sections in this paper).



The depositional regime at the Flaming Cliffs has generally been determined to represent eolian deposition with some fluvial component, although the sedimentology of this locality is currently under review by Dingus and Loope (personal commun.). In places there is an extensive bioturbation, as evidenced by root casts and bore holes (Lefeld, 1971).

#### Chimney Buttes

During the 1993 Mongolian Academy of Sciences–American Museum of Natural History expeditions to the Gobi Desert, a small exposure was visited between the town of Bulgan and the Bayn Dzak locality. Dashzeveg suggested that the locality be called Chimney Buttes. This exposure is extremely small; however, a few significant specimens were found there including an articulated skeleton of *Velociraptor mongoliensis* (Norell and Makovicky, 1999). Other typical Djadokhta-like taxa were recovered as well, including oviraptorid-type eggs and adults and juveniles of *Protoceratops andrewsi*. Multituberculate and lizard specimens were found in small concretions.

Although extremely close to the locality of Tugrueen Shireh, lithologically Chimney Buttes more closely resembles the Flaming Cliffs in that the rocks are bright red in color and extremely fine grained. To date, no detailed geologic work has been done at this site.

#### Tugrueen Shireh (Tugrikin-Shireh)

Also in the general area of Bayn Dzak, lies Tugrueen Shireh, a locality probably most famous for the discovery of the fighting dinosaurs (a *Velociraptor* and a *Protoceratops* locked in mortal combat; see Jerzykiewicz et al., 1993: fig. 11; see also Osmólska, 1993 for different interpretations). Unlike the Flaming Cliffs, the sands of Tugrueen Shireh are brilliant white to tan in color, and are considered to be the result of eolian deposition (Fastovsky et al., 1997).

The dinosaur fauna of Tugrueen Shireh is classically Djadokhta (see Jerzykiewicz and Russell, 1991); specimens of *Protoceratops andrewsi* are abundant, and *Velociraptor mongoliensis* elements (see Norell and Makovicky, 1997, 1999) commonly occur along

with small animals like therian and nontherian mammals and lizards.

Tugrueen Shireh preserves fossils in spectacular fashion, perhaps allowing behaviors to be estimated. For example, the “fighting dinosaurs” have been interpreted as indicative of animals overcome in the heat of battle (contra Osmólska, 1993), whereas death assemblages of *Protoceratops andrewsi*, all oriented in the same direction, may indicate some behavior of these animals in response to wind direction (Fastovsky et al., 1997). This phenomenon is also documented at Bayan Mandahu (Jerzykiewicz et al., 1993).

Lizard specimens collected from this locality are referred to nine taxa. These include *Isodontosaurus gracilis*, *Flaviagama dzerzhinskii*, *Adamisaurus magnidentatus*, *Miemosaurus tugrikinensis* (see later comments), two new iguanians described in this paper, *Cherminotus longifrons* (see later section for details), *Dzhadochthosaurus giganteus*, and *Gurvansaurus canaliculatus* (see Alifanov, 1996).

#### Bayan Mandahu

Bayan Mandahu (fig. 1) in north central China is the only Djadokhta-like locality that has yielded significant collections outside of Mongolia. It is placed in the Djadokhta Formation on the basis of lithology and a common fauna (Jerzykiewicz et al., 1993). The Late Cretaceous beds in the nearby area (Bayan Tu) were first reported by the American Museum of Natural History Central Asiatic Expeditions (Spock, 1930: Go Yoto Formation), and later by Sino-Swedish expeditions (see Bohlin, 1953). The Bayan Mandahu locality was discovered and extensively sampled by paleontologists of the Sino-Canadian Dinosaur expeditions during the years 1986–1990 (see Currie, 1993; Dong, 1993). Lizard collections from this locality belong to 17 genera in eight families. These were described by Gao and Hou (1996).

Although Bayan Mandahu shows many faunal similarities to the Djadokhta, it also shows similarities with the Barun Goyot Formation and is aberrant in yet other aspects. For instance, the protoceratopsian fauna of Bayan Mandahu may contain all three Djadokhta protoceratopsians (i.e., *Protoceratops*

*andrewsi*, *Bagaceratops rozhdestvenskyi*, and *Udanoceratops tschizhovi*). Jerzykiewicz et al. (1993) were, however, tentative in their identifications of these taxa beyond *Protoceratops andrewsi*, and more detailed study needs to take place before we can definitively indicate that all three of these taxa are present at Bayan Mandahu (P. J. Currie, personal commun., 1998). Turtles (Brinkman and Peng, 1993), mammals, and crocodilians were also recovered. Curiously, mononykine alvarezsaurids are completely missing, and elements of the lizard fauna are also slightly different from other Djadokhta localities (see later discussion).

The environment of Bayan Mandahu apparently had more of an eolian component than any other Djadokhta-like site studied thus far, except for perhaps Tugrueen Shireh. Like the latter locality, protoceratopsians are found in death assemblages sometimes buried in an almost vertical pose (Jerzykiewicz et al., 1993: fig. 12). Mass mortality sites of *Pinacosaurus grangeri* are also found in sand-dune deposits.

#### Udan Sayr

Udan Sayr is a small locality to the north of the Barun Saichan Uul. It has yielded a small assemblage including the large protoceratopsian *Udanoceratops tschizhovi* (Kurbanov, 1992). This locality was visited by the MAE in 1995, 1996, and 1997. Several lizard and mammal specimens were collected there, including an exquisitely preserved skull with mandibles of *Gobiderma pulchrum* described in this paper. The lithology at Udan Sayr is bright red to orange and similar to some of the rocks at the Flaming Cliffs. No detailed geologic investigations have occurred at this locality.

#### Ukhaa Tolgod

During early July of 1993, the field party of the Mongolian Academy of Sciences–American Museum of Natural History expedition discovered Ukhaa Tolgod—one of the most prolific Djadokhta-like localities yet discovered (Dashzeveg et al., 1995; Novacek, 1996; Norell, 1997b). Ukhaa Tolgod is exposed as a series of small cliffs, hills, and bluffs (fig. 2). In this area spectacular fossils

were recovered including several oviraptorids, some represented by embryos and adults on nests (Norell et al., 1994; Norell et al., 1995). Nearly 500 mammal specimens were discovered, along with a thousand lizards (Gao and Norell, 1996). The fauna shows strong Djadokhta similarities in that *Protoceratops andrewsi* and *Pinacosaurus grangeri* are common. Several mononykine alvarezsaurids (Chiappe et al., 1998), dromaeosaurids, and troodontids were also found (Norell et al., 1996). Occasional footprints can be seen in cross-section on some exposures (Loope et al., 1998: fig. 3b).

Deposition of fossils at Ukhaa Tolgod was studied by Loope et al. (1998). These authors show that the fossiliferous sediments that were initially interpreted as predominately eolian sediments (Novacek et al., 1994; Dashzeveg et al., 1995) are in fact strata formed by runoff flowing from sand dunes during heavy rainstorms. These low-energy runoff flows covered dead or dying animals and buried others in their burrows. This sort of deposition is novel for Djadokhta-like rocks. Currently this work is being extended to some of the other localities to see if this model applies elsewhere (L. Dingus, personal commun., 1998).

#### Zos

Zos is a small locality that is adjacent to Ukhaa Tolgod; it is a system of ravines that run into a canyon through the Gilbert Ul. Lithologically, Zos is hard to classify, however, it appears to be more fluvial than Ukhaa Tolgod. At Zos the rocks are predominately red sandstone. Protoceratopsian specimens were collected, but have not been definitively identified. New and unusual mammal and crocodile specimens were also collected. Interestingly, there is a Nemegt-type facies (containing a Nemegt-type fauna) that intertongues with the Djadokhta-like rocks at Zos. Stratigraphically, this locality lies below Ukhaa Tolgod. Several lizard specimens were collected from the Zos locality. These include the holotype of a new iguanian (see description below).

#### BARUN GOYOT LOCALITIES

##### Khulsan

Khulsan is a large locality in the Nemegt Basin (fig. 1). It is the type locality of the

Barun Goyot Formation (Gradzinski and Jerzykiewicz, 1974a). Gradzinski and Jerzykiewicz (1974a, 1974b) considered the sediments of the Barun Goyot at Khulsan to be primarily eolian, however, due to an absence of caliches and a greater proportion of clay and siltstones, they concluded that Barun Goyot conditions were less arid than Djadokhta ones. This is further supported by the presence of obviously fluvial components (such as conglomerates) in a greater frequency in Barun Goyot rocks than in Djadokhta ones (Gradzinski et al., 1977). Compared to the Djadokhta Formation, relatively little published work has appeared on the Barun Goyot Formation, or the Khulsan locality, aside from several papers describing the fauna (e.g., Sulimski, 1975).

The fauna at Khulsan appears to be different from classic Djadokhta localities. Several mammals appear to be distinct (Kielan-Jaworowska, 1974). The same is true for the dinosaurs as no species level taxa (beyond the possible occurrence of *Velociraptor mongoliensis*) are reported from Khulsan and any Djadokhta site. However, detailed study of the mammals (Novacek et al., in prep) and the lizards (see later discussion) seems to suggest that some of these perceived differences have been overstated. Lizard fossils from this locality are referred to 17 species. Descriptions of these lizard taxa are covered in papers by several authors (Sulimski, 1975; Borsuk-Bialynicka, 1984; Norell et al., 1992; Alifanov, 1993b; this paper).

#### Khermeen Tsav

Khermeen Tsav is a large locality, where two separate rock units occur. The stratigraphically higher white beds are equivalent of the loosely defined Nemegt Formation that produce a fauna with tarbosauroids, big hadrosaurs, and ornithomimids. Beneath these are characteristic red rocks (the Red Beds of Khermeen Tsav of Gradzinski et al., 1977) that contain a rich Djadokhta-like fauna of protoceratopsians (*Bagaceratops rozhdestvenskyi*), velociraptorine dromaeosaurs, oviraptorids, and the ankylosaur *Saichania chulsanensis*. Several extremely well-preserved birds, including embryos, were recovered from this locality (Elzanowski, 1977, 1981).

More than 20 lizard taxa have been described based on the specimens from this locality. These include six iguanians, 14 scincomorphs, and four anguimorphs (Sulimski, 1972, 1975, 1984; Borsuk-Bialynicka, 1984, 1985, 1988; Alifanov, 1988, 1993a, 1993b, 1996; Norell and Gao, 1997). Several lizards from this locality are also known from Djadokhta beds (e.g., *Adamisaurus*, *Globaura*, *Slavoia*); whereas several other taxa commonly seen in the Djadokhta localities (e.g., *Isodontosaurus*, *Mimeosaurus*) are unknown from this locality.

Lithologically, the above-mentioned localities are predominantly formed of well sorted and cross bedded red sandstones, suggesting the presence of large dune fields in the Late Cretaceous. Some fluvial sediments are also present, indicative of at least ephemeral water in the interdunal environments. Although a variety of mechanisms have been proposed regarding the origin of these deposits, current consensus is that some, if not most, represent predominantly eolian deposits (Jerzykiewicz et al., 1993; Eberth, 1993; Fastovsky et al., 1997), with Ukhaa Tolgod being a notable exception (Loope et al., 1998). These interpretations are, however, under review (Dingus and Loope, personal commun.).

The lithology of sediments at Ukhaa Tolgod and other Djadokhta and Djadokhta-like formations, which often contain "mature caliche paleosols" (Jerzykiewicz, 1995: 244), suggests that this region was an arid desert when these rocks were deposited. Nevertheless, intermittent water was present, both as ponds and as small seasonal streams (Jerzykiewicz, 1995; Jerzykiewicz et al., 1993). At some localities extensive bioturbation and root casts point to the presence of some plant cover.

Variation among these localities has two components: temporal and geographic. Models have been proposed for each. Geographically, Eberth (1993) proposed that the Djadokhta-like beds were part of a large, Late Cretaceous basin where depositional conditions were fairly uniform throughout, similar to many modern Central Asian basins like the Tarim. In a temporal context, assuming sequential superposition of Djadokhta, Barun Goyot, and Nemegt rocks, Jerzykiewicz et al. (1993: fig. 14) proposed that the arid Dja-

dokhta environment was sequentially replaced by less arid Barun Goyot conditions and finally mesic Nemegt ones.

How these formations, or how individual localities, interrelate temporally is difficult to address. On the basis of "comparative studies of dinosaurs and mammals," Gradzinski et al. (1977) suggested that the Barun Goyot was temporally younger than the Djadokhta. Although many authors used supposed faunal differences among these localities to order them in time (for a consideration of the lizards see later discussion in this paper), subsequent intensive collecting at many these localities caused many of these faunal differences to evaporate (Dashzeveg et al., 1995; Gao and Norell, 1996; Dong, 1993; Jerzykiewicz et al., 1993). Furthermore, since the Djadokhta and the Barun Goyot do not lie in superposition, it is impossible to determine their direct stratigraphic relationships. Consequently there is little evidence to separate these localities temporally. Intraformationally, some relationships are present. For instance, in the area around Bayn Dzak it is possible to determine that the Tugrugen Shireh locality lies above the red rocks of Bayn Dzak, and Chimney Buttes (L. Dingus, personal commun., 1998). Furthermore, the relationships of the sublocalities at Ukhaa Tolgod have been determined (Dingus et al., in prep.).

Because no rocks suitable for radiometric

dating have been identified in these sediments and there is a lack of reliable paleomagnetic data (a situation that is being remedied; L. Dingus, personal commun., 1998), the absolute age of these localities is impossible to determine at this time. Nevertheless, several ages have been proposed. All of these are based on little or no direct evidence beyond faunal similarity at very high levels. For instance, Gradzinski et al. (1977) suggested that the age of Djadokhta is ?late Santonian/early Campanian and Barun Goyot ?middle Campanian; whereas other authors (Fox, 1978; Lillegraven and McKenna, 1986; Jerzykiewicz and Russell, 1991) suggested that the Djadokhta and Barun Goyot formations are approximately equivalent in age, respectively, to the middle and late Campanian (or the North American Judithian). Recently, new biostratigraphic evidence for the age of Djadokhta-like sediments in Mongolia and northern China was presented (Averianov, 1997). This age estimate is based on the common occurrence of isolated teeth of a number of mammals in the Darbasa Formation of southern Kazakhstan and at Mongolian localities. These mammals seem to exhibit Djadokhta similarities (although it should be stressed that they are quite fragmentary). In Kazakhstan, the Darbasa Formation yields both terrestrial and marine faunas, the latter exhibiting an early Campanian fauna (Averianov and Nessov, 1995).

## SYSTEMATIC PALEONTOLOGY

### SQUAMATA OPPEL, 1811

#### IGUANIA COPE, 1864

**DEFINITION:** The most recent common ancestor of Iguanidae\*, Agamidae\* and Chamaeleonidae, and all of its descendants (Estes et al., 1988).

**REMARKS:** The monophyly of the Iguania is well supported by a number of character states (Estes et al., 1988). The Iguania include extant familial groups such as the Iguanidae\*, Agamidae\*, and the Chamaeleonidae, and fossil groups such as the Arretosauridae Gilmore, 1943. The monophyly of the Iguanidae\* and the Agamidae\* is still questionable (Frost and Etheridge, 1989), but

there is evidence to support the splitting of the Iguania into two major subgroups: the nonacrodontan iguanians and the acrodontans (Macey et al., 1997).

#### IGUANIDAE (SENSU LATO: NONACRODONTAN IGUANIANS)

##### *Ctenomastax parva*, new genus and species

Figures 3–4

**ETYMOLOGY:** *ktenos* + *mastax* (Gr., f.), comb-jaw; referring to the comblike arrangement of the marginal teeth of this lizard; *parvus* (L.), meaning "little."

**HOLOTYPE:** IGM 3/61 (MAE 89/93-70), incomplete skull with partial right and clear



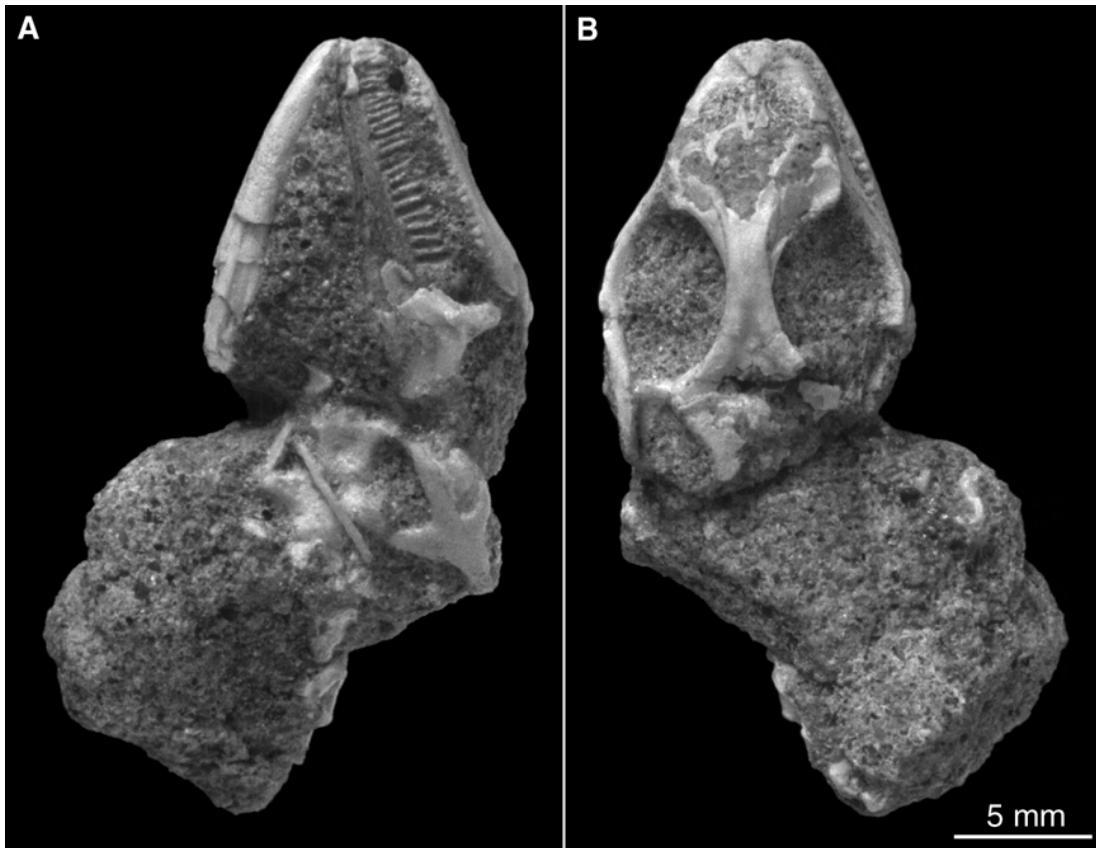


Fig. 3. *Ctenomastax parva*, new genus and species: **A**, **B**, IGM 3/61 (holotype), incomplete skull with mandibles from Zos, ventral and dorsal views.

impression of the left mandible; preserved in red fine-grained sandstones.

**TYPE LOCALITY AND HORIZON:** Zos, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation.

**KNOWN DISTRIBUTION:** Zos and Khulsan localities, Djadokhta and Barun Goyot formations.

**DIAGNOSIS:** Distinguished from other non-acrodontan iguanians (or iguanids) in having the following derived character states: slender, fine teeth arranged in a “comb-like” configuration along the tooth row; tooth crowns short and peglike; maxillary tooth row slightly heterodont with anterior and posterior teeth larger than those in the middle part of the tooth row; anterior one third of Meckelian canal enclosed without fusion of the dentary tube; retracted splenial covering

only the posterior two thirds of Meckelian canal.

**REFERRED SPECIMEN:** IGM 3/62 (MAE 131), incomplete skull with mandibles, first nine vertebrae and an incomplete scapula; from Khulsan (preserved in gray fine-grained sandstones); Upper Cretaceous Barun Goyot Formation.

#### DESCRIPTION

The new taxon is known from two specimens. The diagnostic features of the teeth and jaw structures are best shown on the holotype (fig. 3), whereas the skull roof and the palatal region are well preserved on the referred specimen. The following description is based on both specimens.

**SKULL ROOF:** Skull is delicately built with

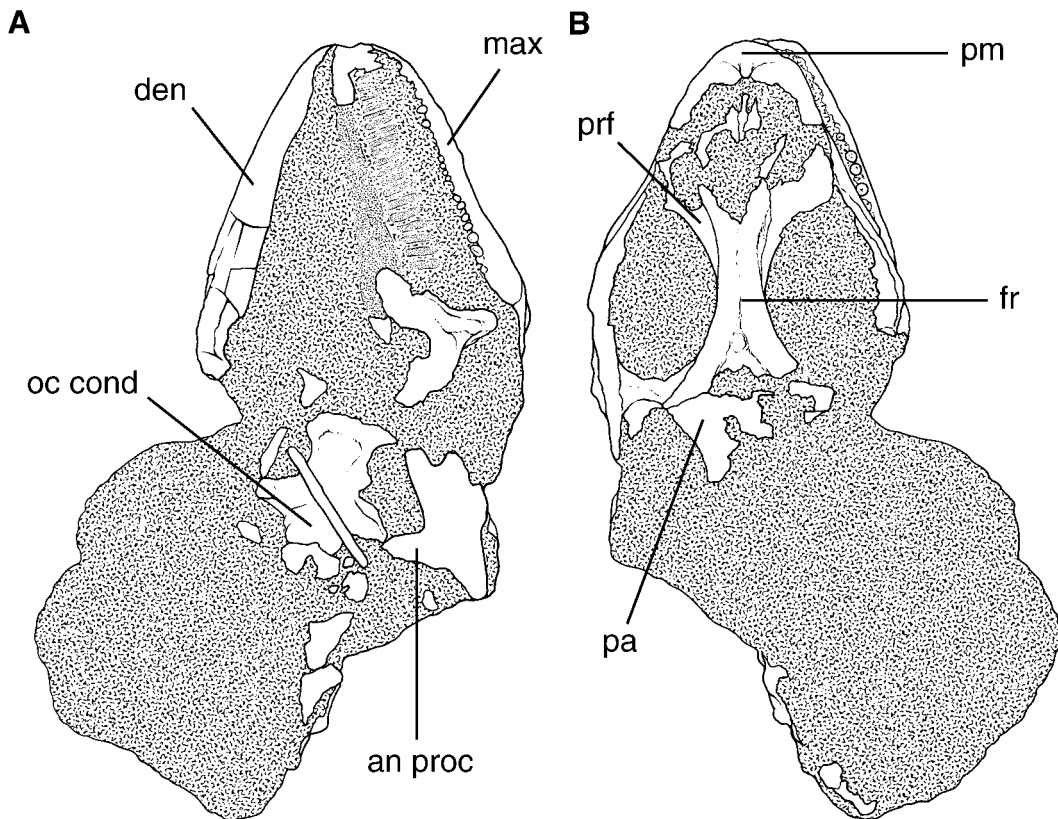


Fig. 3. Continued.

a pointed snout. The premaxillae are fused as a single element and exhibit a prominent dorsal spine separating the nares. Six small unicuspid premaxillary teeth are present. The nasals are paired and extend posteriorly to the level of the posterior borders of the prefrontal bosses. As in other iguanians, the frontals are fused as a single bone and are constricted between the orbits. Ventrally, shallow subolfactory flanges form a trough for the olfactory tract. The dorsal surface of the frontal is smooth anteriorly, but posteriorly is lightly ornamented with rugosities anterior to the parietal foramen. The frontoparietal suture is transverse, with a small parietal foramen opening at the suture (best shown on IGM 3/62; see fig. 4).

The prefrontal is overlapped anteriorly by the dorsal process of the maxilla. The prefrontal is exposed primarily on the dorsal table of the skull and carries a prefrontal boss. It also has a well-developed frontal process,

which medially articulates with the frontal and posteriorly extends to the midlevel of the orbit. The anteroventral (orbital) process forms the anterior wall of the orbit, but ventrally does not contact the palatine. This process medially borders the orbitonasal fenestra (term *sensu* Oelrich, 1956). The prefrontal contacts the lacrimal. Along this suture lies a small notch (the lacrimal foramen).

The postorbital and postfrontal are unfused, separate elements. The left postfrontal on the holotype is slightly shifted medially beneath the frontal and parietal, but it shows a forked condition with a slender anterior process and a short posterior process clasping the frontoparietal suture. The postorbital slightly broadens posteriorly on the skull table where it intrudes into the supratemporal fenestra.

The parietal table is short and roughly trapezoidal. Laterally the parietal table is strongly concave with a medial constriction.

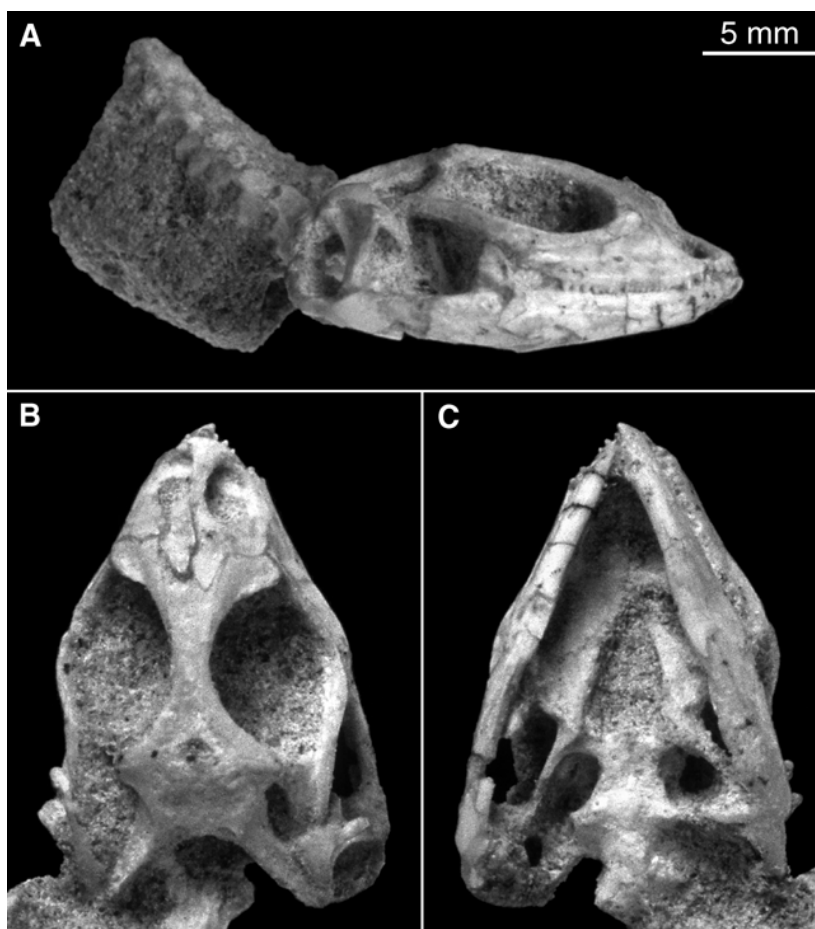


Fig. 4. *Ctenomastax parva*, new genus and species: A–C, IGM 3/62 (referred specimen), incomplete skull with mandibles from Khulsan, lateral, dorsal, and ventral views.

Ventrolaterally it has a steep flange for the attachment of the temporal muscle, which extends continuously to the lateral surface of the supratemporal process of the parietal. The dorsal surface of the parietal table is ornamented with small bumps with rugosities. This sculpturing is more developed than that on the frontals. The posterior border of the parietal table is not a simple transverse margin. Rather, this margin consists of two lateral notches separated by a flat, posterior extension of the parietal table dorsal to the foramen magnum (fig. 4B). The supratemporal process of the parietal is longer than the parietal table. In dorsal view, the supratemporal process is triangular in cross-section adjacent to the main body of the parietal. Posteriorly

it becomes laterally compressed, forming a crest as it turns posterolaterally to contact the quadrate. The supratemporal is preserved on both sides. It attaches to the lateral surface of the supratemporal process of the parietal, and extends anteriorly to the midlevel of the supratemporal process.

In lateral view, the maxilla has a relatively high dorsal process, which forms part of the posterior border of the narial opening. The premaxillary process of the maxilla is short, overlapping the lateral extension of the premaxilla. An even stronger anteromedial process extends and meets its counterpart behind the premaxilla (on both the holotype and the referred specimen). Such a contact was previously interpreted as an acrodontan syna-

pomorphy (Estes et al., 1988), but its occurrence in this and other nonacrodontan iguanians (see below) from the Gobi indicates that the character merits reevaluation. The maxilla carries 19 highly pleurodont teeth (see below) on the holotype and 18 on the referred specimen. Dorsal to the maxilla, the ventral rim of the orbit is formed by the anteroventral process of the jugal and a small lacrimal. As in other iguanians, the postero-dorsal process of the jugal extends to meet the squamosal ventral to the postorbital. The squamosal is missing on the holotype, but is preserved on both sides of the referred specimen. It has a slightly widened base that articulates with the quadrate, and a slender anterior process contacting the postorbital and abutting the jugal.

The quadrate is straight and lightly built. Its dorsal end expands posteriorly slightly. It has a well-developed cephalic condyle that is covered by the squamosal in the holotype. The anterior surface of the quadrate is a vertical plate with a smooth surface penetrated by a small quadrate foramen dorsal to the ventral condyle. This foramen forms the passageway for an anastomotic branch of the anterior tympanic vein and a small anastomotic branch of the posterior condylar artery (Oelrich, 1956). The lateral (tympanic) crest is vertical and curves slightly posteriorly forming the margin of the tympanic membrane. The medial border of the anterior surface of the quadrate is marked by the medial crest which ventrally has a small notch for insertion of the quadrate process of the pterygoid. The ventral condyle is much smaller than the cephalic condyle and sets in the articular fossa of the lower jaw, which has an anterior buttress enhancing the jaw joint (fig. 4A). The posterior crest is much more robust than the tympanic crest. It originates on the cephalic condyle as a prominent ridge that curves ventrally and disappears dorsal to the ventral condyle. Lateral to this crest is a dorsally expanded triangular fossa. The postero-medial surface of the quadrate is also triangular. The thin medial crest is oblique in posterior view. The posterior opening of the quadrate foramen is dorsal to the quadrate-ptyergoid articulation.

**PALATAL ELEMENTS:** Much of the palatal region can not be examined on the type spec-

imen. However, preparation of the palatal region of the referred specimen (IGM 3/62) shows that the preserved left vomer has a clear midline edge separating it from the right vomer (not preserved). In iguanians, vomer fusion occurs only in chamaeleonids (Rieppel, 1981), and the paired condition is a primitive character state for squamates generally (Estes et al., 1988). The suture between the vomer and the palatine cannot be clearly delimited, but the palatine is slightly widened and has a small lateral process that overlaps the palatal process of the maxilla. The lateral edge of the palatine forms the entire medial border of the suborbital fenestra, which is narrow and slightly elongated. The medial edge is slightly damaged, but shows no indication of a midline contact with its counterpart to close the interptyergoid vacuity. Posteriorly, the palatine has an irregular diagonal sutural contact with the ptyergoid. Posterolaterally, the suture originates at the posterior border of the suborbital fenestra, but extends anteromedially, ending at the midlevel of the interptyergoid vacuity. The ptyergoid has a short and wide anterior (or palatal) process, which is about half the length of the posterior (or quadrate) process. Due to its oblique sutures with the palatine, the anterior process of the ptyergoid is roughly triangular. The lateral process of the ptyergoid is even shorter and forms the weakly developed ptyergoid flange. Dorso-medial to the lateral process, the eptyergoid sets in a small columellar fossa at the base of the quadrate process. All the palatal elements are toothless.

**BRAINCASE:** The floor of the braincase is well preserved on both specimens, but the dorsal part of the lateral wall of the braincase is not preserved. Only the ventral half of the right eptyergoid is preserved as a vertical pillar. The basiptyergoid process of the basisphenoid is short and slender and articulates with the grooved medial surface of the ptyergoid. The ventral surface of the basisphenoid is slightly depressed, as seen in many other iguanians. Posteriorly, the basisphenoid is sutured to the basioccipital. This suture is slightly arched anteriorly (fig. 3A, 4C). The basioccipital posterolaterally forms the small spheno-occipital tubercle, which is ventrally directed. Laterally it displays a



roughly triangular occipital recess. Antero-lateral to the occipital recess, the recessus vena jugularis (or vena capitis lateralis of others) is poorly preserved. It is a relatively shallow trough where the posterior opening to the Vidian canal is located anteriorly dorsal to the base of the basiptyergoid process and within the basisphenoid. The foramen ovale lies anterior to the occipital recess. The facial foramen is not preserved on either side of the type.

Although the occiput is badly damaged, some elements are still identifiable on IGM 3/62. The supraoccipital is not preserved. The right paroccipital process is missing, and the left is displaced below the supratemporal arch and in front of the quadrate. The occipital condyle is formed predominately by the basioccipital, with little contribution from the exoccipitals. Dorsolateral to the occipital condyle, the exoccipital is partially preserved on both sides. It forms the posterior rim of the occipital recess, and contributes in small part to the spheno-occipital tubercle and the lateral part of the occipital condyle. The better preserved right side seems to show that the exoccipital is broken at the hypoglossal foramina.

**MANDIBLE:** Both mandibles are well preserved on the referred specimen, but the diagnostic medial side of the dentary and teeth are best exposed on the holotype, in which a matrix impression shows the sutures and enclosure of the Meckelian canal. Both the holotype and the referred specimen show that the canal is closed anteriorly for about one third of its length; the presence of a clear suture indicates that the dentary tube is enclosed but not fused. The posterior two thirds of the canal is medially covered by a narrow splenial. The anterior inferior alveolar foramen and the anterior mylohyoid foramen are located in close approximation. The former foramen is larger than the latter and is located at the anterior end of the splenial, whereas the anterior mylohyoid foramen lies at the ventral border of the splenial. Location of the posterior mylohyoid foramen (= angular foramen of other authors) cannot be determined on either of the specimens, as a matter of preservation. The splenial terminates posteriorly at the level of the coronoid summit of the jaw.

Posterodorsal to the splenial, the medial exposure of the coronoid is triradiate, lacking the posterodorsal process seen in some extant iguanians (see Frost and Etheridge, 1989: fig. 4). Ventral to the coronoid, the anterior part of the angular is exposed as a tongue-like extension, which turns from lateral to the medial side of the jaw, separating the splenial and the dentary to the level of the anterior inferior alveolar foramen. Immediately behind the posteroventral process of the coronoid, the mandibular fossa opens as a narrow and shallow groove extending posteriorly towards the craniomandibular joint. As shown on both the holotype and the referred specimen, the angular process is strongly developed, directed medially and not hooked at all.

In lateral view, the dentary occupies the anterior half of the mandible and posteriorly terminates at the level of the anterior surangular foramen. This proportion is a derived condition among iguanians, as *Sphenodon* and some extant iguanians have a greater proportion of the dentary in relation to the postdentary part of the jaw. Neither of the two specimens has the lateral coronoid process preserved. But the referred specimen displays a clear articular surface anterior to the anterior surangular foramen, indicating that the lateral coronoid process has a triangular anterior border and covers the dorsal part of the dentary-surangular suture (fig. 4A). A small coronoid process of the dentary slightly covers the anterior surface of the dorsal process of the coronoid bone. The posterior extent of the dentary is not preserved on either specimen, but based on observation of the referred specimen, it seems to terminate below the anterior surangular foramen. The latter specimen seems to have a small notch on the dentary for articulation with the surangular and angular bones.

The posterior surangular foramen, much smaller than the anterior one, is located posteriorly near the dorsal border of the jaw and anterior to the craniomandibular joint. As in many other iguanian lizards, the articular and prearticular are fused. The retroarticular process is slightly stronger than the angular process and is directed posteriorly, in contrast to the deflected condition in several lizard

groups including gekkotans, scincoids, and varanids (see Estes et al., 1988). The process has a depression on its dorsal surface, which provides the insertion for the dorsal fibers of the pterygomandibularis muscle (Oelrich, 1956).

**DENTITION:** The marginal teeth are generally peglike in lateral view, but are highly pleurodont, having over two thirds of the tooth height attached to the lateral parapet of the jaws. As the teeth have very slender shafts and are closely spaced, they show a comblike arrangement along the tooth row. The crowns are unicuspid, having no cusps but displaying weak lateral crests.

The marginal teeth of *Ctenomastax parva* are weakly heterodont: the first two or three teeth on the maxillary and dentary tooth rows are enlarged and are more or less caniniform, the middle teeth are much smaller than the anterior ones, and a few posterior teeth are larger than those in the middle part of the tooth row. However, there is no differentiation of crown pattern along the tooth row. The complete maxillary tooth row includes 19 positions on the holotype and 18 on the referred specimen. The complete dentary tooth row is best shown on the holotype, in which a total of 23 teeth are preserved as clear impressions. As mentioned before, the premaxilla is a single element that bears six small unicuspid teeth.

#### COMPARISON AND DISCUSSION

The new taxon *Ctenomastax parva* shares the following characters with other iguanians: frontals are fused and constricted between the orbits; presence of a frontal shelf that anteriorly underlies the nasals; parietal foramen located anteriorly on the frontoparietal suture; and presence of an angular process on the retroarticular process of the lower jaw. Other characters listed in Estes et al. (1988) as iguanian synapomorphies are not preserved on the specimen.

Two nonacrodontan iguanians described by Borsuk-Bialynicka and Alifanov (1991) from Khulsan (*Igua* and *Polrussia*) have short, wide, and rectangular parietal tables. By contrast, *Ctenomastax parva*, known from the same locality, has a trapezoidal parietal table. All of the specimens of these

three taxa are small and nearly equivalent in size, indicating that differences in the shape of the parietal table are not due to ontogenetic or allometric factors. Furthermore, *Igua* has tricuspid teeth that are very different from the peglike dentition of *Ctenomastax parva*. *Polrussia* has unicuspid teeth, that "protrude high above the parapet of the jaw" (Borsuk-Bialynicka and Alifanov, 1991). *Ctenomastax parva* with its low crowned teeth clearly differs from *Polrussia*. Furthermore, the new taxon lacks the fusion of the dentary tube seen in *Polrussia*.

A notable character in *Ctenomastax parva* is the contact of the maxillae behind the premaxillary spine. This character was regarded as an acrodontan synapomorphy by Estes et al. (1988) based on its distribution in extant iguanians (but see Jollie, 1960). However, the dentition of the new species is highly pleurodont, the postfrontal remains as a separate element from the postorbital, and the Meckelian canal is closed anteriorly. These characters strongly indicate that the new species represents a nonacrodontan iguanian (or iguanid), and cannot be classified in the Acrodonta. Furthermore, this same character occurs in several other nonacrodontan iguanians from the Gobi, and suggests such a contact could well be a primitive character state among iguanians.

The relationships of the new species with other nonacrodontan iguanians is currently unclear. Like some other nonacrodontan iguanians described from the Gobi Desert, *Ctenomastax parva* shares a large number of characters with crotaphytine iguanians: (1) lacrimal foramen not enlarged; (2) skull roof not strongly rugose; (3) jugal and squamosal not broadly juxtaposed; (4) parietal table trapezoidal; (5) parietal foramen in frontoparietal suture; (6) supratemporal on lateral side of supratemporal process of parietal; (7) dentary not expanded onto labial face of coronoid; (8) labial blade of coronoid absent; (9) anterior surangular foramen above posteriormost extent of dentary; (10) dentary tube not fused; (11) splenial relatively long anteriorly; (12) marginal teeth pleurodont. Many of these characters are plesiomorphic for the Iguania, providing little information regarding the relationships of the

new lizard except for possibly indicating its primitive status.

***Temujinia ellisoni***, new genus and species

Figures 5–6

ETYMOLOGY: *Temujin*, Mongolian name of the world conqueror Genghis Khan; species epithet after Mick Ellison, Principal Artist at the American Museum of Natural History, who skillfully prepared the photographs and outline drawings for this work.

HOLOTYPE: IGM 3/63 (MAE 121/93-93), incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Ukhaa Tolgod, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

KNOWN DISTRIBUTION: Ukhaa Tolgod and Tugrueen Shireh localities, Djadokhta Formation.

DIAGNOSIS: Differing from other iguanians in having the following derived character states: postfrontal forms slender bar between orbit and supratemporal fenestra; parietal foramen opens largely on frontal side of frontoparietal suture; posterior margin of parietal symmetrically notched for insertion of dorsal axial muscle; presence of vertical ridges and grooves on dorsal process of coronoid for insertion of mandibular adductor muscle; anterior surangular foramen opens dorsally behind dorsal process of coronoid; anterior half of Meckelian canal closed by dentary without fusion; mandibular fossa narrow and elongate; marginal teeth low crowned and strongly swollen; tooth crowns weakly tricuspid; angular process of mandible wide and strong, directed medially.

REFERRED SPECIMENS: IGM 3/64–3/69 (MAE 145/94-40, 75/93-89, 235/93-130, 319/93-147, 39/93-90, MAE 94-37), all topotypic incomplete skulls with mandibles (see discussion below); IGM 3/70 (MAE 19/93-6), fragmentary skull with mandibles from Tugrueen Shireh (Tugrikin-Shireh).

DESCRIPTION

SKULL ROOF: The premaxillae are not preserved on the holotype, but are present on several referred specimens (IGM 3/64, 3/66, 3/68). The premaxillae are fused into a single element with a slender spine. None of the

specimens preserve complete nasals, but impressions on the holotype and IGM 3/70 indicate that the nasals are paired and laterally in contact with the maxillae. The frontals are fused and have an interorbital constriction. The holotype shows a frontal shelf is present anteriorly to underlay the nasal and an anterolateral spike is developed between the nasal and prefrontal. The dorsal surface of the frontals is lightly ornamented with rugosities. The frontoparietal suture is transverse, with the parietal foramen slightly chipping the anterior margin of the parietal, but largely opening on the frontal side of the suture (see fig. 5A).

The parietal table is roughly trapezoidal, and the dorsal surface is weakly ornamented anteriorly with rugosities, as on the frontals. The maximum width of the parietal table is anteriorly at the frontoparietal suture and the minimum width at the posterior margin (slightly wider than half the width at the frontoparietal suture); therefore, the parietal table has no obvious constriction at the middle level. However, the parietal laterally develops a relatively deep flange, indicating a dorsal origin of the temporal muscle. As a distinct character of the species, the posterior margin of the table is symmetrically notched for the insertion of dorsal axial musculature (*spinalis capitis*). The supratemporal process of the parietal is slightly longer than the table and extends posterolaterally at a roughly 45° angle in relation to the midline of the skull. The process is strongly compressed laterally, having a dorsal crest and a deeply sloped lateral surface for attachment of temporal muscles.

The prefrontal has an elongate frontal process, which extends posteriorly along the lateral edge of the frontal to the midpoint of the dorsal border of the orbit. The new species shares this character with *Ctenomastax* (see above) and extant *Oplurus* (see Blanc, 1977: fig. 26), but the phylogenetic significance of this character state needs to be evaluated on the basis of a broader survey. Anterolaterally, the prefrontal forms a very weak prefrontal boss. The anteroventral (orbital) process is slightly concave anteriorly, forming the anterior wall of the orbit and ventrally contacts the widened palatine. This process medially borders the orbitonasal fenestra and laterally

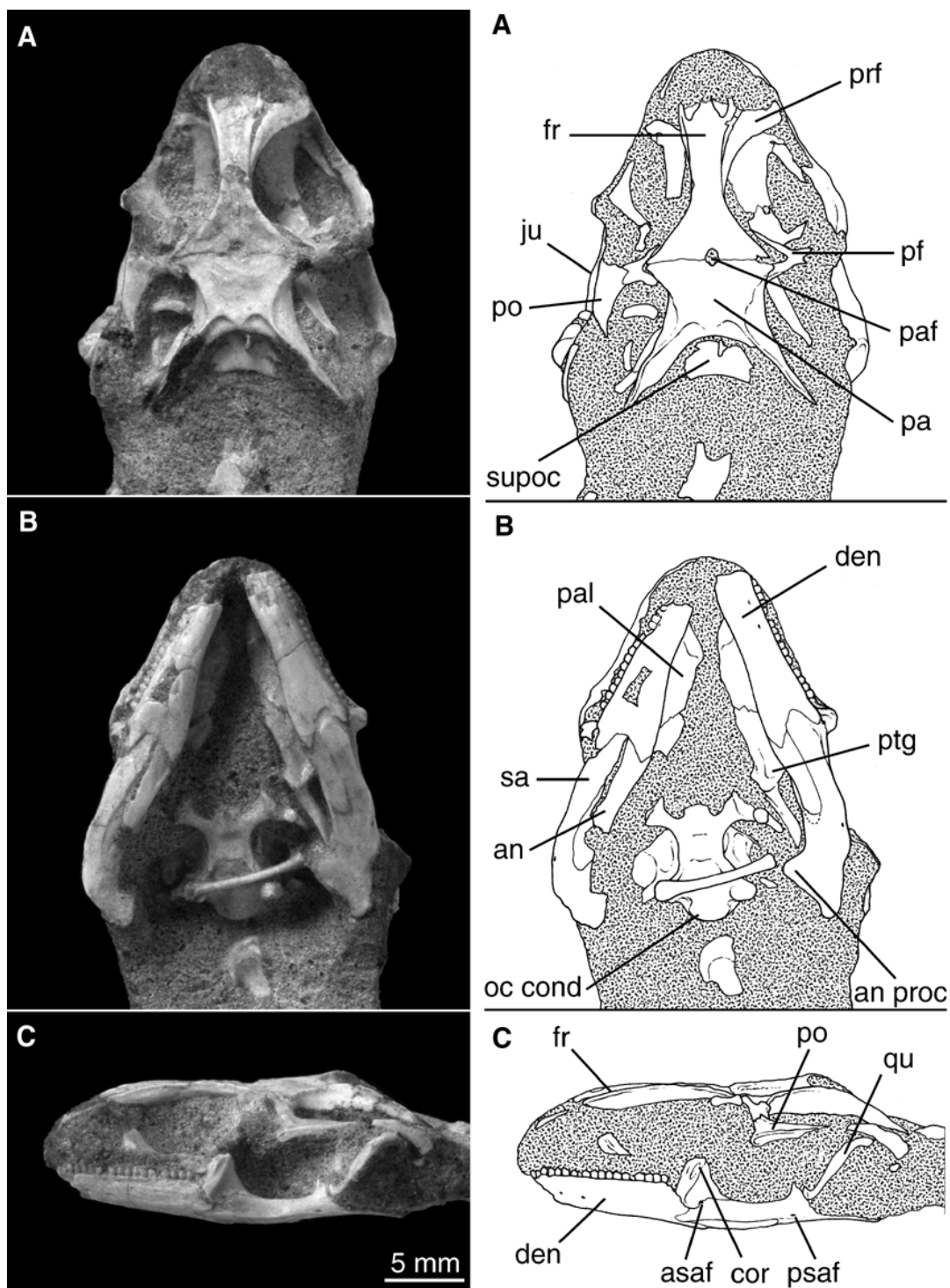


Fig. 5. *Temujinia ellisoni*, new genus and species: A–C, IGM 3/63 (holotype), incomplete skull with mandibles from Ukhaa Tolgod, dorsal, ventral, and lateral views.



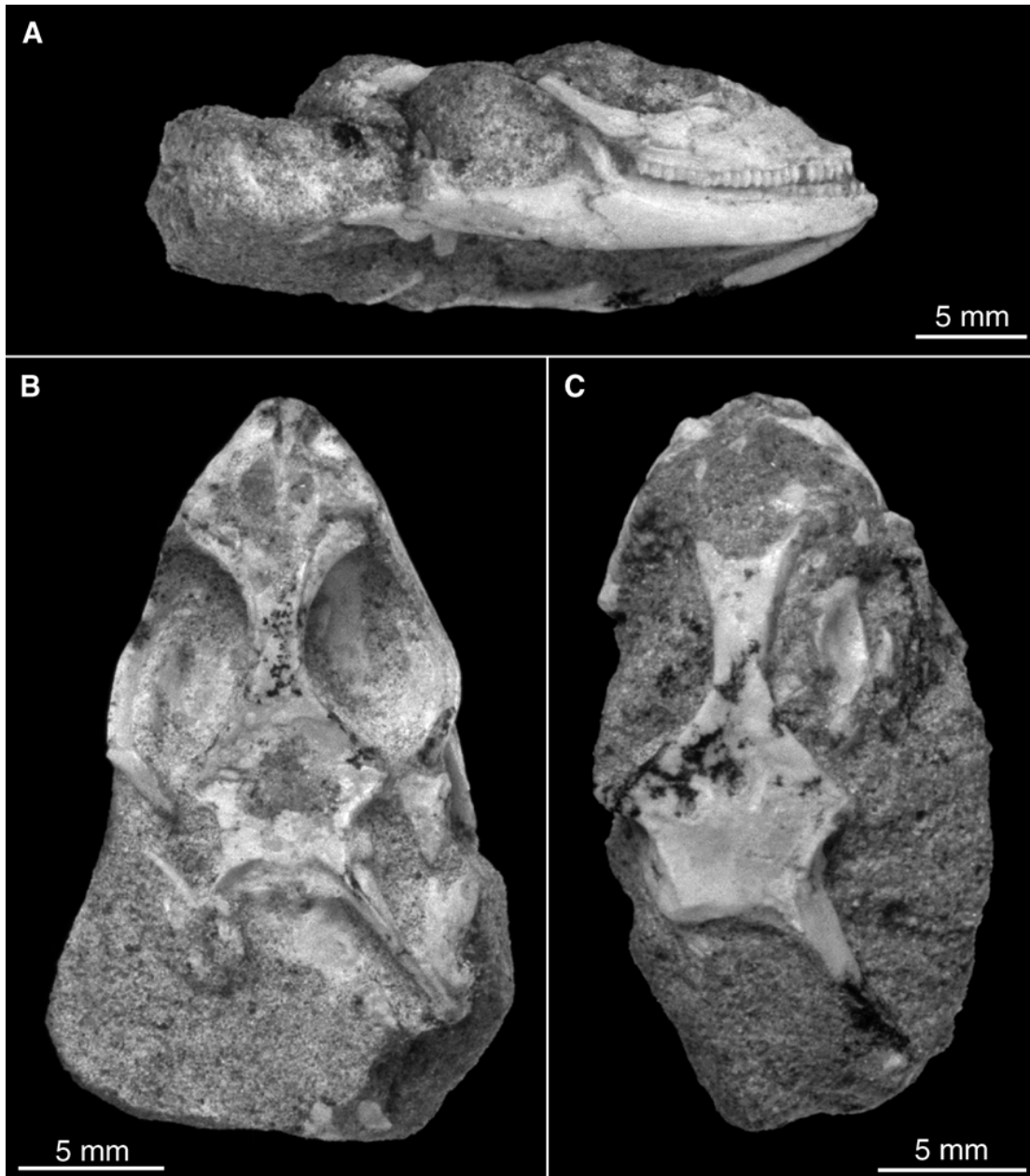


Fig. 6. *Temujinia ellisoni*, new genus and species (referred specimens, topotypic): **A**, IGM 3/69, incomplete skull with mandibles, right lateral view; **B**, IGM 3/64, incomplete skull with mandibles, dorsal view; **C**, IGM 3/65, incomplete skull with mandibles, dorsal view.

contacts the lacrimal bone. The lacrimal foramen is small, differing from the enlarged condition seen in acrodontans. The relationship of the prefrontal with the nasal is unclear, but at least the large part of the antero-

medial edge of the prefrontal is separated from the nasal by a slender anterolateral process of the frontal (figs. 5A, 6B).

The postfrontal and postorbital are clearly delimited by a V-shaped suture, and a small

wedge of the postorbital fits in the lateral edge of the postfrontal. The postfrontal is reduced, but is present as a slender bar separating the orbit from the supratemporal fenestra (not confined to the orbital rim); it is medially forked to clasp the frontoparietal suture. Such a postfrontal differs from that in extant iguanians, which is confined to the posterodorsal margin of the orbit (see de Queiroz, 1987; Estes et al., 1988). The posterior process is short and robust, fitting in a small notch on the parietal, but the anterior process is long and slender, almost twice the length of the posterior process. The body of the postfrontal is thickened and is more rod-like than platelike, differing from other iguanian species. The postorbital is subtriangular with a large, wide anterior process and a pointed posterior process that contacts the squamosal. The lateral edge of this element is slightly grooved for the posterodorsal process of the jugal, which contacts the anteroventral side of the squamosal (the posterior tip of the jugal process is preserved with the squamosal).

The squamosal is missing on the right side but completely preserved on the left. This element is also transversely expanded like the postorbital. It has no dorsal process, but its posterior end is hooked laterally in dorsal view. The supratemporal is not preserved on the holotype, but other specimens (e.g., IGM 3/66, 3/68) show a small splint, which lies between the squamosal and the supratemporal process of the parietal as in many other lizards.

The maxilla, jugal, and lacrimal are preserved on the right side of the holotype. These elements are also preserved on several referred specimens. The maxilla is relatively low and carries a dorsal process, the summit of which is slightly anterior to the midpoint of the tooth row. As in *Ctenomastax parva*, an anteromedial process of the maxilla contacts the opposite element behind the dorsal spine of the premaxillae (best shown in IGM 3/64, 3/68). The maxilla bears teeth and tooth spaces for 21–22 positions (see description of dentition below). The posterodorsal process of the jugal on the holotype is broken above the coronoid process and at the middle part of the postorbital rim. However, IGM 3/64 preserves a complete bar (see fig. 6B) that

extends first posterodorsally then nearly horizontally to contact the postorbital and the squamosal. The anteroventral process is mounted on the dorsal edge of the maxilla and forms most of the ventral rim of the orbit. Anterior to the jugal is a small lacrimal, which forms the anteroventral corner of the orbit.

**PALATAL ELEMENTS:** The vomers are not preserved on the holotype, but the articular surface on the palatine indicates the vomers are paired as in other iguanians except for chamaeleonids. The palatine has a vomerine process. Posteriorly the palatine is wide, forming most of the floor of the orbit. Anteromedially within the orbit, a small process meets its counterpart, forming the ventral border of the orbitonasal fenestra. Posteriorly it lacks sutural contact along the midline, leaving a narrow opening of the interpterygoid vacuity (pyriform recess of Oelrich, 1956; Estes et al., 1988). Anterolaterally within the orbit, a small lateral process of the palatine overlaps the palatal flange of the maxilla, and it is through this process that the infraorbital canal penetrates the palatine. The palatine contributes the anterior two thirds of the medial border of the suborbital fenestra, with the posterior one third formed by the pterygoid. As in many other lizards, the ectopterygoid forms both part of the posterior as well as the lateral border of the fenestra, and its anterolateral process does not extend to meet the palatine.

The anterior (palatine) process of the pterygoid has a wide base and contacts the palatine along a transverse suture when viewed dorsally. Ventrally, however, the suture is oblique with a short anterior extension of the pterygoid along the ventromedial edge of the palatine (fig. 5B). The short lateral process is articulated with the ectopterygoid, and ventrally forms a weak pterygoid flange. Dorsally near the base of the posterior (quadrate) process, a small socket (the fossa columella) is developed for the epipterygoid articulation. However, the epipterygoid on the holotype is displaced on both sides, so the ventral end of the left epipterygoid abuts the basiptyergoid process, and the right epipterygoid lies horizontally across the ventral surface of the basioccipital (fig. 5B). A deep notch, forming the synovial joint, lies slight-

ly anteroventral to the basiptyergoid process. As in many other lizards, the notch has an anterior buttress, preventing the process from sliding forward. Posterior to the joint, the laterally smooth and convex quadrate process is medially grooved, possibly allowing a sliding motion of the basiptyergoid process. The posterior end of the process becomes laterally compressed and extends to support the quadrate.

**BRAINCASE:** The braincase floor is well preserved on the holotype and several of the referred specimens (e.g., IGM 3/68). On the holotype, the basisphenoid is complete except for the parasphenoid process, which is missing, possibly because it was cartilaginous in life. The basiptyergoid process has a slender shaft but a strongly expanded condyle for articulation with the pterygoid. The main part of the basisphenoid has a small depression on its ventral surface, and carries a short posterolateral process extending to the base of the spheno-occipital tubercle. Owing to the development of this lateral process, the basisphenoid-basioccipital suture is laterally oblique rather than transverse. The basioccipital is roughly equivalent in size with the basisphenoid. Located laterally, at the midlevel of the basioccipital, the spheno-occipital tubercle is more ventrally than posteriorly directed. The occipital condyle is robust in relation to the size of the basioccipital. Corresponding lateral components of the exoccipital form two thirds of the occipital condyle, while a medioventral one third is composed of basioccipital.

Dorsolateral to the braincase floor is a deep and wide trough, which is the recessus vena jugularis (term of Oelrich, 1956). The lateral wall of the trough is formed by a well-developed crista prootica of the prootic, but the medial wall is composed of both the prootic and a dorsal extension of the basisphenoid (without contribution from the basioccipital). Anteriorly within the recessus, the posterior opening of the Vidian canal penetrates the basisphenoid and opens posterodorsal to the base of the basiptyergoid process. The facial foramen for the facial nerve (VII) opens on the arched roof of the recessus. More posteriorly, the foramen ovale opens dorsolateral to the spheno-occipital tubercle, and is separated from the occipital re-

cess by a prominent ridge (crista interfrenalis of Säve-söderbergh, 1947; Oelrich, 1956). Within the occipital recess, two openings are clearly identifiable: dorsal to the recess is a smaller foramen perilymphaticus, and deep in the recess is the larger foramen rotundum.

The lateral wall of the braincase lacks a clearly defined alar process of the prootic (best shown on IGM 3/68, 3/70), and thus the dorsal part of the epiptyergoid lays against the otic capsule directly (IGM 3/68). The alar process provides an origin of the pseudotemporalis profundus (see Oelrich, 1956). Lack of an alar process indicates fundamental differences in the development, or the origin, of these muscles compared to other iguanians that have this process. Ventral to the anterior semicircular canal, a weak trigeminal notch is developed as the passageway for the trigeminal nerve (V). Anteroventral to the notch, the inferior process of the prootic (best shown on IGM 3/70) is well developed and anteriorly sutures to the well-ossified pila antotica. The posterior process of the prootic is triangular, extending posterolaterally along the anterior surface of the paroccipital process and terminating near the tip of the process. Dorsally at the base of the posterior process, a minute foramen (?endolymphatic foramen) opens near the prootic-supraoccipital suture on the prootic.

In posterior view, the supraoccipital is hexagonal, having a very low occipital crest limited to the anterodorsal part of the bone. Part of the anterior and most of the posterior semicircular canals are covered by the supraoccipital. The posterior dorsal surface of the supraoccipital is a slightly convex and smooth slope, and its posterior edge is arched anteriorly as the dorsal rim of the foramen magnum. The supraoccipital is sutured laterally with the prootic and posterolaterally with the exoccipital. Lateral to the foramen magnum, the exoccipital serves multiple functions as in many other lizards: it forms a posterolateral wall of the braincase, the lateral border of the foramen magnum, the basal part of the paroccipital process (fused with the opisthotic), the posterior rim of the occipital recess, and part of the occipital condyle. In posterior view, the exoccipital forms a triangular surface, which medially sutures

with the spheno-occipital tubercle and laterally borders the occipital recess by its crista tuberalis (best shown on the holotype and IGM 3/68). Lateral to the occipital condyle, the triangular surface is penetrated by three foramina, which are arranged as a triangle: dorsally lies the foramen for the vagus nerve (X), and ventrally are two foramina for the hypoglossal nerve (XII). This condition is different from *Anolis carolinensis* and *Ctenosaura pectinata*, in which three rami of the hypoglossal nerve emerge through three separate foramina in the exoccipital bone (Willard, 1915; Oelrich, 1956).

**MANDIBLE:** The mandibles on the holotype are well preserved except for the anterior tips, which are missing due to breakage. In lateral view, the dentary makes up roughly the anterior half of the mandible, having a strongly convex lateral surface. The left dentary is better preserved than the right, and is broken anteriorly at the fourth or the fifth tooth position (determined by comparison with IGM 3/64). Posteriorly, the dentary is slightly notched for the short anterior extension of the surangular and angular. The posterior extremity of the dentary terminates at the level below the summit of the coronoid. The ventral border of the mandible is slightly flattened, as the jaw is not strongly compressed laterally, but is rather convex.

The coronoid has no lateral blade. Instead it displays a robust dorsal process with two prominent vertical ridges on its lateral surface for attachment of the mandibular adductor muscle. The surangular occupies the dorsal posterior half of the mandible and has an anterior process fitting into the posterior notch of the dentary together with the anterior process of the angular. The lateral surface of the surangular has a strong horizontal crest (adductor crest) for attachment of the jaw muscles. The anterior surangular foramen (figs. 5C, 6A) is located dorsal to the crest and right at the coronoid/surangular suture posteroventral to the dorsal process of the coronoid. The posterior surangular foramen is much smaller than the anterior foramen (about half the size of the latter), and is located below the adductor crest and anteroventral to the craniomandibular joint. Posterodorsally, the surangular bears a promi-

nent dorsal process, which forms the anterior buttress for the craniomandibular joint.

The angular is a narrow tonguelike element exposed ventral to the surangular. Anteriorly it fits into the posterior notch of the dentary below the surangular, and posteriorly it terminates well anterior to the angular process and ventral to the posterior surangular foramen. Sharply different from the condition in *Anchaurosaurus gilmorei*, the angular in this species forms part of the ventral border of the postdentary part of the jaw, but is not exposed on the medial side of the jaw.

In medial view, the anterior one third of the Meckelian canal on the holotype is closed by a strong medial and upward enrolling of the ventral edge of the dentary; however, the enclosure of the dentary tube is unfused. Most of the referred specimens consistently show the same morphology as the holotype, but IGM 3/69 has the canal slightly open medially. The splenial is reduced, restricted to the posterior two thirds of the Meckelian canal. Posteriorly, it terminates at the same level as the posteroventral process of the dentary. The anterior inferior alveolar foramen and the anterior mylohyoid foramen penetrate the splenial close to the midpoint of the tooth row.

The mandibular fossa is a very narrow and elongate slit, opening horizontally between the prearticular and the surangular; it has an anterior border immediately behind the posteroventral process of the coronoid and posteriorly extends to a point below a prominent process of the surangular anterior to the craniomandibular joint. At the posterior end of the mandible, the prearticular is entirely fused with the articular and is partially fused with the surangular; only a short suture posterior to the angular can be delimited from the latter element. Medial to the craniomandibular joint, the prearticular bears a wide and strong angular process, which is perpendicular to the retroarticular process in direction. The retroarticular process is best preserved on the holotype and IGM 3/69 (figs. 5B, 6A). Both the specimens show that the process is posteriorly directed, having its lateral border curved medially at the base.

**DENTITION:** The premaxillary teeth are not preserved on the holotype, but other specimens (e.g., IGM 3/64, 3/68) show that the



fused premaxilla carries five to six unicuspid teeth. The maxillary teeth are best preserved on IGM 3/69, which shows a nearly complete tooth row containing 20 positions. A complete maxillary tooth count can be estimated as 22 based on comparison of this specimen with IGM 3/64. The dentary teeth are best preserved on the holotype and IGM 3/69, and a complete dentary tooth row as shown on the latter specimen contains a total of 25 positions.

The tooth attachment is pleurodont, having about two thirds of the columnar tooth shaft attached to the relatively deep lateral parapet of the jaws. The teeth in lateral view have short crowns. The first two or three maxillary teeth are unicuspid, followed by several bicuspid teeth, then well-defined tricuspid teeth in the middle and posterior part of the tooth row. The tricuspid crowns are laterally swollen, having a prominent central cusp and smaller but symmetrical lateral cusps (see figs. 5C, 6A). From anterior to posterior along the tooth row, the teeth become increasingly stouter and the tricuspid cusps become more pronounced.

#### COMPARISON AND DISCUSSION

Recognition of the new taxon *Temujinia ellisoni* is primarily based on the holotype. Several specimens (e.g., IGM 3/68, 3/69, 3/70) can be confidently referred to the same species, whereas the referral of several other specimens (IGM 3/65, 3/66, 3/67) to the species is tentative. In comparison with the holotype, the latter three skulls are more slenderly built with a more pointed snout. However, these specimens possess most of the diagnostic features of the species (see above), supporting referral to the same species as the holotype. IGM 3/65 shows a frontal tab overlapping the parietal (indicating a less movable frontoparietal hinge) and the parietal foramen opens within the frontal tab (see fig. 6C). However, because this is the only specimen showing this feature and the other two specimens with similar skull configurations are poorly preserved, we cannot determine the significance of this feature.

The new species *Temujinia ellisoni* is clearly referable to the Iguania on the basis of the following diagnostic characters of the

group (see Estes et al., 1988 for evaluation): frontals are fused and constricted between orbits; frontal shelf anteriorly underlies the nasals, with frontals exposed anterolaterally as prominent spikes; prefrontal bosses are present; postfrontal is reduced; parietal foramen is displaced anteriorly; and the presence of an angular process of the mandible. Possession of these iguanian synapomorphies, but lack of acrodontan autapomorphies (see Estes et al., 1988) indicate the nonacrodontan position of the new taxon within the Iguania.

Compared with other nonacrodontan iguanians from the Gobi, this taxon differs from *Anchaurosaurus* (Gao and Hou, 1995, 1996) in having the frontal process of the prefrontal extended to the middle level of the orbit, much weaker frontal bosses, and short-crowned and swollen teeth. It differs from *Igua* and *Polrussia* in having a short, trapezoidal parietal table with longer supratemporal process, and differs from the above-described *Ctenomastax* primarily in having short-crowned and tricuspid teeth.

Compared with extant nonacrodontan iguanians, it is worth noting that the new species shares the following characters with the Madagascan *Oplurus* (see Blanc, 1977): the frontal process of the prefrontal is strongly elongate; the parietal table is short and trapezoidal, with a lateral flange extending onto the lateral surface of the supratemporal process; the palatal elements are expanded transversally; the mandibular fossa opens as an elongate narrow slit. The phylogenetic significance of these shared characters merits further investigation.

One interesting cranial feature displayed in *Temujinia ellisoni* is the forked postfrontal (see also description of *Ctenomastax parva*). A forked postfrontal that clasps the frontoparietal suture is absent in extant iguanids and this character has been interpreted as a synapomorphy of Scleroglossa (Estes et al., 1988; Scincogekkonomorpha of Sukhanov, 1961). However, presence of such a forked condition in the Late Cretaceous iguanids from the Gobi indicates that the status of this character in squamate evolution requires reevaluation. As these may represent basal iguanians, the forked condition may well be a primitive state for lizards generally, and the

nonforked condition in extant iguanians is probably a derived condition within the clade.

Another notable feature about this new taxon is the maxillary contact behind the premaxillary spine. Among the Late Cretaceous iguanians from the Gobi, both *Temujinia elisoni* and *Ctenomastax parva* show such a contact. As discussed above, occurrences of such a contact in these Cretaceous nonacrodontan iguanians raise the question about the apomorphic status of the character for acrodontans and indicate that the character merits further evaluation.

***Zapsosaurus sceliphros*,**  
new genus and species

Figure 7

ETYMOLOGY: *zaps* + *sauros* (Gr., m.), meaning storm lizard; *skeliphros* (Gr.), meaning thin or slender, in reference to the lightly built skull of the new species.

HOLOTYPE: IGM 3/71 (MAE 255/92-10), incomplete skull articulated with mandibles.

TYPE LOCALITY AND HORIZON: Tugrueen Shireh, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Jerzykiewicz et al., 1993; Fastovsky et al., 1997).

KNOWN DISTRIBUTION: Only known from the type locality and horizon.

DIAGNOSIS: Distinguished from possibly closely related *Anchaurosaurus gilmorei* by having the following character states: prefrontal bosses weakly developed; posterior border of parietal strongly flanged for attachment of axial musculature; Meckelian canal closed below anterior three-fourths of tooth row; splenial strongly reduced, covering only posterior one fourth of Meckelian canal; lateral surface of coronoid dorsal process bears vertical crest associated with a ventral tubercle; presence of distinct medial flange of surangular anteromedial to craniomandibular joint; mandibular fossa strongly shortened, posteriorly terminating halfway between coronoid and craniomandibular joint; marginal teeth having short shafts, but strongly flared crowns.

REFERRED SPECIMEN: IGM 3/72 (MAE 20/93-15), left upper and lower jaws (topotypic).

DESCRIPTION

**SKULL ROOF:** The holotype skull is undistorted and is preserved in a dark brown coarse-grained sandstone concretion. The premaxillae are not preserved on the holotype or the referred specimen. The left nasal is incompletely preserved, but is the only remnant of this element present. Its posterior end is slightly displaced ventral to the frontal; however, a depression clearly indicates that the frontal has an anterior tab, which is overlapped by the nasal as in other iguanians. The fused frontals are more slender than in *Anchaurosaurus gilmorei*, and the frontoparietal suture is slightly posterior to the level of the coronoid process of the lower jaw. As in *Anchaurosaurus gilmorei*, the parietal foramen opens at the frontoparietal suture, but is significantly enlarged on the parietal side. Only an anterior rim occurs on the frontal (fig. 7C). The parietal table is short and trapezoidal. It differs from *Anchaurosaurus gilmorei* in having a strongly developed posterior shelf or flange, which is divided by a weak median ridge and is laterally extended onto the base of the supratemporal process. The process is slender and strongly elongate, bearing a sharp dorsal crest. Attached to the posterolateral surface of the supratemporal process, the supratemporal bone is a much stronger element than in *Anchaurosaurus gilmorei*, and it has a flat dorsal surface.

The prefrontal is preserved on both sides. It has a weak prefrontal boss, contrary to the strong lateral projection seen in *Anchaurosaurus gilmorei* (see Gao and Hou, 1995: fig. 1). Posteromedially, the prefrontal has a slender frontal process whose posterior extent lies at the midlevel of the orbit. The postfrontal is probably separated from the postorbital (indicated by the articular surface on the frontal), but the actual status of this element cannot be ascertained because of poor preservation. Extant nonacrodontan iguanians normally retain a reduced postfrontal (Estes et al., 1988). A comparison with *Anchaurosaurus gilmorei* is impossible, as this region of the skull is not preserved on any known specimens of the latter species.

The squamosal is incompletely preserved on the right side, and it has been slightly displaced medially. The bone has a broad pos-

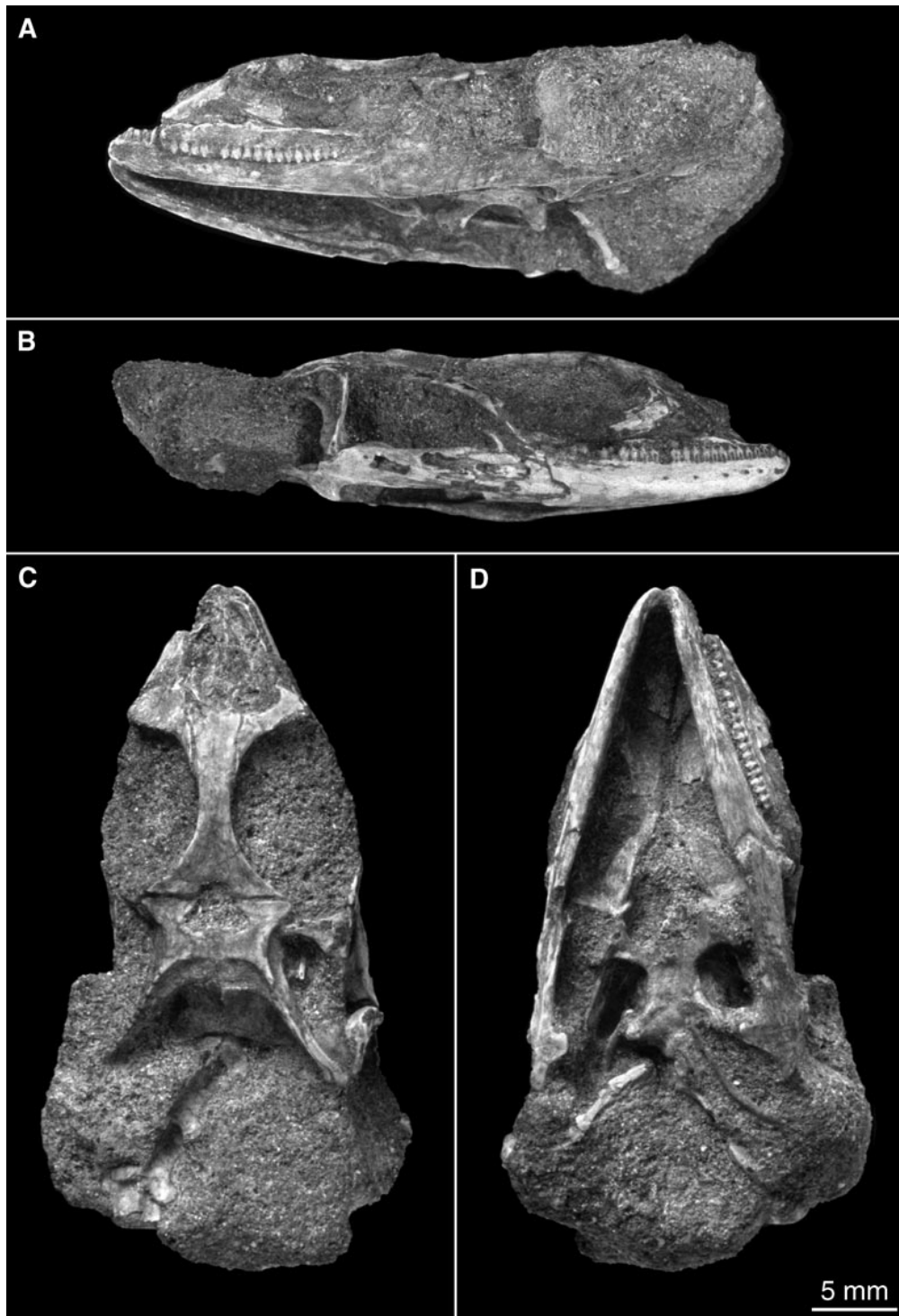


Fig. 7. *Zapsosaurus sceliphros*, new genus and species: **A–D**, IGM 3/71 (holotype), incomplete skull with mandibles from Tugrugeen Shireh, lateral, dorsal, and ventral views.

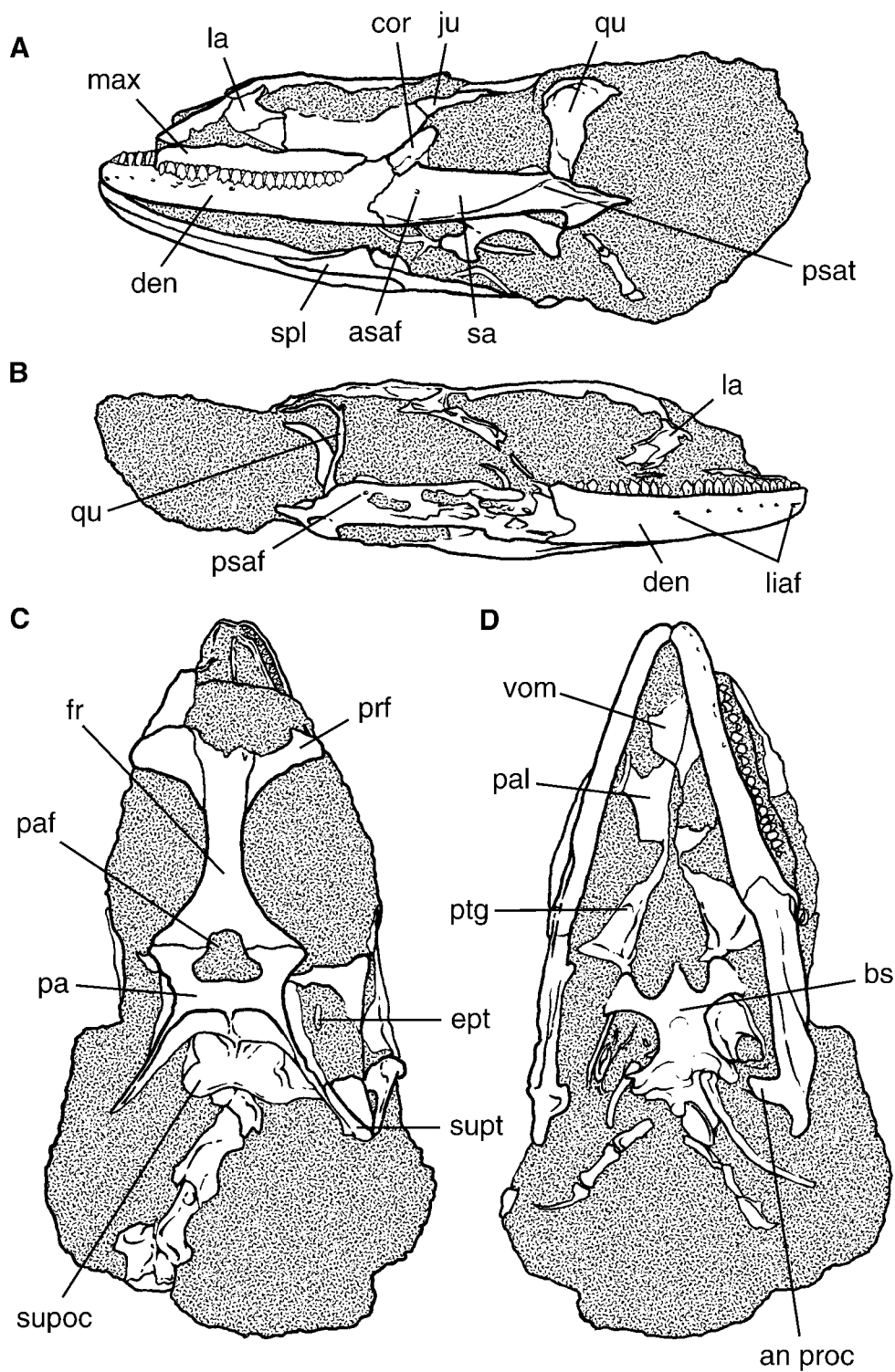


Fig. 7. Continued.



terior end, limiting the size of the supratemporal fenestra. Because the bone is poorly preserved, the contact of this element with the postorbital and the jugal cannot be identified. The quadrate is straight and is more slender than in *Anchaurosaurus gilmorei*. The cephalic condyle expands strongly medioposteriorly to form a triangular table and has a well-developed foramen penetrating its dorsal surface. The anterolateral surface of the quadrate is smooth and slightly convex. The quadrate foramen opens above the ventral condyle on this surface. However, the anteromedial surface is strongly concave to form a wide and vertical groove dorsal to the ventral condyle. In lateral view, the tympanic crest is thin, straight, and vertical. The tympanic crest is oriented at a 90° angle to the horizontal lateral border of the cephalic condyle, giving the lateral crest for the tympanic membrane an L-shape. The posterior surface of the quadrate is divided into two surfaces by a vertical posterior crest, which is weakly arched anteriorly. The lateral part is strongly concave to form a deep fossa, and the medial part is slightly concave and forms an inverted triangular-shaped surface as the medial crest diminishes ventrally. The posterior opening of the quadrate foramen penetrates the medial surface on the lower one third of the bone, close to the posterior crest. The ventral condyle is transversely expanded and is saddle-shaped with a concave ventral surface. The right epipterygoid is preserved and exposed in dorsal view (fig. 7C). It attaches to the lateral surface of the prootic, but its contact with the parietal cannot be confidently determined as the bone may have been slightly displaced posteriorly.

Only the left maxilla is preserved, and it is incomplete. It has a low dorsal process that bends medially to contact the nasal, prefrontal, and the anterolateral process of the frontal. The posterior border of the process is notched for a well-developed lacrimal. The posterior process of the maxilla has a nearly transverse suture with the jugal, and in this aspect differs from *Anchaurosaurus gilmorei* (see Gao and Hou, 1995: fig. 1). The maxilla has 18 well-preserved teeth, and probably four to five additional anterior teeth are missing owing to breakage (see below).

The jugal is broken on the left side, but a

clear impression allows the morphology of this element to be described. Its anteroventral process is relatively deep, roughly rectangular, and forms the ventral border of the orbit together with the lacrimal. The posterodorsal process forms the posterior bar of the orbit and dorsally contacts the postorbital.

**PALATAL ELEMENTS:** All of the palatal elements are toothless (fig. 7D). Better preserved on the right side than the left, the vomers are paired and slightly elongate. The palatines are wide, but have no midline contact. The suborbital fenestra is slightly elongate, extending to the midlevel of the palatine. The fenestra is medially bordered by the palatine and the pterygoid, and is laterally bordered by the maxilla and the ectopterygoid. The ectopterygoid in palatal view has a triangular base, which is sutured medially with the widened pterygoid, and has a ventral process forming small part of the weakly developed pterygoid flange. The ectopterygoid forms the posterior border of the suborbital fenestra, and the anterolateral process extends to the midlevel of the suborbital fenestra. The pterygoid has an elongate palatine process, which thins anteriorly and is sutured to the palatine along its medial edge to form the medial border of the interpterygoid vacuity. The posterior part of the process broadens and has an oblique lateral edge for articulation with the palatine. The posterior edge of the lateral process inflects dorsally to form the pterygoid flange. The quadrate process is essentially a blade that is convex laterally and concave medially. Like in many other iguanians, a notch is developed medially at the base of the process that forms the joint with the basiptyergoid process of the basisphenoid. The posterior extremity of the process becomes a slender blade, attaching to the medial border of the quadrate.

**BRAINCASE:** The basisphenoid and the basioccipital form the braincase floor. These elements are unfused and separated by a clear suture (fig. 7D). The base of the rostrum of the basisphenoid is slightly thickened, and has a small depression posterior to it. Anterolaterally, the basiptyergoid process is short, but has a strongly expanded condyle directed anterolaterally at a 45° angle to the midline. Posterolaterally, the basisphenoid bears a short process attaching to the ventral

surface of the basioccipital and extending to the base of the sphenoccipital tubercle. The basioccipital forms the posterior part of the floor and ventral part of the lateral wall of the braincase, and a major part of the occipital condyle.

Dorsolateral to the floor of the braincase, the recessus vena jugularis is well preserved on both sides of the holotype. The lateral wall of the recessus is formed by the prootic with a sharp crest (crista prootica), but the medial wall is formed by three elements: dorsally by the prootic and ventrally by the basisphenoid and basioccipital. A posterior opening of the Vidian canal penetrates the medial wall of the recessus. It opens between the base of the basipterygoid process and the basisphenoidbasioccipital suture, with no involvement from the prootic. A small facial foramen penetrates the prootic and opens on the medial wall of the recessus. The foot of the right stapes as preserved covers the foramen ovale, but the shaft is not preserved. The foramen ovale is located dorsal to the occipital recess. A slender bone extends posteriorly from the occipital recess. Although similar in position to the stapes, it is long and slightly curved, indicating it is a dislocated hyoid element. Another hyoid element is preserved on the left side posteroventral to the braincase floor.

Most of the occipital aspect of the skull is not exposed, because the skull is articulated with several cervical vertebrae. However, some features of the occiput can be observed from dorsal and ventral views. In dorsal view, the supraoccipital carries a weakly developed median crest for attachment of the ligamentum nuchae (Oelrich, 1956). Laterally parallel to the crest, the posterior semicircular canal swells dorsally, but no suture can be delimited between the supraoccipital and the exoccipital. In ventral view, the paroccipital process is shorter than in *Anchaurosaurus gilmorei* and extends more laterally than posteriorly. The fissurelike vague foramen (for cranial nerves X, XI) and the rounded hypoglossal foramen (for cranial nerve XII) are very close to one another, and are both located dorsolateral to the occipital condyle.

**MANDIBLE:** The mandibles are well preserved on both sides, with slight damage to the right coronoid and the postdentary region. In

lateral view, the dentary has a smooth surface and carries seven mental foramina. The last foramen is located at the midlevel of the tooth row. Like in *Anchaurosaurus gilmorei* (Gao and Hou, 1995), the dentary is posteriorly bifurcated and notched for the blunt surangular, with little involvement of the angular bone. The posterodorsal (coronoid) process is shorter but stronger than the posteroventral (Meckelian) process, which extends on the ventral border of the jaw and wedges between the surangular and the angular. The coronoid has a lightly built dorsal process, the lateral surface of which carries a vertical crest for the external jaw adductor. This crest ventrally ends with a prominent process. This condition is different in *Anchaurosaurus gilmorei*, where the coronoid process is robust, lacks a vertical crest, but has a low and robust tubercle. Like in *Anchaurosaurus gilmorei*, the coronoid of the new species has no lateral blade, but a small wedge between the dentary and the surangular.

The surangular occupies most of the postdentary part of the jaw in lateral view. It has a large lateral surface and a prominent crest for the attachment of the jaw adductor muscle. As in *Anchaurosaurus gilmorei*, the anterior surangular foramen is located in a low position anteriorly in the middle of the bone, and the posterior surangular foramen opens on the crest posteriorly near the craniomandibular joint (fig. 7A, B). The angular is incompletely preserved on the left side, and left clear impressions on the right. This element is small and barely exposed in lateral view. It wedges between the surangular and the prearticular in ventral view and between the dentary and the splenial in medial view. The angular foramen (preserved on the left side) is extremely small, and opens on the medial side of the jaw close to the posterior end of the splenial. The prearticular (fused with the articular) is the second largest element of the postdentary part of the jaw. Its contact with the surangular and the posteroventral process of the dentary is exposed, as the angular bone that normally covers this suture is not preserved. The prearticular medially carries a prominent and slightly hooked angular process, and a posteriorly directed retroarticular process. The articular fossa for the mandibular joint with the quadrate condyle lacks an anterior or posterior buttress, therefore, the joint seems to be more freely

movable. Posterior to the jaw joint, the retroarticular process is weakly developed and posteriorly directed. The dorsal surface of the process is concave, but has no foramina opening in it.

In medial view, the anterior three-fourths of the Meckelian canal is closed, without fusion of the dentary tube. The anterior end opens near the symphysis. The posterior one fourth of the canal is medially covered by a greatly reduced splenial, which has its posterior extension terminating anterior to the angular foramen. The anterior process of the surangular extends and wedges between the splenial and the anteroventral process of the coronoid. The dorsal rim of the surangular is anteriorly rounded as commonly seen in other lizards, but posteriorly a distinct flange is strongly developed anteromedial to the craniomandibular joint and above the mandibular fossa (fig. 7C). Such a strong flange is absent in other lizards. Functionally, this flange may serve as an insertion of the pterygomandibularis muscle (see Oelrich, 1956). Also different from *Anchaurosaurus gilmorei* (see Gao and Hou, 1995: fig. 1), the mandibular fossa in *Zapsosaurus sceliphros* is strongly reduced into a short and shallow groove, extending only to the midpoint between the coronoid process and the craniomandibular joint.

**DENTITION:** The morphology of the marginal teeth is best observed on the incomplete left maxilla, which has 18 tricuspid teeth preserved. The teeth are much shorter and more slender than in *Anchaurosaurus gilmorei*, and the crowns are more strongly flared, having the small lateral cusp separated from the prominent central cusp by a clearly defined groove (fig. 7A). Owing to breakage of the maxilla, a complete tooth count of the upper dentition cannot be obtained, but can be estimated at 23–24 teeth. The right dentary contains 27 positions for the complete tooth row, and these are all tricuspid except for the anteriormost five that are unicuspid. The number and morphology of the premaxillary teeth cannot be determined.

**VERTEBRAE:** On the holotype (IGM 3/71), the first three cervicals (the atlas-axis complex and the third vertebra) and part of the fourth are preserved in articulation. The atlas is a simple ringlike structure, the elements of which remain unfused. The axis is elongate

and has a low but well-developed crown, which extends posteriorly and overlaps part of the third cervical. Each of the cervicals has a well-defined ventral keel.

Several caudals are preserved in association with the skull. Two anterior caudals are dislocated to the left orbit, and each of these shows an autotomy fracture posterior to a single pair of transverse process. This condition corresponds with the so-called “*Sceloporus*-type” of caudal autotomy as described by Etheridge (1967).

#### COMPARISON AND DISCUSSION

The new taxon shares several characters with *Anchaurosaurus gilmorei* including: skull elongate with relatively pointed snout; parietal table trapezoidal, but with long, slender supratemporal process; parietal foramen opens at the frontoparietal suture, but is enlarged on the parietal side. These indicate a close relationship of the two forms. However, *Zapsosaurus sceliphros* is clearly distinguishable from *Anchaurosaurus gilmorei* by the characters listed in the diagnosis.

Both *Zapsosaurus sceliphros* and *Anchaurosaurus gilmorei* are relatively large lizards in comparison with other Cretaceous iguanians known from the Gobi. These taxa are from the same geological formation (Djadokhta Formation), but do not co-occur at the same localities. *Anchaurosaurus gilmorei* is known from Bayan Mandahu near the southern border of the Gobi, and *Zapsosaurus sceliphros* from the Tugrugeen Shireh locality, which is some 400 km northwest of the former locality.

Although Gao and Hou (1995) noted that *Anchaurosaurus gilmorei* shares 11 character states with crotophytines, the relationships of *Anchaurosaurus gilmorei* and *Zapsosaurus sceliphros* to other iguanians are unclear. Alifanov (1996) classified *Anchaurosaurus* in the Crotophytidae together with the Eocene *Arretosaurus* Gilmore, 1943. Examination of the known material of *Arretosaurus*, including the holotype (AMNH 6706), indicates no shared derived character states supporting the grouping of these taxa in the same family. Until a thorough study of the phylogenetic relationships of the Gobi and other basal ig-

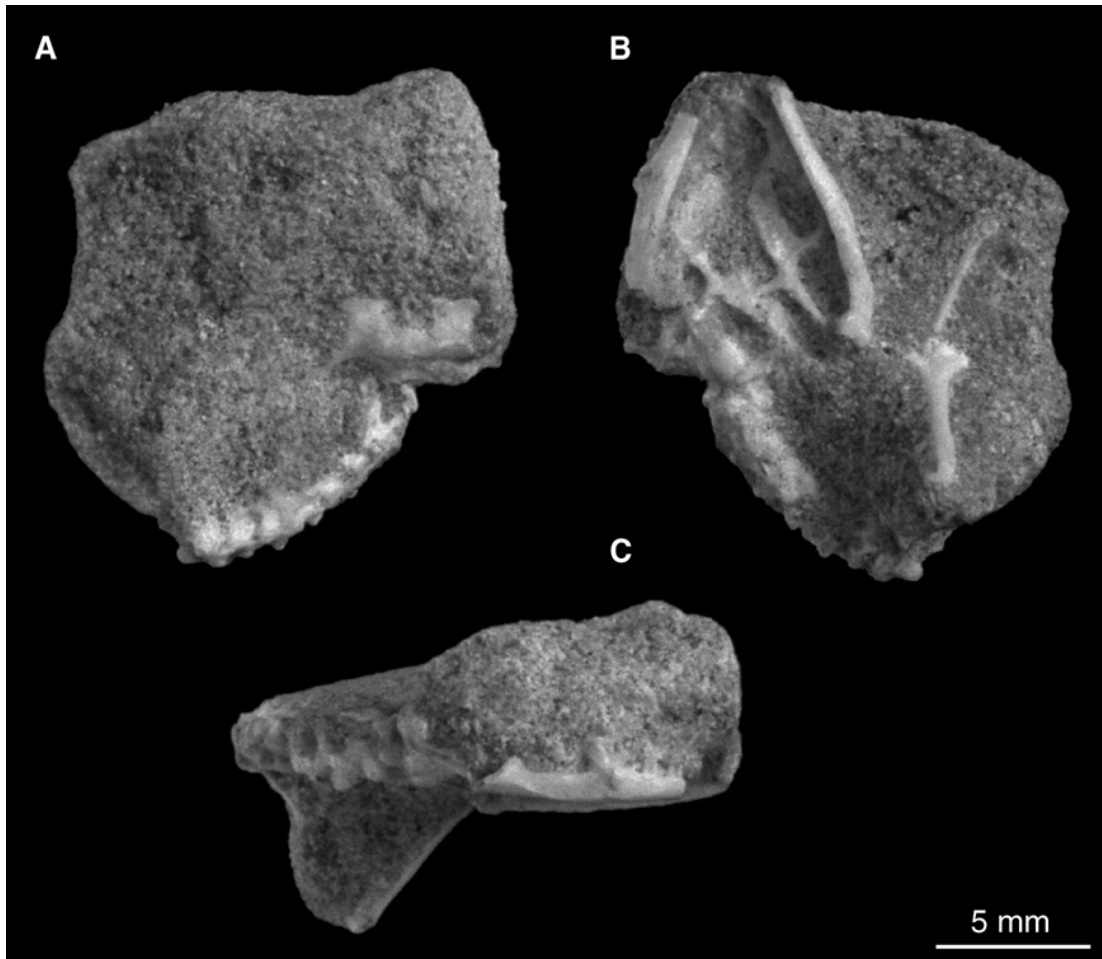


Fig. 8. *Polrussia mongoliensis*: A–C, IGM 3/73, incomplete skull articulated with mandibles and cervical vertebrae, dorsal, ventral, and lateral views.

uanians is completed, the interrelationships of several nonacrodontan iguanians including *Anchaurosaurus* and *Zapsosaurus* remain unclear.

*Polrussia mongoliensis*

Borsuk-Bialynicka and Alifanov, 1991

Figure 8

HOLOTYPE: ZPAL MgR-I/119, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khulsan, Nemegt Basin, Mongolia; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Known only from the type locality and horizon.

REVISED DIAGNOSIS: Distinguished from

other nonacrodontan iguanians by the following derived character states: frontals slenderly elongate and strongly narrowed; spheno-occipital tubercle greatly reduced as remnant knob; splenial retracted to slightly anterior to posterior end of tooth row; Meckelian canal entirely closed by fusion of dentary tube; posterior extension of dentary terminates at level of dorsal process of coronoid; marginal teeth having slenderly cylindrical shafts and pointedly unicuspid crowns.

REFERRED SPECIMEN: IGM 3/73 (MAE 219/92-45), partial skull with mandibles and cervical vertebrae; collected from Khulsan.

REMARKS: IGM 3/73 is referred to *Polrussia mongoliensis* based on several diagnostic



features of the species shown on the specimen: the splenial is retracted to slightly anterior to the posterior end of the dentary tooth row; the Meckelian canal is entirely closed by fusion of the dentary tube; posterior extension of the dentary terminates at the level of the coronoid dorsal process; and the marginal teeth are slenderly built, with pointed, unicuspid crowns.

Although fragmentary, IGM 3/73 is only the second specimen (other than the holotype) known for the species. The new specimen reveals some unknown morphology and clarifies some uncertainties about the species. The configuration of the parietal is uncertain on the holotype, but the new specimen shows the element is rectangular and has an unossified region indicating a fontanelle. In palatal view, the new specimen shows no midline contact of the palatines, contrary to the speculation "judging from the position of the right bone" on the holotype (Borsuk-Bialynicka and Alifanov, 1991: 338). Also from the new specimen, the pterygoid teeth are retained, but palatine teeth are absent. The sphenoccipital tubercle is greatly reduced into a small knob.

Regarding the relationships of *Polrussia mongoliensis*, Borsuk-Bialynicka and Alifanov (1991: 340) stated that "on the basis of the present knowledge the Opluridae, nonanole Polychridae, Tropidurinae and Leiocephalinae may not be excluded as possible relatives of *Polrussia*." It is worth noting, however, that *Polrussia mongoliensis* shares with *Igua minuta* at least one character state: the parietal is rectangular with a large fontanel. Pending an actual phylogenetic analysis, this character state may indicate a closer relationship of the two species.

#### ACRODONTA COPE, 1864

**DEFINITION:** The most recent common ancestor of extant Agamidae\* and Chamaeleonidae and all of its descendants (Estes et al., 1988; see Frost and Etheridge, 1989; see also remarks below).

**DIAGNOSIS:** The Acrodonta as above defined can be diagnosed by some 13 derived character states (see Estes et al., 1988 for list of characters and citations).

**REMARKS:** The Acrodonta include two fa-

miliar level subgroups: the Agamidae\* and the Chamaeleonidae, with the latter subgroup being considered to be the "offshoots of agamid stock" (Camp, 1923). The monophyly of the Chamaeleonidae is well supported (Estes et al., 1988; Frost and Etheridge, 1989), but monophyly of the Agamidae\* is uncertain (Frost and Etheridge, 1989).

Several lizard taxa from the Gobi Desert as described below are tentatively placed in the Acrodonta, as they all have acrodont dentition; however, they seem to form a monophyletic clade (see below) that may not be part of the crown-group Acrodonta. A thorough phylogenetic analysis with incorporation of these Gobi taxa is badly needed, and following the results of such an analysis, current classification of the acrodontan lizards may have to be revised.

#### PRISCAGAMINAE BORSUK-BIALYNICKA AND MOODY, 1984

The Priscagaminae are a group of acrodontan iguanians known from the Upper Cretaceous deposits in the Gobi Desert. The group includes *Mimeosaurus*, *Priscagama*, *Phrynosomimus*, and possibly *Pleurodontagama* (see Alifanov, 1996 for different classification of these taxa). The possible monophyly of the group is supported by the following potential synapomorphies: dermal roof elements of skull ornamented with small, rounded tubercles (Borsuk-Bialynicka and Moody, 1984); lateral coronoid process present as platelike and ventrally extended flap (Borsuk-Bialynicka and Moody, 1984; Gao and Hou, 1995); both anterior and posterior mylohyoid foramina present on medial side of jaw (Borsuk-Bialynicka and Moody, 1984).

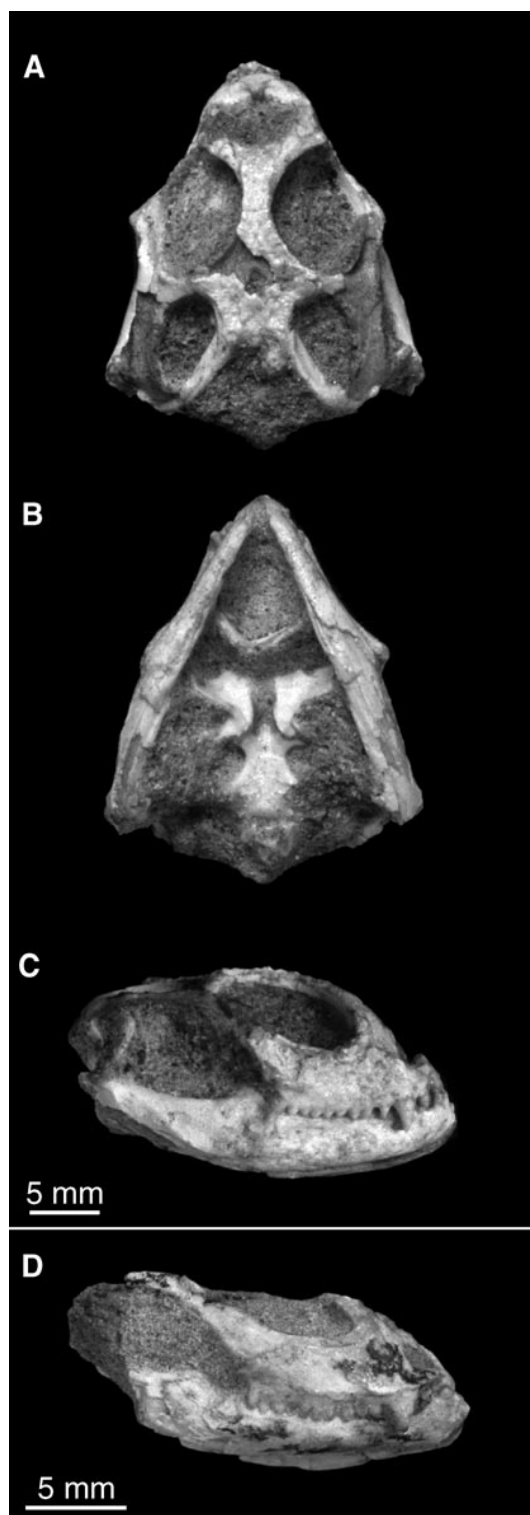
#### *Mimeosaurus crassus* Gilmore, 1943

Figure 9

**HOLOTYPE:** AMNH 6655, left maxilla fused with jugal.

**TYPE LOCALITY AND HORIZON:** Bayn Dzak (Shabarakh Usu), Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (see Gilmore, 1943).

**KNOWN DISTRIBUTION:** Bayn Dzak, Ukhaa Tolgod, Zos Wash, Bayan Mandahu localities



(Gilmore, 1943; Gao and Hou, 1996; this paper); Djadokhta Formation.

**REVISED DIAGNOSIS:** Distinguished from other acrodontan iguanians by having the following derived character states: strong reduction of premaxilla; maxilla short, deep, and subrectangular in fusion with jugal; maxillary tooth row short, straight, with first two teeth conspicuously enlarged and caninelike; lateral process of coronoid flattened with distinct vertical crest anteriorly.

**REFERRED SPECIMENS:** IGM 3/74 (MAE 83/93-89), IGM 3/75 (MAE 63/93-153); both incomplete skulls with mandibles and both from Ukhaa Tolgod. IGM 3/76 (MAE 96-105), incomplete skull with mandibles from the Zos Wash locality.

**REMARKS:** Although known since the 1940s, only a few well-preserved skulls of *Mimeosaurus crassus* have been collected. The new specimens from Ukhaa Tolgod and the adjacent Zos Wash locality, together with those collected from Bayan Mandahu (Gao and Hou, 1995), consistently display a unique set of characters. We emend the species diagnosis, accordingly (see above).

The new specimens reveal important new information about the skull morphology and dentition of this iguanian species. Well-preserved skulls (e.g., IGM 3/76 from Zos Wash) show a remnant postfrontal hidden beneath the posterior rim of the orbit (fig. 9A). Comparison with the holotype (AMNH 6655) not only confirms the referral of these new specimens to this taxon, but also reveals that this lizard had a conspicuously heterodont dentition. As Gilmore (1943) originally described, the first two maxillary teeth are enlarged and caninelike, with the second being the largest; however, some specimens (e.g., IGM 3/75, 3/76; see fig. 9C, D) show that this type of heterodonty is more conspicuous than others (the anterior dentary teeth are strongly protruding anterior to the

←

Fig. 9. *Mimeosaurus crassus*: A–C, IGM 3/76, incomplete skull with mandibles from Zos Wash, dorsal, ventral and lateral views; D, IGM 3/75, fragmentary skull with mandibles from Ukhaa Tolgod, right lateral view.

premaxilla), suggesting that the variants may represent different sexes.

Based on a single very fragmentary skull (PIN No. 3143/102) from Tugrugeen Shireh (Tugrikin-Shireh) in the Djadokhta Formation, Alifanov (1989a) named a second species, *Mimeosaurus tugrikinensis*, but provided no evidence by which it can be distinguished from the type species. Gao and Hou (1995) questioned the validity of the nominal species (*M. tugrikinensis*) and treated it as a subjective junior synonym of *Mimeosaurus crassus* (see Alifanov, 1996 for different opinion).

Regarding the relationships and classification of *Mimeosaurus crassus*, Alifanov (1996) grouped it with *Gladidenagama* in his “tribe Mimeosaurini,” and classified the tribe in the Hoplocercidae (subfamily Pleurodontagaminae). The diagnosis of the tribe Mimeosaurini presented by Alifanov (1996) is: “process of tooth replacement ceases in postnatal period of ontogeny. Central point of the jaw teeth expressed, with lateral shelves. Posterior process of maxilla wide.” Unfortunately, none of these character states are actually diagnostic of this group, and the Mimeosaurini as defined by Alifanov is an artificial taxon. We lack access to *Gladidenagama* specimens, but we see no rationale for placing *Mimeosaurus* in the Hoplocercidae, which are a group of nonacrodontan iguanians commonly called the “morunasaur.” Morunasaur have highly pleurodont and multicuspid teeth (see Frost and Etheridge, 1989), and this group bears no close relationship with *Mimeosaurus* within the Iguania.

*Priscagama gobiensis*

Borsuk-Bialynicka and Moody, 1984

Figure 10

HOLOTYPE: ZPAL MgR-III/32, incomplete skull articulated with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Barun Goyot Formation—Khermeen Tsav and Khulsan; Djadokhta Formation—Bayn Dzak, Bayan Mandahu, and Ukhaa Tolgod localities (Borsuk-

Bialynicka and Moody, 1984; Gao and Hou, 1996; this paper).

REVISED DIAGNOSIS: Distinguished from other acrodontan iguanians including *Mimeosaurus crassus* by the following derived character states: skull lightly built, and flattened; pointed snout elongate; dorsal process of maxilla close to midpoint of tooth row, with anterior extension of maxilla; basiptyergoid process of basisphenoid asymmetrically widened, having strong posterolateral extension; lower jaw elongate, angular process reduced as slender spike and hooked anteriorly.

REFERRED SPECIMENS: IGM 3/77 (MAE 62/93-153), IGM 3/78 (120/93-93), both incomplete skulls with mandibles from Ukhaa Tolgod; IGM 3/79 (MAE 130), incomplete skull with mandibles from Khulsan.

REMARKS: Besides the two specimens mentioned above, a much larger skull from Ukhaa Tolgod (IGM 3/80, MAE 307/93-162; fig. 10C, D) is referred to the same species with question. The anterodorsal part of this skull is missing, but the lower jaws are complete. The mandible is elongate and curved as in *Pleurodontagama aenigmatodes* (see Borsuk-Bialynicka and Moody, 1984), but the teeth (triangular and essentially acrodont) are indistinguishable from *Priscagama gobiensis* (see below). The lower jaw has 16–18 teeth, in spite of elongation of the jaw.

No significant differences in skull morphology have been found to distinguish *Pleurodontagama* from *Priscagama* (Borsuk-Bialynicka and Moody, 1984). Discovery of the new specimen (IGM 3/80) further obscures the two forms. In general, the two nominal taxa share character states such as an elongate antorbital part of the skull and a pointed snout, the squamosal has a hooked posterolateral process, the parietal foramen is significantly smaller than in *Mimeosaurus* and other related iguanians from the Gobi, and the strongly reduced angular process has a slender anteriorly hooked spike. However, the very small sample size and the incompleteness of the available specimens do not allow determination whether the differences are an individual variant or phylogenetically significant. Currently, differences in shape and arrangement of the marginal teeth are the

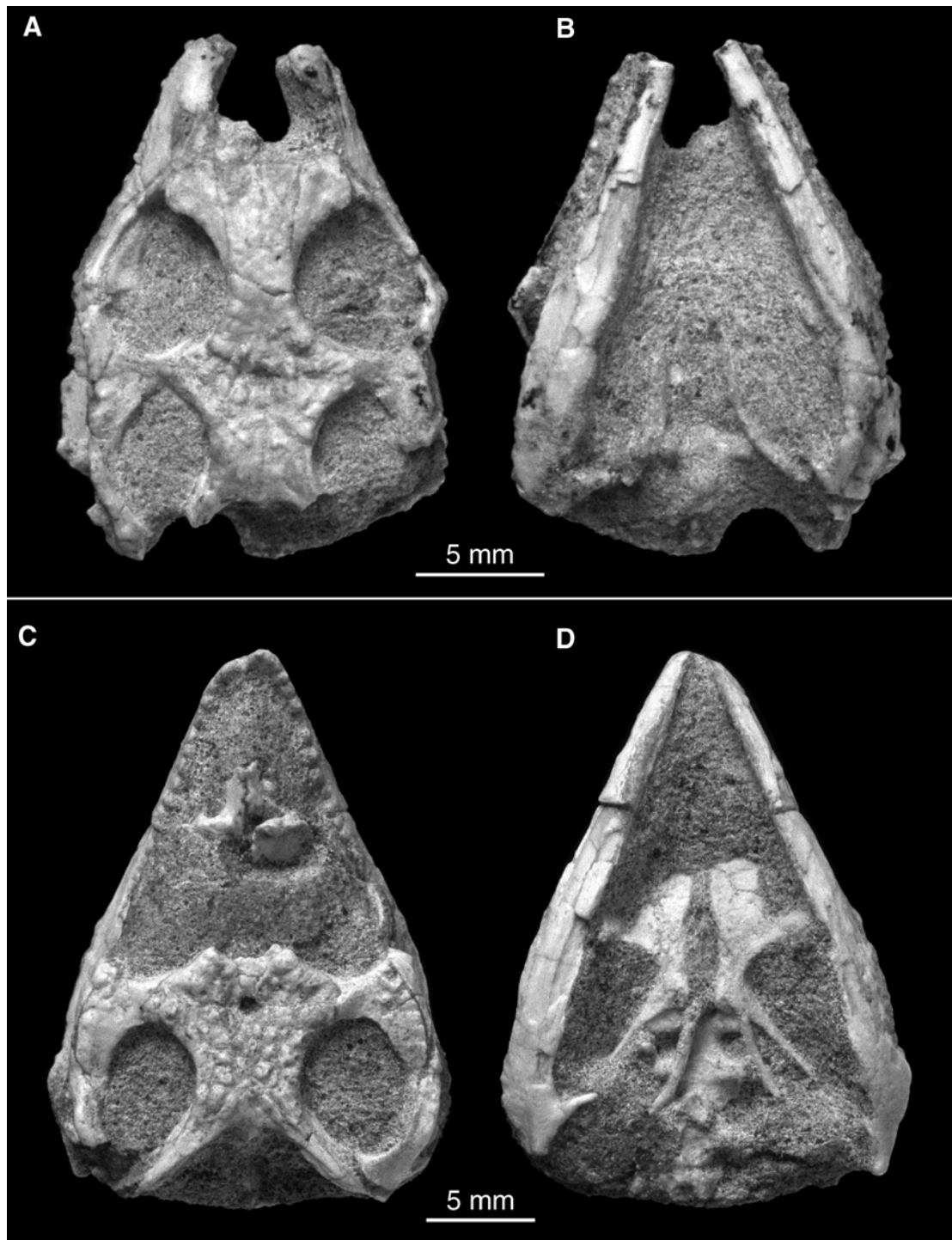


Fig. 10. *Priscagama gobiensis*: A, B, IGM 3/77, incomplete skull with mandibles from Ukhua Tolgod, dorsal and ventral views; C, D, IGM 3/80, incomplete skull with mandibles from Ukhua Tolgod, dorsal and ventral views.



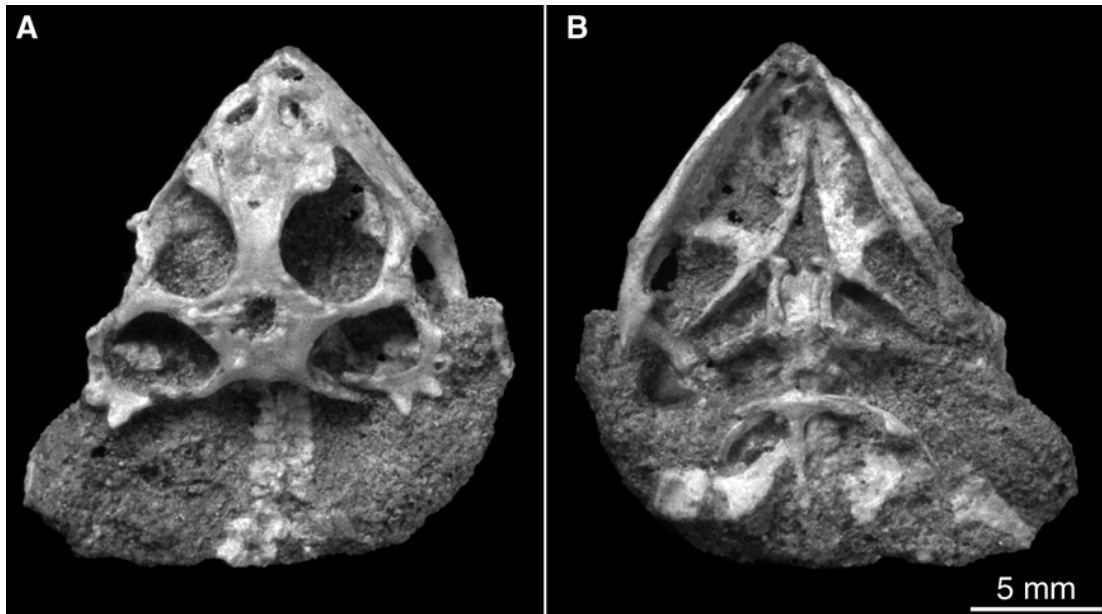


Fig. 11. *Phrynosomimus asper*: **A**, **B**, IGM 3/81, nearly complete skull with mandibles (articulated with several vertebrae and partial pectoral girdle), dorsal and ventral views.

only criteria on which the two forms can be distinguished from one another.

*Phrynosomimus asper* Alifanov, 1996

Figure 11

**HOLOTYPE:** PIN No. 3142/318, nearly complete skull with mandibles. [note: the figure of the holotype is incorrectly inscribed in Alifanov (1996: fig. 4); see discussion below.]

**TYPE LOCALITY AND HORIZON:** Khermeen Tsav locality; Upper Cretaceous Barun Goyot Formation, Mongolian Gobi Desert.

**KNOWN DISTRIBUTION:** Barun Goyot Formation—Khermeen Tsav and Khulsan localities; Djadokhta Formation—Ukhaa Tolgod.

**DIAGNOSIS:** Sharing with other acrodontan iguanians derived characters such as absence of postfrontal, and acrodont dentition on main part of marginal tooth row. Distinguished from other acrodontans including *Mimeosaurus* in having the following autapomorphies: skull short and equilaterally triangular; presence of prominent bony spikes on squamosal and parietal; loss of lateral process of squamosal; well-developed medial process of squamosal separates supratemporal

and supratemporal process of parietal; presence of robust lateral projection on jugal; anterior inferior alveolar foramen opens ventral to anteroventral process of coronoid at splenial-dentary suture; retroarticular process of mandible short and laterally compressed.

**REFERRED SPECIMENS:** IGM 3/81 (MAE 258/92-63), nearly complete skull with mandibles from Khulsan (Area of Wall); IGM 3/82 (MAE 96-31), IGM 3/83 (MAE 152/93-40), both incomplete skulls with mandibles from Ukhaa Tolgod.

#### DESCRIPTION

The three specimens listed above represent the only material known for the species other than the holotype. Notably they were not collected at the type locality Khermeen Tsav. Among these newly recovered specimens, IGM 3/81 (fig. 11) consists of a nearly complete skull with mandibles, several articulated vertebrae and a partial pectoral girdle. Although the skull is dorsoventrally compressed, all the elements are in articulation and show no significant damage. A description of this specimen is given below for bet-

ter understanding of the morphology of this bizarre acrodontan species.

**SKULL ROOF:** The premaxilla is a single bone with a short and wide spine projecting posterodorsally. The spine slightly separates the nasals anteriorly. The slightly distorted tooth-bearing border of the premaxilla is not exposed, and the number of premaxillary teeth cannot be determined. However, it can be observed that the tooth-bearing part of the bone is only slightly wider than the spine.

The nasals are short and paired, with a clear midline suture. A lateral process of the nasal forms the posterior border of the narial opening, and contacts both the prefrontal and the dorsal process of the maxilla. The frontals are fused and are constricted between the orbits as in other iguanians. The frontals underlie the nasals anteriorly, and are exposed anterolaterally with a slender spike intervening the nasal and the prefrontal. The spike is short, not reaching the maxilla; thus it does not separate the nasal from contacting the prefrontal. The posterior border of the frontals widens to twice the width of the anterior border, and has a transverse suture with the parietal. A proportionally large parietal foramen opens at the frontoparietal suture. The subolfactory flange (*crista cranii*) is weakly developed as a low curb forming a trough for the olfactory tract. The dorsal surface is ornamented with small bony knobs.

The parietal table is trapezoidal, having a strongly widened anterior border and a much narrower posterior width (fig. 11A). This configuration is different from *Phrynosoma*, in which the table is generally rectangular (see Etheridge, 1964: fig. 2). The dorsal surface of the parietal table is ornamented with small bony knobs around the parietal foramen, but the most prominent ones are located at the base of the supratemporal process. The supratemporal process is very slender, and it extends laterally behind the medial process of the squamosal and fits in a groovelike facet of the latter element. This pattern of articulation of the two elements is different from *Phrynosoma* in which the two processes directly abut (see e.g., Etheridge, 1964: fig. 2). In *Phrynosomimus asper*, the supratemporal process of the parietal does not contact the quadrate. The posterior border of the parietal table is formed as a sharp and curved ridge,

below which is a well-developed down-growth or flange that has a depression on each side for insertion of the axial muscles.

The prefrontal is slightly enlarged, but lacking a hooked lateral process as seen in *Phrynosoma*. The dorsal part of the prefrontal forms a small triangular shelf roofing the anteromedial corner of the orbit, and is ornamented with small bony knobs like other roofing elements. Extending close to the midlevel of the orbit, the frontal process of the bone is proportionally much more slender than in *Priscagama* and *Mimeosaurus*. A much stronger anteroventral process forms the anterior wall of the orbit and ventrally contacts the palatine. Laterally at the corner of the orbit, a minute bone represents the vestigial lacrimal. The lacrimal foramen is small, opening between the lacrimal and the prefrontal.

The maxilla is separated from the jugal, unlike the fused condition in *Mimeosaurus* (see below). With slight dislocation of the premaxilla, the right maxilla shows a well-developed anteromedial process extending to the midline. This extension indicates that the maxillae were in contact behind the premaxillary spine (an acrodontan condition, Estes et al., 1988; but see discussion above). Like in *Mimeosaurus*, several small and rounded tubercles are developed along the ventral border of the orbit and the posterodorsal process of the jugal. The latter bone has a very prominent tubercle projecting laterally at the posteroventral corner of the bone, but it lacks the hooked posteroventral process seen in some extant acrodontans.

The postfrontal is lost, and the postorbital is the sole element separating the orbit from the supratemporal fenestra. Although boomerang-shaped in dorsal view, this element is triradiate: it has a medial process sutured with the posterolateral process of the frontal, a weak anterolateral process articulated with the jugal, and a much stronger posterolateral process articulated with the squamosal.

The squamosal is the most characteristic element of this species, which has four prominent spikes along its posterior and lateral borders. The bone is curved medially, forming most of the posterior and lateral borders of the rounded supratemporal fenestra. The squamosal lacks a lateral process, and in this

respect differs from *Priscagama* and *Mimeosaurus*, in which the same element is triradiate with prominent lateral processes. Lateral to the postorbital, the squamosal contacts the jugal as generally seen in other iguanians.

Both quadrates are well preserved. The quadrate is slender and vertically straight. Dorsally, the slightly expanded cephalic condyle contacts both the squamosal and the paroccipital process but lacks a contact with the supratemporal process of the parietal. The supratemporal is incompletely preserved on both sides. The articulation pattern of the supratemporal with the squamosal and the parietal cannot be ascertained, although an articular surface on the supratemporal process of the parietal indicates that the supratemporal may approach the base of the process.

**PALATAL ELEMENTS:** The vomers are short and paired, having a sutural contact along the midline (fig. 11B). The palatines are slightly widened, but are clearly separate and diverge posteriorly for the interpterygoid vacuity (pyriform recess). Laterally each palatine has a short process that contacts the maxilla. The pterygoid has an elongate palatine process that is laterally sutured with the palatine and anteriorly approaches (but does not seem to contact) the vomer. It has a very short lateral process contacting the ectopterygoid behind the suborbital fenestra, and a long and slender posterior process extending to contact the quadrate. The ectopterygoid forms the posterior border of the suborbital fenestra, and has a very prominent ventral process (pterygoid flange) for attachment of the pterygoideus muscle. All the palatal elements are toothless.

**BRAINCASE:** In ventral view, the braincase floor is partly covered by a few dislocated foot elements. The well-exposed middle part of the braincase floor is largely formed by the basisphenoid (fused with the parasphenoid), whereas the basioccipital contributes to only the far posterior part of the braincase floor. The sphenoccipital tubercle is short and ventrally directed, with a small occipital recess opening more posteriorly than laterally. The crista prootica is poorly developed, and thus the recessus vena jugularis is very shallow and lacks a well-defined lateral wall. Anteriorly within the recessus, a posterior opening of the Vidian canal is identifiable

and it penetrates the prootic bone. Posteriorly in the recessus, the foramen ovale is identifiable as an opening anterior to the occipital recess. Slightly anterior to the foramen ovale is the facial foramen, which is very small and opens posteriorly.

**MANDIBLE:** Mandibles on both sides are preserved and anteriorly articulated at the symphysis. In keeping with the proportions of the skull, the mandibles are short and slender. In lateral view, the dentary has a posteroverventral extension terminated at the level of the last tooth position, but its posterodorsal articulation with the coronoid is obscured by the upper jaw as preserved. The surangular is poorly preserved on both sides. The position of the anterior surangular foramen cannot be determined, but the posterior surangular foramen can be identified on the right mandible. It is a large foramen in relation to the size of the jaw, and it opens far anteroventrally from the craniomandibular joint.

The dentary medially forms a deep subdental shelf, which has no dental gutter as in other acrodontans. The Meckelian canal is closed by the splenial, except for the anterior part which opens close to the symphysis. The splenial is narrow and long, having an anterior extension terminating anteriorly at the level of one fourth of the length of the dentary tooth row. A small anterior mylohyoid foramen penetrates the splenial, but the anterior inferior alveolar foramen opens at the splenial-dentary suture at the level below the anteroventral process of the coronoid bone. The splenial has a tongue-like posterior extension between the angular and the anterior process of the prearticular, and this extension terminates at a point anterior to the mandibular fossa. In medial view, the coronoid is triradiate, lacking the posterodorsal process seen in extant acrodontans (e.g., *Physignathus*, see Frost and Etheridge, 1989: fig. 4). The coronoid is not well preserved, but the right side seems to show a lateral flap as in *Mimeosaurus* and other priscagamines. The mandibular fossa is a narrow opening, extending posteriorly to the level above the angular process, which is very short and directed anteromedially. Similar to the condition in *Phrynosoma* (see Etheridge, 1964), the retroarticular process is laterally compressed and vertical (fig. 11B).

**DENTITION:** Like in *Mimeosaurus* and many other acrodontans, the marginal teeth in *Phrynosomimus asper* are triangular and acrodont. Due to slight distortion of the snout, the premaxillary teeth are not exposed, and thus the number and morphology of the teeth on this element cannot be identified. The right maxilla has eight teeth and probably two to three anterior ones are not preserved, and anterior to the fourth tooth from the rear is a significant space that may indicate a tooth position; therefore, the complete maxillary tooth row may contain up to 12 teeth.

The dentary teeth on both sides are enclosed by the arch of the upper jaws, but in medial view the right mandible shows nine teeth and probably three to four vacant positions; therefore, the complete dentary tooth row probably contains 12–13 positions. The teeth progressively increase in size towards the posterior end, and the three posteriormost teeth each have a resorption pit, indicating possible tooth replacement, although these are essentially acrodont teeth.

**PECTORAL GIRDLE:** The preserved pectoral girdle includes incomplete scapulae, coracoids, clavicles and an interclavicle. The “T”-shaped interclavicle is slenderly built, differing from that in *Phrynosoma* which has the stem greatly reduced (see Etheridge, 1964: fig. 4). The clavicles on both sides are in articulation with the interclavicle, although the right element is slightly displaced posteriorly. The clavicle is basically boomerang-shaped, having a small process (not hooked) at its midpoint. Coracoid plates are preserved on both sides, but the secondary coracoid and its fenestra cannot be observed. Both left and right scapulae are incompletely preserved, but show no significant differences from other known iguanians.

#### COMPARISON AND DISCUSSION

Alifanov (1996) named and described *Phrynosomimus asper* on the basis of a single specimen (PIN No. 3142/318), which is incorrectly labeled as “(d) *Gladidenagama semiplena*, sp. nov. (holotype, PIN No. 3142/319)” in his illustration (Alifanov, 1996: fig. 4). The new specimens display the same unusual skull configuration with spikes on the

squamosal. Small, triangular acrodont teeth are also present. On the basis of these diagnostic features, the three new specimens can be confidently identified as *Phrynosomimus asper*. As mentioned above, the new specimens represent the only material known for the species other than the holotype. In addition, the discovery of two specimens (IGM 3/82, 3/83) from Ukhaa Tolgod extends the stratigraphic distribution of this peculiar acrodontan lizard from the type horizon (Barun Goyot Formation) to the Djadokhta Formation.

A problem stemming from the ambiguous description of the holotype specimen (PIN No. 3142/318) concerns its tooth count. Alifanov (1996) diagnosed the species as having a “total of maxillary teeth no less than 15; from which five belong to the additional series,” but later described it as having 17 (two caninelike teeth plus 15 postcanine teeth). Although described as having two “caninelike” anterior teeth, none of the figures that Alifanov provided actually show such teeth. Because the holotype is poorly illustrated and incorrectly labeled, the actual number of maxillary teeth cannot be ascertained for that specimen; however, if the lower jaw (Alifanov, 1996: figs. 7f, o: showing seven positions on the posterior half of the tooth row) is correctly illustrated, the maxillary tooth count on the holotype may well have been overestimated. The best preserved new specimen (IGM 3/81) shows only 11–12 maxillary teeth.

The new specimen described above (IGM 3/81) is preserved in light brown and poorly cemented sandstones. The short triangular skull with a spiked squamosal is strikingly similar to North American *Phrynosoma*, perhaps suggesting a similar burrowing life style. The Gobi lizard, however, is clearly an acrodontan as evidenced by its triangular acrodont teeth. Furthermore, the presence of small osteodermal tubercles on the skull roof and development of a lateral flap of the coronoid are indicative of a relationship with the priscagamines.

The absence of a postfrontal is another character, besides the acrodont dentition, on which this taxon is referred to the acrodontans. All extant acrodontans have the postfrontal lost (Estes et al., 1988), although



some fossil specimens (e.g., IGM 3/76: *Mi-meosaurus*) retain a small bone. In addition, the loss of this element may be convergently acquired in some nonacrodontan iguanians, including *Phrynosoma*, crotaphytines, most sceloporines, and oplurines (Etheridge and de Queiroz, 1988).

#### IGUANIA INCERTAE SEDIS

##### *Isodontosaurus gracilis* Gilmore, 1943

Figures 12, 13

**HOLOTYPE:** AMNH 6647, incomplete mandibles with well-preserved teeth.

**TYPE LOCALITY AND HORIZON:** Bayn Dzak (Shabarakh Usu), Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation.

**KNOWN DISTRIBUTION:** Djadokhta Formation—Bayn Dzak, Bayan Mandahu, Ukhaa Tolgod, Zos, and Tugrugeen Shireh localities (Gilmore, 1943; Alifanov, 1993a; Gao and Hou, 1996; this paper).

**REVISED DIAGNOSIS:** Sharing with other iguanians the following derived character states: frontals fused and constricted between orbits, presence of jugal/squamosal contact, parietal foramen opens at frontoparietal suture, and presence of angular process in lower jaw. Differing from all acrodontan iguanians primarily in having highly pleurodont dentition.

Distinguished from all nonacrodontan iguanians by a large number of derived character states: squamosal significantly widened with lateral flange; quadrate process of pterygoid strongly expanded and laterally compressed as winglike; coronoid dorsal process not exposed laterally, but entirely covered by coronoid process of dentary; strongly developed coronoid process of dentary carries prominent lateral crest for attachment of bodenaponeurosis of external mandibular adductor muscles; lateral surface of lower jaw develops distinct fossa below coronoid process for the superficialis of external mandibular adductor muscles; angular extends antero-medially to midlevel of dentary tooth row; ventral border of lower jaw develops distinct trochlear notch for *M. pterygomandibularis*; marginal teeth reduced in number, containing no more than 14 maxillary and 16 dentary teeth; tooth crowns increasingly dilated posteriorly and compressed laterally, with pos-

terior border lapping anterolateral border of next posterior crown, last tooth much reduced.

**REFERRED SPECIMENS:** Ukhaa Tolgod—IGM 3/84 (MAE 96-113), nearly complete skull with mandibles; IGM 3/85–3/89 (MAE 27/93-192, 42/93, 49/93-163, 161/93-40, and 94-16-1), all incomplete skulls with mandibles. Zos—IGM 3/90 (MAE 94-54), incomplete skull with mandibles. Tugrugeen Shireh—IGM 3/91 (MAE 261/92-123), nearly complete skull with partial postcranial skeleton; IGM 3/92 (MAE 23/93-28), partial skull with mandibles; IGM 3/93, 3/94 (MAE 221/93-8, 88/93-19), both partial skull with mandibles.

#### DESCRIPTION

The new specimens referred to *Isodontosaurus gracilis* include the best preserved skulls known for the species, which reveal taxonomically important features of this poorly known taxon. The species is previously known mostly from tooth-bearing jaw material. In view of the fact that the skull features of the species are extremely poorly known, a description of the cranial morphology is given below, based on the new material.

**SKULL ROOF:** The premaxillae are fused, bearing six conical teeth (IGM 3/85, 3/86, 3/91). The dorsal spine of the element is slender and elongate and is distally slightly spatulate. The nasals are paired, having their anterior one third intervened by the dorsal spine of the premaxillae along the midline. The lateral border of the nasal contacts both the maxilla and the prefrontal, as an anterolateral process of the frontal is not well developed. Like in other iguanians generally, the frontals are fused and constricted between the orbits. A frontal shelf (best shown on IGM 3/84, 3/92) is well developed anteriorly, and the shelf dorsally has a pair of depressions for the posterior processes of the nasals. The anterior part of each frontal is slightly widened, and laterally has a flange for articulation with the prefrontal (shown on IGM 3/84, 3/92; figs. 12A, 13C). The posterior part of the element is very wide, with a maximum width three times that of the interorbital width. The frontoparietal suture is



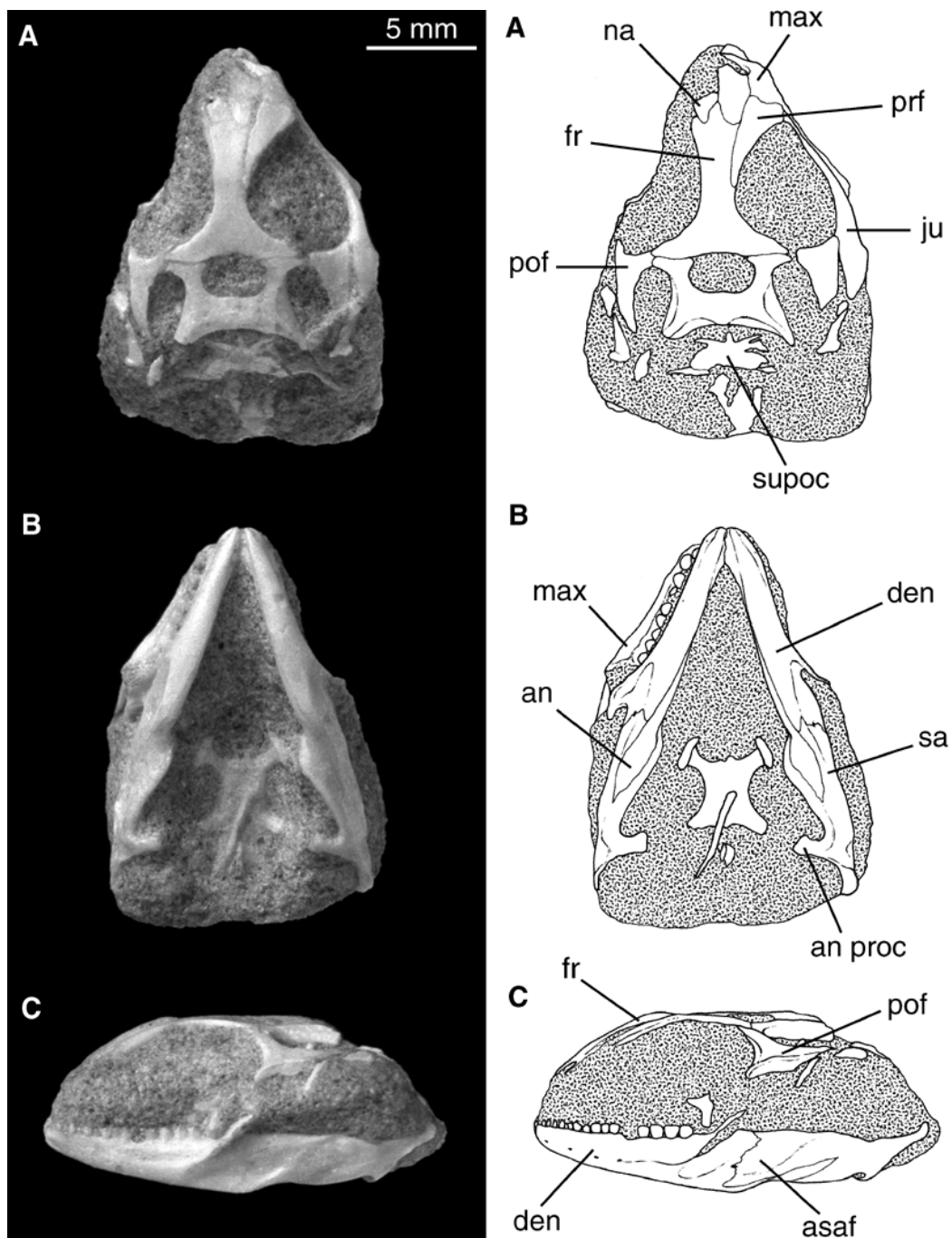


Fig. 12. Iguania incertae sedis, *Isodontosaurus gracilis*: A–C, IGM 3/84, incomplete skull with mandibles from Ukhaa Tolgod, dorsal, ventral, and lateral views.

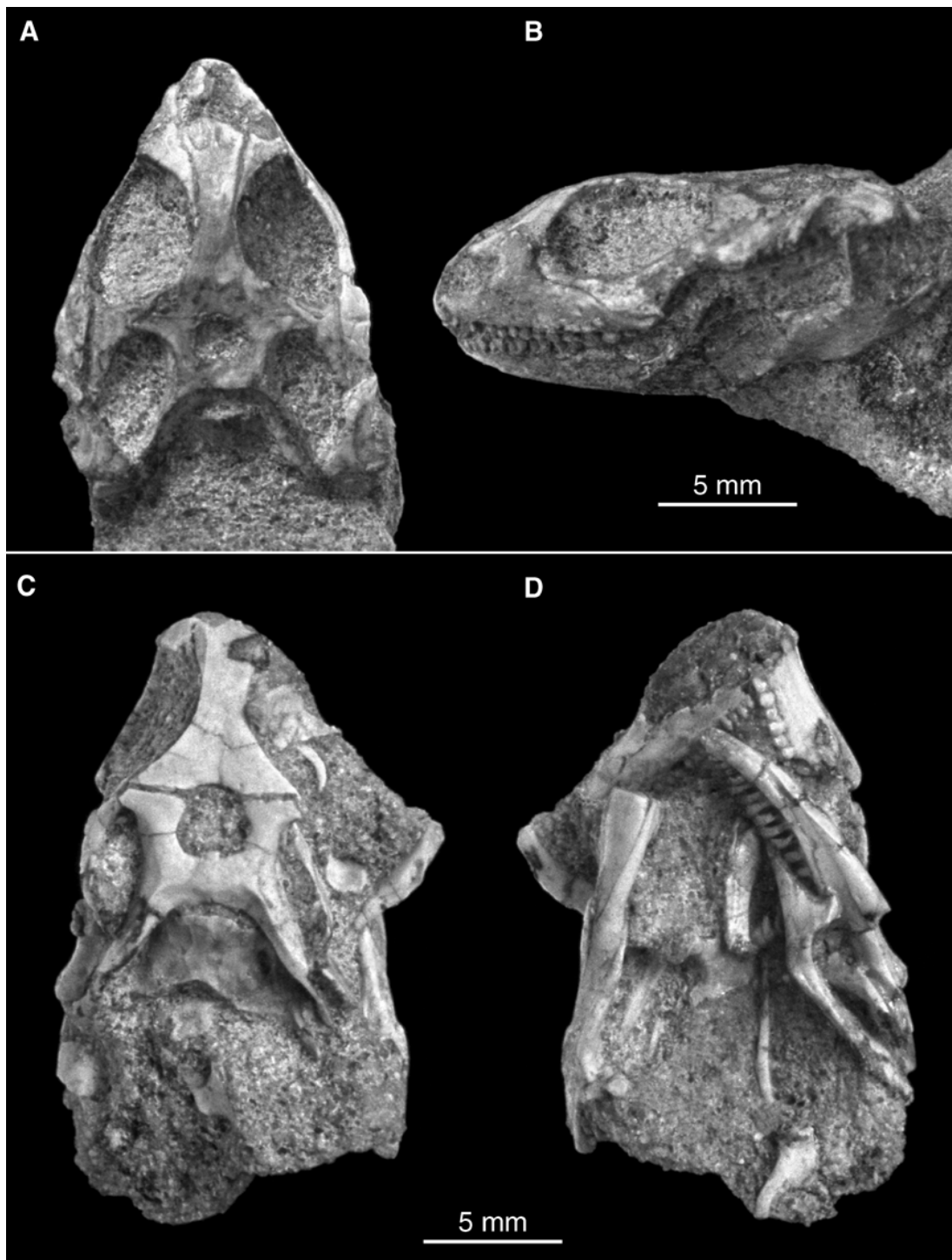


Fig. 13. *Iguanodon* incertae sedis, *Isodontosaurus gracilis*: **A**, **B**, IGM 3/91, cranial part of a skeleton preserved in concretion from Tugrugeen Shireh, dorsal and left lateral views; **C**, **D**, IGM 3/92, incomplete skull with mandibles from Tugrugeen Shireh, dorsal and ventral views.

simply transverse, but the posterior border of the frontal is slightly notched for the parietal foramen.

The parietal table is short and roughly trapezoidal. A large part of the parietal table is penetrated by a well-developed fontanelle, which is confluent with the parietal foramen (a feature also seen in several but not all other nonacrodontan iguanians from the Gobi). The lateral border of the parietal table is flanged for origins of the temporal muscles. The posterior border of the table is also weakly flanged for attachment of the axial muscles. The supratemporal process of the parietal, best preserved on two specimens from Tugrugeen Shireh (IGM 3/91, 3/92), is slightly longer than the parietal table. For most of its length, the process carries a sharp dorsal crest and is sloped both medially and laterally making the process roughly triangular in cross-section. The process distally does not contact the quadrate, but is weakly articulated with the squamosal and the supratemporal bone (see below).

The maxilla is short, and is firmly articulated to the lacrimal and jugal; these together form a roughly rectangular lateral wall of the skull below the orbit. The maxilla has a triangular posterior process bulging laterally. This configuration of the element is similar to that in *Mimeosaurus crassus*, but it is not fused with the jugal and has no bony ornamentation along its dorsal border. Anteriorly the maxilla bears a well-developed antero-medial process (IGM 3/84, 3/85, 3/89, 3/91), which extends behind the premaxillary spine approaching or contacting the opposite structure. The nasal process of the maxilla is located dorsally above the anterior part of the tooth row. The process curves medially to articulate with the nasal and prefrontal, but seems to have no contact with the frontal as the anterolateral process of the latter is not well developed. Posterior to the nasal process, the maxilla is dorsally articulated with a small lacrimal and the entire length of the anterior process of the jugal; thus, the maxilla does not participate in the formation of the ventral border of the orbit. The maxilla of different individuals variably carries 10–14 teeth (see below).

The prefrontal is well preserved on two specimens (IGM 3/84, 3/91). The frontal pro-

cess of the element is proportionally long, extending to the midlevel of the orbit along the lateral border of the frontal. The ventral process of the prefrontal (IGM 3/92) curves downward to form the anterior wall of the orbit, and has a small notch on its lateral border for the lacrimal foramen; therefore, the foramen must open at its suture with the lacrimal bone. The postfrontal is fused with the postorbital to form a postorbitofrontal (IGM 3/84, 3/91), but one specimen (IGM 3/92) shows a remnant “suture” on the left element (no suture at all on the right side).

As mentioned above, the anteroventral process of the jugal forms a large part of the ventral border of the orbit, and it has a triangular base that slightly bulges laterally. The element, however, lacks a posteroventral process. The posterodorsal process of the jugal strongly slants posteriorly, and the distal half of the process is spatulate contacting both the postorbital and the squamosal (figs. 12A, 13B).

The squamosal (best preserved on IGM 3/91) is widened, with a lateral extension for the attachment of the temporal muscles. The lateral border of the wing is curved medially, and is posteriorly linked with a hooklike lateral process. A large part of the squamosal covers the cephalic head of the quadrate, but its anterior extension curves laterally and articulates with the jugal bone. The posterior end of the squamosal carries a short but well-defined dorsal (medial) process, forming the posterior rim of the supratemporal fenestra and contacting the supratemporal process of the parietal. The posterior border of the squamosal is slightly notched for articulation with the supratemporal bone (see below).

No supratemporal bone is identified on any of the known specimens of *Isodontosaurus gracilis*. Such an element is normally developed as a splint wedging between the supratemporal process of the parietal and the squamosal (but see Frost and Etheridge, 1989). In this species, however, it appears to be absent as in some agamids and some other lizards (see Estes et al., 1988 for citations).

The quadrate is vertically positioned, without distortion (IGM 3/91). It has a thin and straight tympanic crest, lacking a strongly concave conch on its posterior margin. The cephalic condyle is partially covered by the

widened squamosal, but is exposed posteriorly as a strong tubercle above the tympanic crest. As a matter of preservation, the anterior surface of the quadrate cannot be observed without further preparation; but the posterior aspect of the bone is observable on two specimens (IGM 3/91, 3/92). Like in many other lizards generally, the quadrate is posteriorly divided into two parts by a prominent and curved posterior crest that runs dorsoventrally from the cephalic condyle to the ventral condyle. The medial part of the posterior aspect is about half the width of the lateral part, and the medial part has a posterior opening of the quadrate foramen located about one third the height of the quadrate bone above the ventral condyle. The ventral condyle does not show significant expansion, but remains small and slightly saddle-shaped fitting in the articular fossa of the lower jaw.

**PALATAL ELEMENTS:** Slightly displaced palatal elements can be observed on IGM 3/85 and 3/92 (fig. 13D). Both the palatine and pterygoid are toothless elements. The palatine is narrow and elongate, forming the medial border of the suborbital fenestra. Along the medial border of the palatine is a narrow groove (on IGM 3/92), in which fits the slender posterior process of the vomer which approaches or may even contact the pterygoid. The pterygoid has a short anterior process, which is articulated to the medial edge of the palatine. An even shorter lateral process articulates with the ectopterygoid. The posterior (or quadrate) process has a medial trough as in other lizards generally, but the process carries a strongly expanded dorsal wing. A similar condition is seen in extant *Uromastix* (Saksena, 1942: text-fig. 7).

**BRAINCASE:** The supraoccipital is well exposed posterior to the parietal table (IGM 3/91, 3/92). It has a strongly convex dorsal surface, but lacks a clearly defined sagittal crest, nor does it develop a processus ascendens at its anterior border. The element laterally contacts the prootic with a longitudinal suture, and posteromedially has a notch at the dorsal rim of the foramen magnum. The posterolateral border of the bone contacts the exoccipital with a slanted suture. The paroccipital process is short, and has the prootic extended onto its anterolateral surface (figs. 12A,

13C). Also in dorsal view, the anterior and posterior semicircular canals are clearly recognizable in several specimens.

The braincase floor is slightly elongate and rectangular in shape (exposed on IGM 3/84, 3/92). Anteriorly, the cultriform process of the parasphenoid is poorly ossified, as only the basal part is preserved. The basipterygoid process is short, having a slender shaft but strongly expanded end for articulation with the pterygoid. The basisphenoid/basioccipital suture is medially horizontal but laterally diagonal, a primitive condition (Gao and Norrell, 1998). The basioccipital composes a smaller part of the braincase floor than the basisphenoid. The spheno-occipital tubercles are short but proportionally quite robust. The tubercles are more ventrally than laterally directed. Other features of the braincase cannot be observed without further preparation of the specimens.

The epipterygoid is exposed on several specimens (IGM 3/84, 3/85, 3/94). This is a slender pillar as seen in other lizards generally, but its actual position and its contact with the lateral wall and roof of the braincase cannot be observed.

**MANDIBLE:** The mandible of the species shows a set of peculiar features, which are apparently related to its specialized feeding mechanism evidenced by its highly durophagous dentition. The jaw is robustly built. The dentary portion is slightly longer than the postdentary portion. Posterodorsally the dentary bears an extremely well-developed coronoid process, which entirely covers the lateral surface of the dorsal process of the coronoid bone (leaving no lateral exposure of the latter element). This process carries a prominent lateral crest for insertion of the bodenaponeurosis of the external mandibular adductors (see Oelrich, 1956; Rieppel, 1980c). The lateral surface of the mandible below this crest forms a distinct fossa (or depression), providing extra surfaces for insertion of the superficialis portion of the external jaw adductor muscles (see Oelrich, 1956). The fossa is ventrally bordered by a prominent adductor crest formed by both the surangular and the dentary bone. Within the fossa is the meandering dentary/surangular suture, and the anterior surangular foramen



opens on the suture ventral to a short posterior extension of the dentary (fig. 12C).

The posterior surangular foramen is small and opens anterolateral to the craniomandibular joint. Below the anterior surangular foramen, the ventral border of the mandible develops a distinct trochlear notch probably for a tendinous bundle of the pterygomandibularis muscle (of Oelrich, 1956; *M. pterygoideus* of Lakjer, 1926; Haas, 1973). This notch is formed largely by the angular, which has a small lateral exposure and twists medially at the trochlear notch. The retroarticular process is slender, posteriorly directed, and terminates with a tubercle for the insertion of the *M. depressor mandibularis* (Oelrich, 1956). Ventromedially at the base of the retroarticular process, an angular process is well developed and slightly hooked anteriorly (fig. 12B).

The medial aspect of the mandible can be observed on two specimens (IGM 3/84, 3/92). A noticeable feature on this side of the jaw is the long anterior extension of the angular bone. The anterior extent is twice the length of the posterior extension exposed on the lateral surface of the jaw. Anteriorly the angular terminates at the midpoint of the tooth row, anterior to the anterior inferior alveolar foramen. This anterior extension has a long sutural contact with the splenial as in some extant acrodontans (Jollie, 1960), but such a condition cannot be polarized satisfactorily in comparison with rhynchocephalians (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989). The posterior mylohyoid foramen (or angular foramen of other authors) penetrates the angular at the level slightly anterior to the coronoid summit of the jaw (fig. 13D).

The subdental shelf is present and curves along the basal line of the tooth row; a sulcus dentalis (dental gutter), however, is completely lost. The Meckelian canal anteriorly turns ventrally and opens as a groove, but posteromedially is covered by the splenial and the angular bone. The splenial is just slightly deeper than the angular and has a posterior extension terminating at the level of the distinct trochlear notch of the jaw where it contacts the anteroventral process of the coronoid. The anterior inferior alveolar fo-

ramen and the anterior mylohyoid foramen lie closely together (IGM 3/84).

**DENTITION:** As recognized by Gilmore (1943), *Isodontosaurus gracilis* is peculiar in having a highly durophagous dentition. All the marginal teeth are highly pleurodont, with approximately two thirds of the tooth shaft attached to a relatively deep lateral parapet of the jaw (fig. 13D). Tooth replacement is of the typical iguanid type, where new teeth erupt within resorption pits. The tooth shafts are slender and slightly anteroposteriorly compressed; the crowns, however, are strongly dilated anteroposteriorly and compressed laterally, with posterior borders lapping the outside of the next posterior crown. Generally, anterior teeth are small, increasingly becoming enlarged posteriorly; but the last maxillary tooth is often significantly smaller than the adjacent anterior tooth. The ultimate maxillary tooth is more medially located than others and is therefore slightly set off from the main tooth line.

Both small and larger specimens show essentially the same typical dentition; however, the number of teeth in a complete tooth row varies considerably among specimens. For the maxillary tooth row, a complete tooth count ranges from as few as ten teeth (IGM 3/89, 3/90) to as many as 14 (IGM 3/84, IGM 3/91, 3/94); two other specimens (IGM 3/85, 3/86) have 12 maxillary teeth on each side. Dentary teeth can be observed on five specimens (IGM 3/84, 3/85, 3/90–3/92), while other specimens have them concealed by the upper dentition. A complete dentary tooth row contains as few as 12 positions (IGM 3/90) or as many as 16 (IGM 3/84, 3/91, 3/92). One specimen (IGM 3/85) has 14 positions. Therefore, the dentary tooth row normally contains two more positions than the maxillary tooth row in the same specimen.

#### COMPARISON AND DISCUSSION

Gilmore (1943) named *Isodontosaurus gracilis*, and provisionally referred it to the Anguidae on the basis of its resemblance to *Peltosaurus* in tooth morphology. Estes (1983) removed *Isodontosaurus* from the Anguidae and hinted at a scincomorphan relationship. Ignoring the fact that the species



has a highly pleurodont dentition, Borsuk-Bialynicka (1991a) regarded *Isodontosaurus gracilis* as a "true agamid," and Alifanov (1993a) formally classified it in the Agamidae. The monotypic taxon has been given subfamilial and familial ranks (Alifanov, 1993a), which provide no help in elucidating its relationships.

Several specimens (IGM 3/84, 3/91, 3/92), collected from Ukhua Tolgod and Tugrugeen Shireh localities, represent the best preserved skulls known for *Isodontosaurus gracilis*. These specimens, together with several others, show character states that support the referral of *I. gracilis* to the Iguania: frontals are fused and constricted between orbits; presence of a jugal/squamosal contact; parietal foramen opens at the frontoparietal suture (confluent with a fontanelle); and presence of an angular process on the mandible. More importantly, the new specimens reveal several characters that were previously unknown for this lizard (see discussion below).

The peculiar dentition of this bizarre iguanian was noted by Gilmore (1943), but a comparison of the new specimens reveals some previously unknown information. As described above, the number of maxillary teeth ranges from as few as ten to as many as 14, and the number of dentary teeth ranges from 12 to 16. No clear pattern can be identified for correlation of size with number of teeth, as a higher number of teeth occurs in both smaller and larger specimens. However, one recognizable pattern is that the dentary tooth row has two more positions than the maxillary tooth row in the same individual.

Besides the dentition, several other peculiar features of *Isodontosaurus gracilis* should be noted. One of these is the presence of a large parietal fontanelle confluent with the parietal foramen. A similar condition of the foramen is known not only in some non-acrodontan iguanians from the Gobi (e.g., *Anchaurosaurus*, *Zapsosaurus*, *Igua*, and *Polrussia*), but also to a much smaller extent in some extant iguanians: e.g., *Oplurus* (Blanc, 1977), some *Sceloporus* (Wiens and Reeder, 1997), and acrodontan *Uromastyx* (Beddard, 1905; El-Toubi, 1945; Jollie, 1960). Presence of such a fontanelle is a noticeable feature for these Cretaceous iguani-

ans, although the phylogenetic significance of this character requires careful evaluation.

Several other peculiar features of *Isodontosaurus gracilis* are detectable in its lower jaw, and may have developed in association with its specialized feeding mechanism. These include: an unusually well-developed coronoid process of the dentary that covers the entire lateral side of the coronoid bone with a prominent lateral crest for attachment of the bodenaponeurosis of external mandibular adductor muscles; the lateral surface of the mandible has a well-developed fossa for the superficialis muscle; and the ventral border of the mandible develops a distinct trochlear notch that serves as a possible passageway for a tendinous bundle of the pterygomandibularis.

Except for its pleurodont dentition, *Isodontosaurus gracilis* shows striking similarities in skull configuration and palatal features to extant *Uromastyx*, which is commonly placed in the Agamidae (or in Leiolepidinae of the Chamaeleonidae, Frost and Etheridge, 1989). They share similarities such as: parietal foramen is confluent with the parietal fontanelle; jugal is posterodorsally spatulate; posterolateral process of basisphenoid extends onto spheno-occipital tubercle; dentary covers lateral part of the coronoid process; angular strongly extends anteriorly to, or surpassing, midlevel of tooth row. However, these features must be carefully evaluated to determine whether they are phylogenetically significant.

Based on the available evidence, *Isodontosaurus gracilis* can be broadly referred to the Iguania. The relationships of this bizarre lizard within the Iguania, however, are far from clearly understood; and for this reason, we classify it as "Iguania Incertae sedis."

#### GEKKOTA CUVIER, 1817

DEFINITION: The most recent common ancestor of Gekkonidae and Pygopodidae and all of its descendants (Estes et al., 1988; see remarks below).

DIAGNOSIS: The Gekkota as above defined can be diagnosed by as many as 46 derived character states (see Estes et al., 1988 for list of synapomorphies and citations).

REMARKS: Besides the Gekkonidae and

Pygopodidae, two fossil familial groups (Ardeosauridae and Bavarisauridae) are often classified in the Gekkota (Hoffstetter, 1964, 1966; Estes, 1983). However, recent studies have shown that *Ardeosaurus* is possibly related to scincomorphs (Mateer, 1982; Evans, 1993), and *Bavarisaurus* is not a gekkotan but possibly related to either scincomorphs or anguimorphs (Evans, 1993, 1994). *Eichstaettisaurus* is probably the best candidate for a gekkotan among the Jurassic lizards (see Evans, 1993 for discussion). The new taxon described below is tentatively classified in the Gekkota, but resolution of its actual relationships with other known gekkotans depends on future phylogenetic analyses incorporating this fossil taxon.

Although the monophyly of the Gekkota is highly corroborated by a long list of derived character states, the relationships of gekkotans to other major squamate groups are not unambiguous. Cladistic analysis by Estes et al. (1988) has shown a possible Gekkota-Autarchoglossa sister group relationship, but the monophyly of the latter taxon is weakly supported by as few as three possible synapomorphies, none of which are unambiguous (see Estes et al., 1988 for discussion). Various workers have advocated possible affinities of the Gekkota with the Xantusiidae (see Rieppel, 1988 for review and citations; see also Lee, 1998). Consequently, the relationships of the Gekkota within the Squamata merit further investigation.

#### FAMILY INCERTAE SEDIS

##### *Myrmecodaptria microphagosa*, new genus and species

Figure 14

ETYMOLOGY: *myrmex* + *daptria* (Gr., f.), meaning ant eater; *mikrophagos* (Gr.), meaning eating little.

HOLOTYPE: IGM 3/95 (MAE 271/93-65), incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Ukhaa Tolgod, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

KNOWN DISTRIBUTION: Known only from the type locality and horizon.

DIAGNOSIS: Sharing with other gekkotans derived character states such as: frontals

fused and having descending processes in contact below olfactory tract; postorbital absent; lacrimal lost; pterygoid teeth lost; crista prootica extends onto basiptyergoid process; quadrate suspension by paroccipital abutting; and retroarticular process deflected medially.

Differing from all other members of the group in having the following autapomorphies: Skull strongly elongate, having parietal table roughly equal length with frontals; presence of well-defined ventral process anteriorly on ventrolateral flange of parietal; supratemporal arch formed by slender squamosal only; squamosal extends anteriorly to level of frontoparietal suture, and abutting jugal; reduced number of small marginal teeth that are widely spaced and peglike.

#### DESCRIPTION

The holotype (IGM 3/95) is the only known specimen of this taxon. Although having a rounded snout, the skull is strongly elongate, and roughly rectangular in dorsal view. The snout is heavily covered with thick osteoderms that have pitted surfaces, and the external narial opening is not retracted.

SKULL ROOF: The premaxillae are fused and have a relatively wide dorsal spine that forms the medial border of the narial opening. The spine is covered by a thick osteoderm, and thus the pattern of the premaxillanarial articulation cannot be observed. The nasal is partly preserved on the left side, and is also covered with an osteoderm, like the premaxillae. The frontals are fused (fig. 14B), and the olfactory flanges are well developed and in contact ventral to the olfactory tract (gekkotan synapomorphy, see Estes et al., 1988). The frontal articulates anteriorly with the nasal; other articulations are not preserved. Posteriorly the frontal is expanded and has a straight transverse suture with the parietal. The dorsal surface of the frontal is scarred, suggesting a covering of osteoderms.

The parietals are fused without a trace of a midline suture (fig. 14B). The parietal table is narrow and very elongate. In length, it is roughly equivalent to the frontal bone. The dorsal surface of the parietal table is ornamented with osteoderms. The parietal foramen is a minute opening, which is located on the anterior one third of the parietal table.

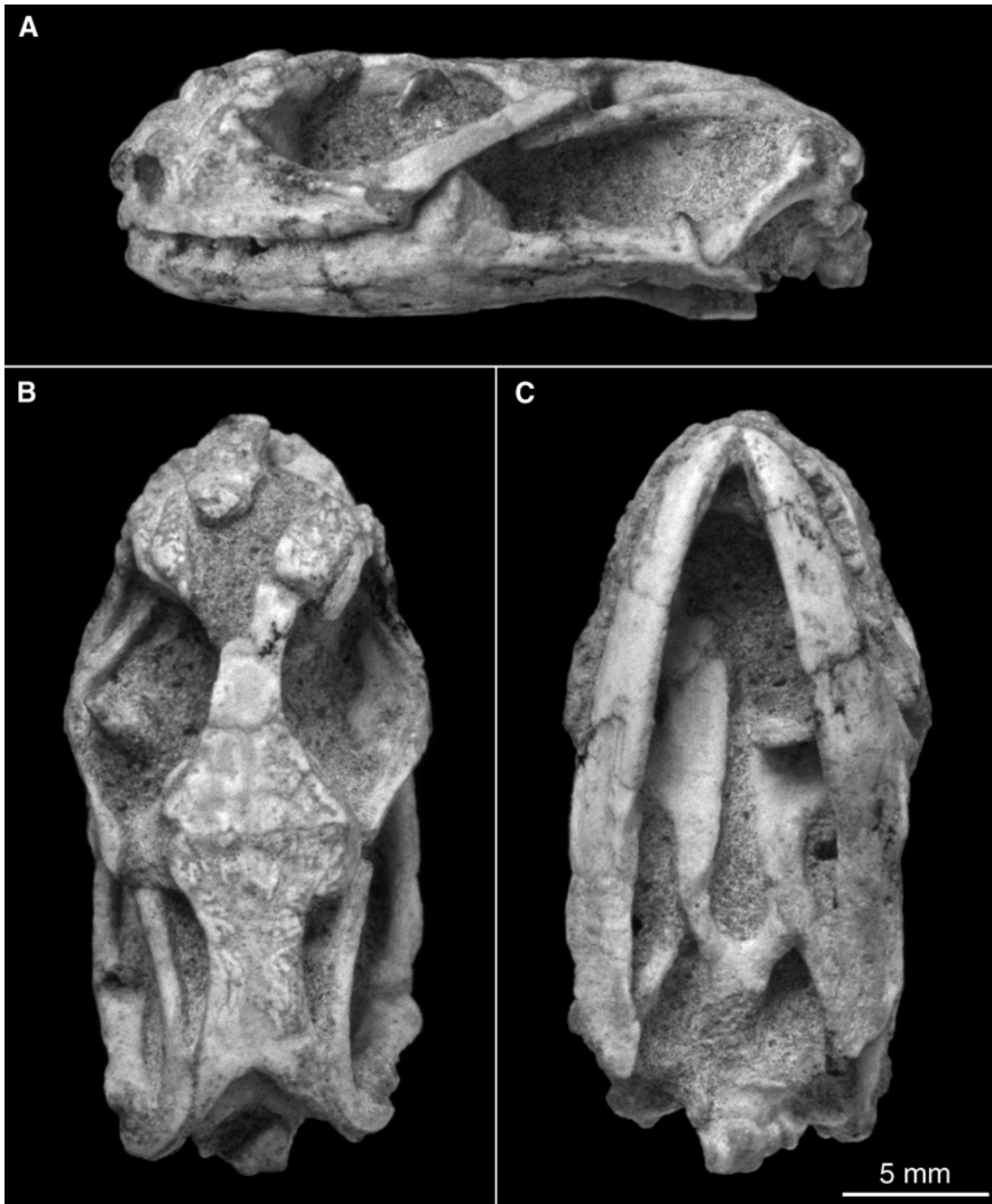


Fig. 14. Gekkota incertae sedis, *Myrmecodaptia microphagosa*, new genus and species: A–C, IGM 3/95 (holotype), incomplete skull with mandibles from Ukhaa Tolgod, left lateral, dorsal, and ventral views.

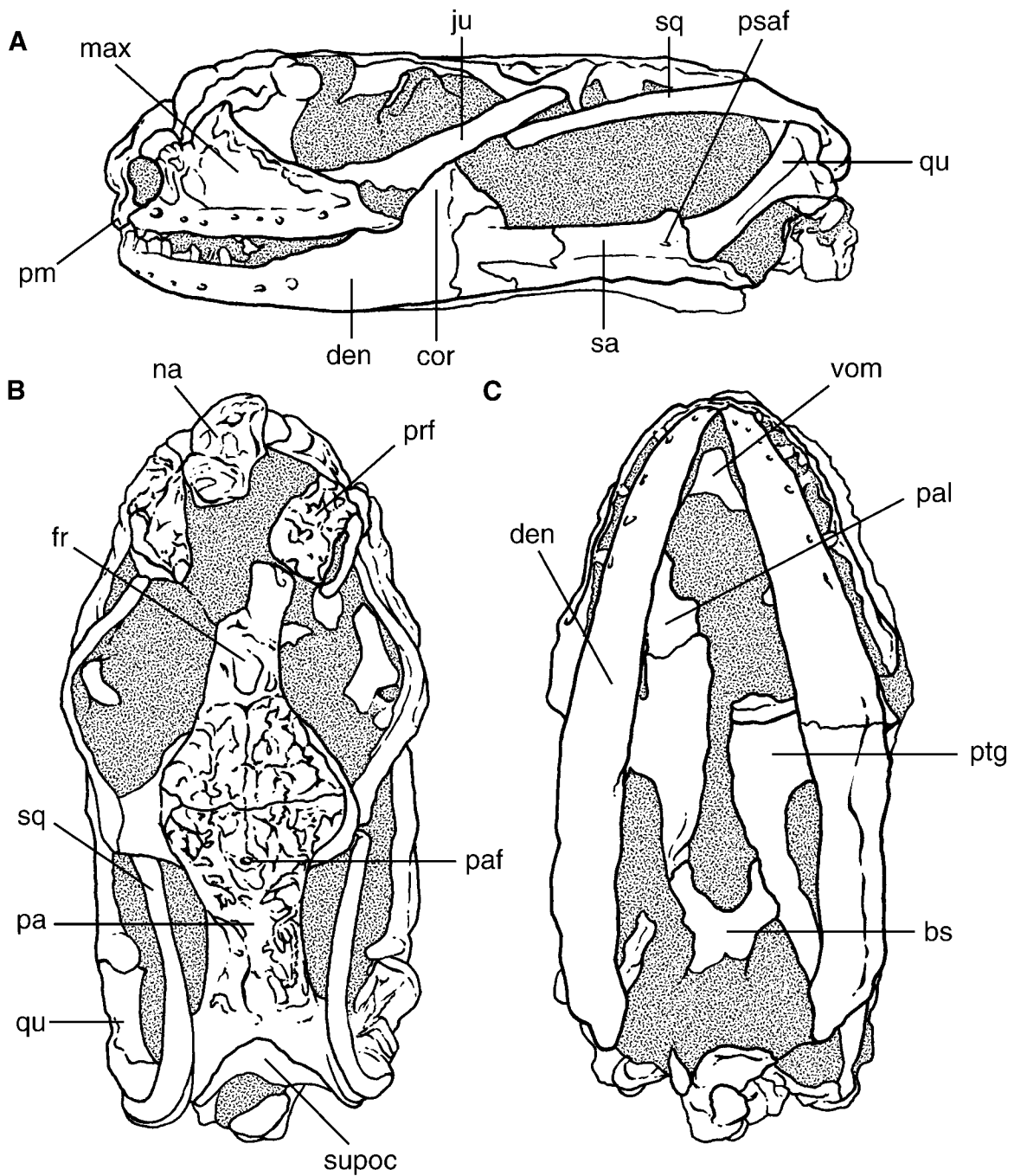


Fig. 14. Continued.



The ventrolateral border of the parietal table has a vertical flange, indicating a ventral origin of the temporal muscles. The anterior part of the flange bears a well-developed ventral process (downgrowth of Estes et al., 1988), which is laterally compressed and anteroposteriorly broadened. Such a process is absent in extant gekkonids and pygopodids (Estes et al., 1988). The process ventrally contacts the prootic (poorly preserved), but it cannot be determined whether it contacts the epipterygoid, as the latter element is not preserved on either side of the skull. The supratemporal process of the parietal is very short, having a length equal to about one third that of the parietal table. The supratemporal process has a roughly triangular base and a slender extension that contacts the paroccipital process (shown on the right side of the specimen).

The maxilla has a very short anterior process articulating with the premaxillae (fig. 14A). A slightly longer anteromedial process extends posterior to the tooth-bearing part of the premaxillae, but does not meet its equivalent counter part. The nasal (or dorsal) process of the maxilla is high, and is located dorsal to the anterior half of the maxillary tooth row (a primitive condition in squamates). The process dorsally articulates to the nasal and the prefrontal, and may contact the anterolateral process of the frontal (indicated by a gap between the nasal and the prefrontal). The lateral surface of the maxilla is covered with osteoderms, and is penetrated by a horizontal row of very small foramina (lateral superior alveolar foramina) parallel to its ventral border. The posterior process of the maxilla forms the ventral border of the orbit, and extends to the midlevel of the orbit where it articulates with the jugal.

The dorsal surface of the prefrontal is small and triangular, and is ornamented with osteoderms. The prefrontal forms the entire anterior wall of the orbit, and ventrally contacts the palatine within the orbit. Like in other gekkotans, the lacrimal is absent and a small lacrimal foramen opens at the prefrontal-maxilla suture (but see Rieppel, 1984). Below the lacrimal foramen is another small opening, representing the inferior orbital foramen. The postorbital is completely lost, leaving the elongate squamosal to form the

entire bar of the supratemporal fenestra. The postfrontal (preserved on both sides) is forked medially to clasp the frontoparietal suture (see discussion above), and is laterally articulated with both the jugal and the squamosal (fig. 14B).

The squamosal is a slender bar extending anteriorly to the level of the frontoparietal suture, where it abuts the jugal and medially contacts the postorbital. The bone is hockey-stick shaped without a trace of a dorsal process. The squamosal has a short contact with the supratemporal process of the parietal posterior to the supratemporal fenestra, but posteriorly this contact is separated by the splint-like supratemporal bone.

The quadrate, preserved on both sides, is in an oblique position slanting dorsoposteriorly. As in extant gekkonids (Rieppel, 1984), the quadrate has a convex anterior slope that forms part of the origin for the external adductor muscles. The cephalic condyle dorsally articulates with the squamosal and the supratemporal, and medially bears a well-defined process contacting the anteroventral part of the paroccipital process (a gekkotan synapomorphy, see Rieppel, 1984; Estes et al., 1988). The medial border of the quadrate is vertically straight, lacking any trace of a pterygoid lappet. The ventral condyle is expanded transversely, and a small quadrate foramen is recognizable anteriorly above the condyle.

**PALATAL ELEMENTS:** In palatal view, the vomers and the palatines are disarticulated and slightly displaced, indicating a reduced contact between these elements (Rieppel, 1984). The palatine is short, wide, and toothless. The anterior half of the pterygoid (toothless) is a broad elongate plate, making the interpterygoid vacuity (pyriform recess) narrow throughout most of its length. Although incompletely preserved on both sides, the quadrate process of the pterygoid is proportionally thick (fig. 14C). It is dorsally convex, but ventrally flattened. The ectopterygoid has a slender anterior extension, which meets the palatine excluding the jugal and the maxilla from the suppressed suborbital fenestra.

**BRAINCASE:** The braincase on IGM 3/95 is poorly preserved. In ventral view, the preserved braincase floor includes part of the

basisphenoid and part of the basioccipital with the occipital condyle. The braincase floor is narrow and elongate, in keeping with the elongation of the skull. In articulation with several fragmentary bones including part of the atlas vertebra, the occipital condyle, formed by the basioccipital and the exoccipital, is partially exposed in ventral view, and seems to be rounded differing from the bipartite condition in extant gekkotans (Rieppel, 1984; Estes et al., 1988).

The lateral wall of the braincase (prootic) is poorly preserved, but it shows an alar process contacting the ventral process of the parietal. Although incompletely preserved, part of the medial wall of the recessus vena jugularis extends onto the basipterygoid process, suggesting that the crista prootica may have extended forward to this point. In dorsal view, the supraoccipital is better preserved and anterodorsally bears a prominent process (processus ascendens; processus anterior tecti of Jollie, 1960). Such a process is absent in extant gekkotans (Bellairs and Kamal, 1981; Rieppel, 1984; Estes et al., 1988). Posterolaterally, the supraoccipital has a sutural articulation with the exoccipital, which forms most of the lateral border of the foramen magnum, and is fused to the opisthotic forming the short paroccipital process. The exoccipital contributes to about one third of the occipital condyle on each side.

**MANDIBLE:** The mandibles are preserved on both sides of the specimen. The articular fossa of the lower jaw accepts the ventral condyle of the quadrate, and has a prominent buttress at its anterior border (fig. 14A). The dentary has a smooth lateral surface with no osteodermal ornamentation but a horizontal row of small mental foramina. Posterodorsally, the dentary sutures with the coronoid and the surangular, and at the junction of the three elements is a small opening representing the surangular foramen. The dentary has a long posteroventral process extending far beyond the apex of the coronoid to the mid-level of the surangular bone. Because such a long process occurs in some other gekkotans and xantusiids (see Rieppel, 1984), in some iguanians (Pregill, 1984; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989), and in more basal rhynchocephalians, it may

well represent a primitive condition for squamates.

In medial view, the splenial covers about three fourths of the Meckelian canal below the tooth row. It has a slender tongue extending anteriorly, but posteriorly terminating in front of the posteromedial process of the coronoid bone. The anterior inferior alveolar foramen opens at the splenial-dentary suture at the level of the anterior one third of the tooth row, and the anterior mylohyoid foramen is close but slightly posteroventral to the former foramen.

Most of the postdentary part of the jaw is formed by the surangular, which has a rounded dorsal surface and a lateral crest for the adductor muscles attached to the jaw. The posterior surangular foramen opens anterior to the craniomandibular joint and lateral to the buttress of the articular fossa. The suture line between the angular bone and its adjacent elements cannot be delimited, and thus, the nature of the angular is uncertain. Medially, the mandibular fossa is narrow and elongate, extending from the posteroventral process of the coronoid to slightly anterior to the craniomandibular joint. The articular and the prearticular are fused without trace of suture. The retroarticular process of the jaw is broad at the base, but narrow toward the end (as opposed to extant gekkotans). The retroarticular process is slightly deflected medially resembling extant gekkotans, but differing from them in having no lateral notch.

**DENTITION:** The marginal teeth are strongly reduced both in size and in number. Most of the premaxillary teeth are not preserved, and the number of teeth on this element cannot be determined, although it can be estimated as six or seven. The maxillary and dentary teeth are peglike, widely spaced from one another with no basal expansion at all. There are approximately 13 tooth positions on each maxilla, but the actual number cannot be determined due to inadequate preservation.

The dentary teeth are better preserved than those on the maxillae. The left dentary has six teeth preserved, and the right side has five, but a complete dentary tooth row probably contains about 15 positions on each side of the jaws. The teeth are pleurodont in terms of implantation, having about half of the

tooth shaft attached to the lateral parapet of the jaw.

#### COMPARISON AND DISCUSSION

On the basis of the phylogenetic framework presented by Estes et al. (1988), two subgroups are included in the Gekkota (but see Kluge, 1967 for different classification): the Gekkonidae (geckos) and the Pygopodidae (snake lizards). The latter family includes about 30 species, which are confined to Australia and its neighboring islands (Mattison, 1989). The group has a fossil record from Australia (Hutchinson, 1997), but is unknown from elsewhere. The former group, Gekkonidae, includes more than 800 species, and has a distribution throughout the tropical and subtropical world including hundreds of oceanic islands (Mattison, 1989). The group has Cenozoic fossil records in both western and eastern hemispheres (see Estes, 1983), but the Mesozoic record of the Gekkonidae is extremely poor and is known only from fragmentary specimens from the Gobi Desert (Alifanov, 1989b; Borsuk-Bialynicka, 1990).

The referral of the new genus and species to the Gekkota is supported by several character states as mentioned above. However, the relationship of the new taxon within the Gekkota remains unknown in the absence of a phylogenetic analysis. In recent literature, there are considerable discussions regarding the higher level phylogeny of gekkotan clades (Rieppel, 1984; Kluge, 1967, 1987; Grismer, 1988; Estes et al., 1988), and conflicting evidence from extant taxa has been the source of disagreement among authors on the placement of the Pygopodidae and Eublepharidae (see Estes et al., 1988 for comments). It has been demonstrated that fossil evidence can overturn a phylogenetic hypothesis based only on extant groups (Gauthier et al., 1988; Kemp, 1988); therefore, incorporating a primitive gekkotan from the Gobi (such as *Myrmecodaptia microphaga*) with extant taxa in a phylogenetic analysis may provide important insights into the character evolution of the group as a whole and help resolve the differences among authors.

Although the exact relationships of the new taxon cannot be ascertained at this stage,

it is clear that the new lizard retains many primitive character states in comparison to extant gekkotans. These include: retention of a rudimentary parietal foramen; a well-developed jugal that forms a complete postorbital bar; the retention of a supratemporal fenestra with a complete upper temporal arch; presence of a processus ascendens of the supraoccipital; a well-developed supratemporal bone; Meckelian canal closed by the splenial without fusion of the dentary tube; splenial extending beyond the midpoint of the dentary tooth row; retroarticular process that is narrow posteriorly; and retroarticular process lacking a lateral notch, and thus, a narrow waist at the base of the process is not developed. Retention of these primitive character states (see Estes et al., 1988 for character evaluation) suggests that the new species from the Gobi may well represent a phylogenetically important basal taxon in the gekkotan clade.

#### SCINCOMORPHA CAMP, 1923

**DEFINITION:** The most recent common ancestor of Scincoidea and Lacertoidea, and all of its descendants (see Estes et al., 1988; see also Presch, 1988).

**DIAGNOSIS:** The Scincomorpha as above defined can be diagnosed by nine synapomorphies (see Estes et al., 1988 for list of synapomorphies and citations).

**REMARKS:** The Scincomorpha include six extant familial groups (Scincidae, Cordylidae, Xantusiidae, Lacertidae, Teiidae, and Gymnophthalmidae), the interrelationships of which are still matters of debate (see Estes et al., 1988; Presch, 1988). Besides the extant families, the Scincomorpha also include several fossil groups (Paramacellodidae, Polyglyphanodontidae, Macrocephalosauridae, and Adamisauridae). Among these, the monophyly of the Paramacellodidae was reviewed by Evans and Chure (1998), while the status of the other three groups is still problematic (see below).

#### TEIIDAE GRAY, 1827

POLYGLYPHANODONTINAE GILMORE, 1942  
(Estes, 1983)

Several taxa described below represent a group of scincomorphs whose classification

has been controversial. These taxa were placed in several different familial groups (Macrocephalosauridae, Polyglyphanodontidae, Adamisauridae, Teiidae) by different authors. More recently, Alifanov (1996) classified these in the Macrocephalosauridae—a familial group the name of which was synonymized with Polyglyphanodontinae by Estes (1983). The monophyly of the Macrocephalosauridae needs to be demonstrated before the familial name can be validated; therefore, we tentatively follow Estes (1983) by placing these problematic taxa in the Polyglyphanodontinae (Teiidae).

*Adamisaurus magnidentatus* Sulimski, 1972

Figures 15, 16

**HOLOTYPE:** ZPAL MgR-II/80, incomplete skull with mandibles.

**TYPE LOCALITY AND HORIZON:** Bayn Dzak, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation.

**KNOWN DISTRIBUTION:** Djadokhta Formation—Bayn Dzak, Bayan Mandahu, and Tugrueen Shireh localities (Sulimski, 1972; Gao and Hou, 1996; this paper); Barun Goyot Formation—Khermeen Tsav and Khulsan localities (Sulimski, 1978; this paper).

**REVISED DIAGNOSIS:** A polyglyphanodontine differing from other members of the group in having the following derived character states: premaxillary spine widened and spatulate; parietal anteromedially develops a rectangular tab overlapping frontals; parietal foramen opens close to frontoparietal suture but on parietal side; jugal expanded with enlarged posteroventral process; ectopterygoid significantly enlarged, with robust ventral process; strong posterior extension of dentary covering large part of surangular, and extending close to posterior surangular foramen; posterior extension of angular bone surpassing posterior surangular foramen and terminating below craniomandibular joint; marginal teeth strongly expanded and bulbous, subacrodont; replacement teeth emerge in crypts below functional tooth row.

**REFERRED SPECIMENS:** Ukhaa Tolgod—IGM 3/96–3/101 (MAE 95-78, 31/93-164, 95-45, 94-10, 45/93-163, 48/93-163), all incomplete skulls with mandibles from Zophies Hill; IGM 3/102, 3/103 (MAE 32/93-

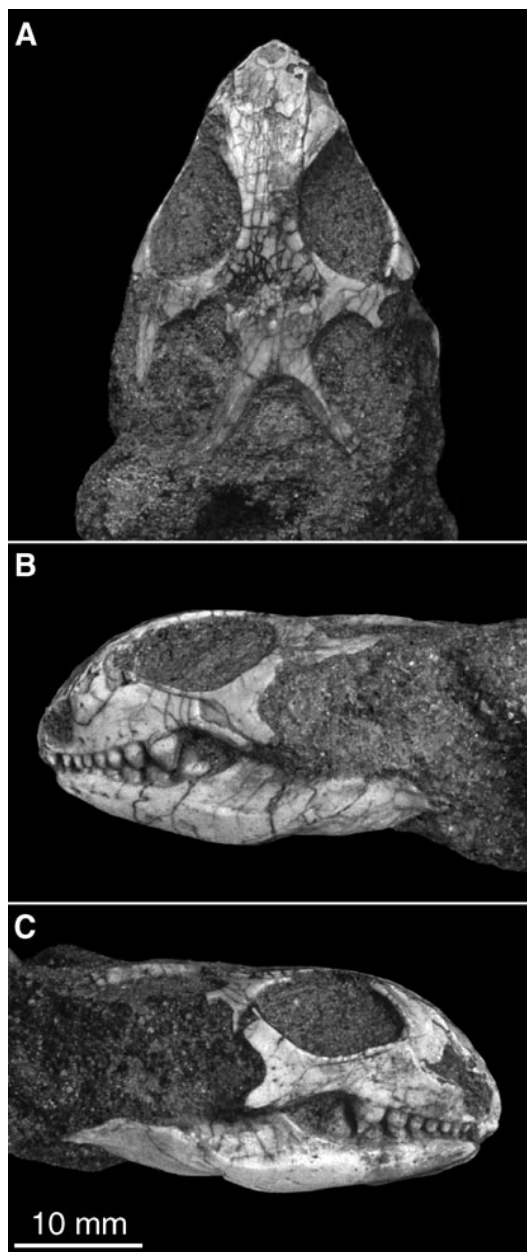


Fig. 15. Scincomorpha, Teiidae (Polyglyphanodontinae), *Adamisaurus magnidentatus*: A–C, IGM 3/116, nearly complete skull with mandibles from Tugrueen Shireh, dorsal, left and right lateral views.



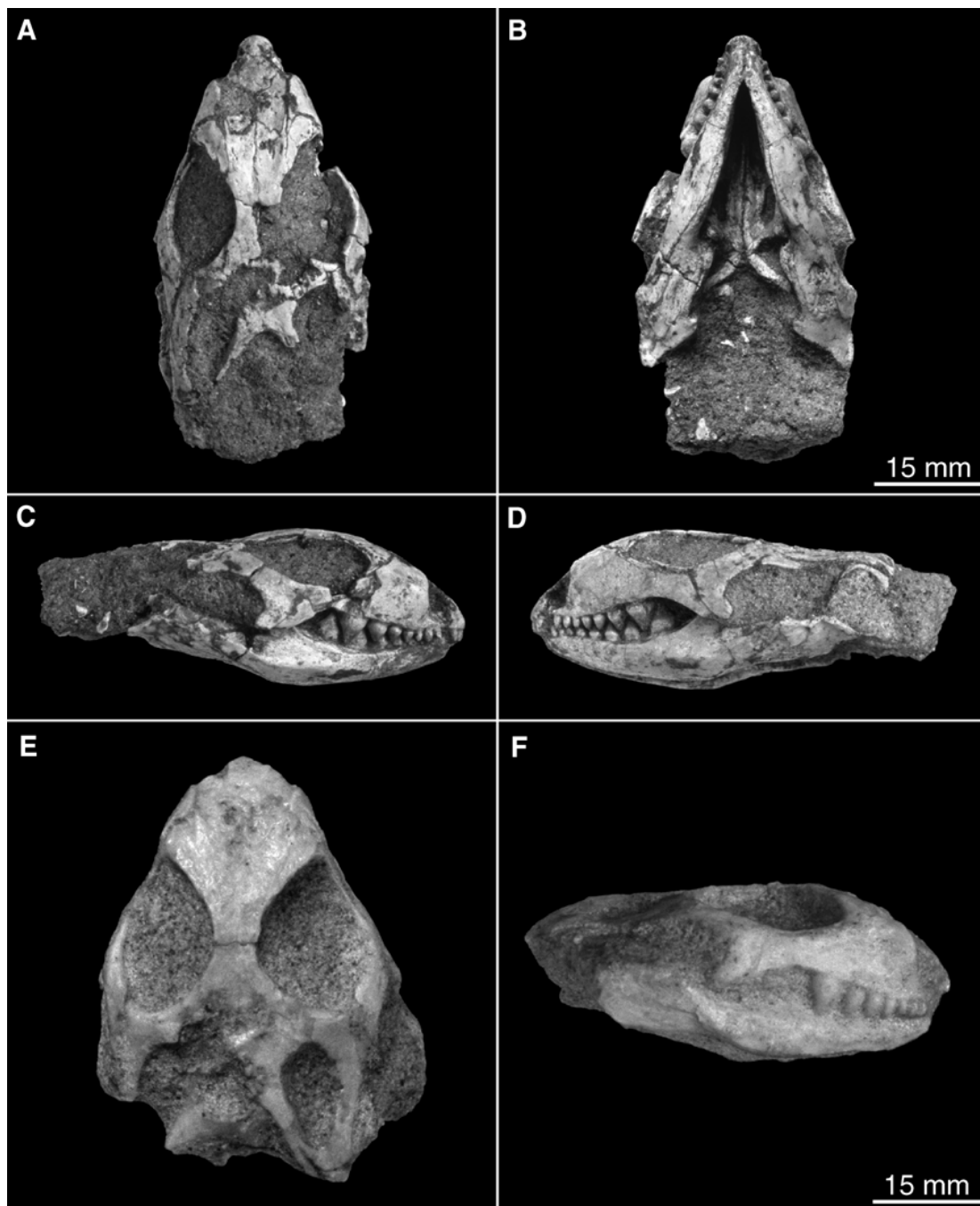


Fig. 16. *Adamisaurus magnidentatus*: A–D, IGM 3/117, incomplete skull with mandibles from Tugrugen Shireh, dorsal, ventral, right and left lateral views; E, F, IGM 3/96, incomplete skull with mandibles from Ukhaa Tolgod, dorsal and lateral views.

91, 38/93-90), incomplete skulls with mandibles from Small Exposure; IGM 3/104-3/106 (MAE 117/93-93, 118/93-93, 122/93-93), fragmentary skulls with mandibles from Zofia Exposure; IGM 3/107, 3/108 (MAE 449/93-124, 94-36), fragmentary skull with mandibles from First Strike; IGM 3/109 (MAE 95-62), fragmentary skull with mandibles from Camel Humps; IGM 3/110 (MAE 138/93-140), fragmentary skull with mandible from Camel Tits Hot Spot; IGM 3/111-3/115 (MAE 64/93-45, 56/93-110, 119/93-93, 107/93-86, and MAE 23), fragmentary skulls with mandibles from Ukhaa Tolgod without sublocality information.

Tugrugeen Shireh—IGM 3/116, nearly complete skull with mandibles articulated with partial postcranial skeleton; IGM 3/117-3/122 (MAE 252/92-14, 18/93-2, 167/93-5, 168/93-5, 226/93-3, 227/93-27), all incomplete skulls with mandibles.

Khermeen Tsav—IGM 3/123-3/125 (MAE 196/92-25, 209/92-39, 211/92-39), all fragmentary skull with mandibles.

REMARKS: Sulimski (1972) first described and referred *Adamisaurus magnidentatus* to the “?Agamidae,” but later (Sulimski, 1978) erected a monotypic family (Adamisauridae) and placed it in the Scincomorpha. Estes (1983) reviewed the available evidence and placed the species in the Polyglyphanodontinae, based on its shared similarities with macrocephalosaurs and *Polyglyphanodon*.

There is much confusion regarding the cranial morphology of this lizard, and several key sutures were incorrectly identified. First, the premaxilla was described as having only two teeth, but well-preserved specimens clearly show five to six teeth (e.g., IGM 3/116, 3/117). Second, the parietal foramen was described and figured as opening at the frontoparietal suture (Sulimski, 1972: fig. 1, 1978: fig. 1), but much better preserved new specimens (e.g., IGM 3/99, 3/115, 3/116) show that the foramen penetrates the parietal, which anteromedially develops a rectangular tab overlapping the frontals (fig. 15A). Third, the dentary was misinterpreted as having a shorter posterodorsal process overlapping the lateral surface of the coronoid and a slightly longer posteroventral process below the anterior surangular foramen (Sulimski, 1978: fig. 1). The new specimens (e.g., IGM 3/116,

3/117), however, undoubtedly show a much stronger posterior process covering a large part of the lateral surface of the surangular bone and extending to the level of the posterior surangular foramen (fig. 15B, C). Fourth, the angular bone was incorrectly reconstructed as terminating far anterior to the posterior surangular foramen (Sulimski, 1978: fig. 1A; contra fig. 1D, F), but well-preserved specimens (IGM 2/116, 3/117) clearly show that the angular extends posterior to the foramen and terminates at the level of the craniomandibular joint.

Before its skull morphology can be clarified, the phylogenetic position of this bizarre lizard cannot be assessed satisfactorily. An extensive description of the skull osteology based on well-preserved specimens and reassessment of the phylogenetic relationships of this problematic taxon will be published in a separate paper, but at this stage, we tentatively classify *Adamisaurus* in the Polyglyphanodontinae (Teiidae) as it apparently shares many character states with *Macrocephalosaurus* and *Polyglyphanodon* (Estes, 1983).

*Gobinatus arenosus* Alifanov, 1993

Figures 17, 18

HOLOTYPE: PIN No. 3142/308, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Khermeen Tsav (Alifanov, 1993b); Khulsan and Ukhaa Tolgod localities (this paper); Upper Cretaceous Barun Goyot and Djadokhta formations.

REVISED DIAGNOSIS: Differing from other closely related scincomorphs in having the following derived character states: Skull strongly narrow and elongate; small osteodermal ornamentation present on skull roof; premaxillary spine elongate and spatulate; basipterygoid process widened as short and roughly squared plate; ventral surface of braincase floor marked with three distinct depressions, one on basisphenoid and two on basioccipital; quadrate foramen present as small pocket with three openings in it; posterior border of angular bone slightly

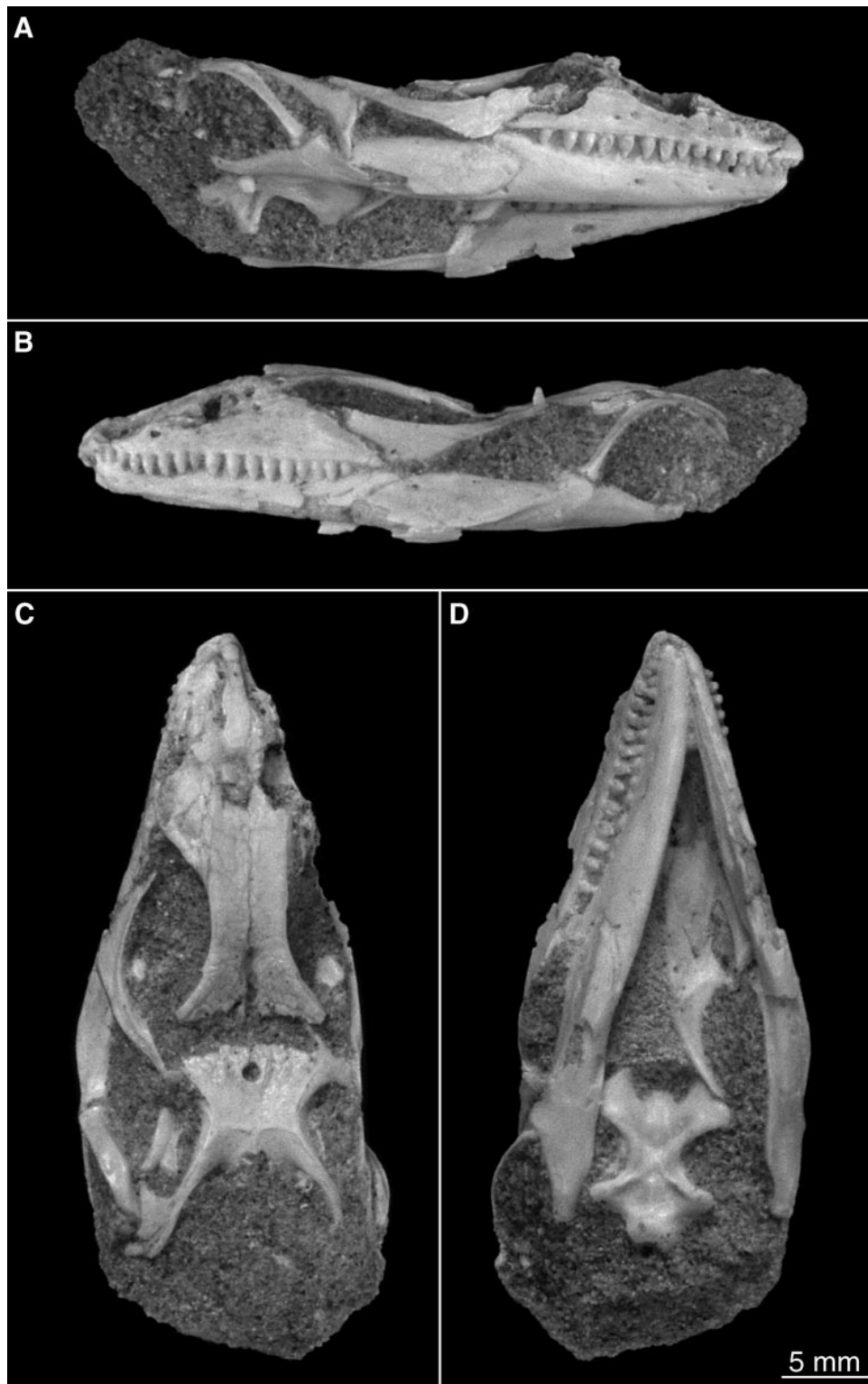


Fig. 17. *Gobinatus arenosus*: A–D, IGM 3/126, incomplete skull with mandibles from Khulsan, lateral, dorsal, and ventral views.

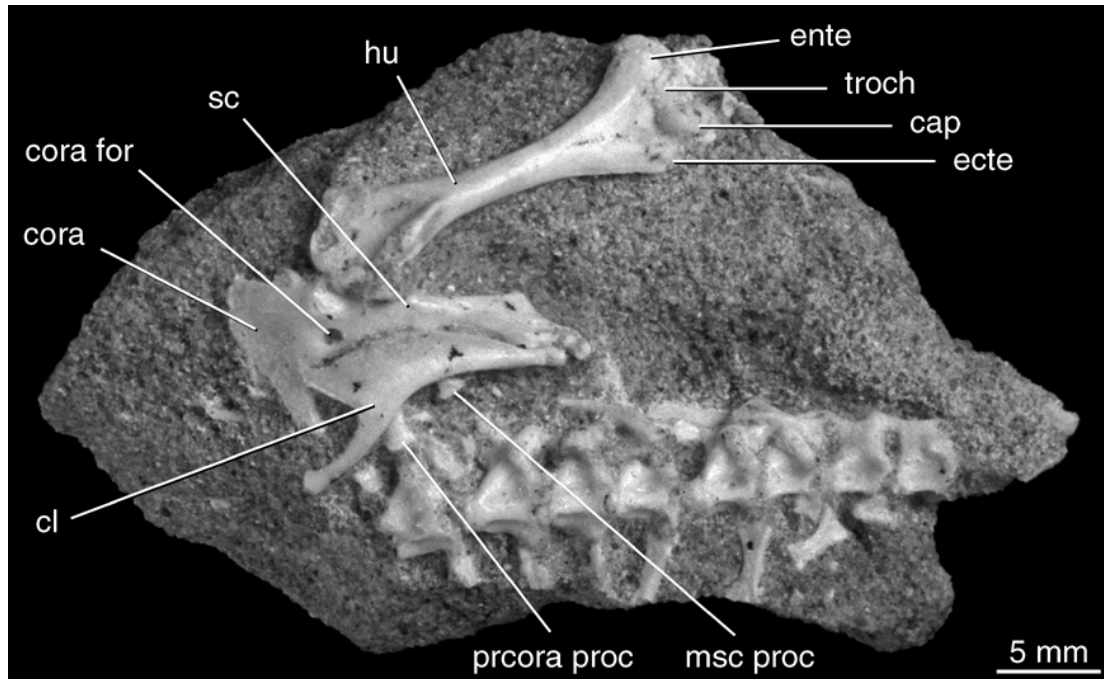


Fig. 18. *Gobinatus arenosus*: partial postcranial skeleton of IGM 3/126, in ventral view (anterior end towards right).

notched; subdental shelf reduced and sulcus dentalis entirely lost; anterior inferior alveolar foramen enlarged; angular extends to level of posterior surangular foramen; retroarticular process slender and strictly directed posteriorly; marginal teeth bulbous but widely spaced along tooth row; tooth crowns unicuspid and slightly recurved.

**REFERRED SPECIMENS:** Khulsan—IGM 3/126 (MAE 61-91), nearly complete skull with mandibles; IGM 3/127 (MAE 212/92-67), incomplete skull with partial right mandible. Ukhua Tolgod—IGM 3/128 (MAE 268/93-65), incomplete skull with mandibles.

#### DESCRIPTION

Although slightly crushed dorsoventrally, IGM 3/126 is the best preserved material known for *Gobinatus arenosus*. This specimen is described below, as it reveals important features that are unknown from the holotype.

**SKULL ROOF:** The premaxillae are fused as a single unit, which carries seven teeth (determined from the broken bases). The ante-

rior surface of the element is smooth and lacks any foramina (anterodorsal premaxillary foramina). The premaxillary spine is extremely elongate; it has a narrow shaft at the base, but the distal part is spatulate (fig. 17C). The nasal process extends to such a posterior position that it separates the nasals for about half of their length along the midline of the skull.

The nasals are paired. Each side of the element has a slender anterior process extending along the lateral border of the premaxillary spine (nasal process of premaxilla), and a short posterior process as a thin plate overlapping the anterior shelf of the frontal. The nasal laterally contacts the dorsal process of the maxilla, and is well separated from the prefrontal by an anterolateral process of the frontal (scincomorph synapomorphy, see Estes et al., 1988).

The frontals are paired, with a clear midline suture. The dorsal surface of the element is ornamented with osteodermal rugosities, the complexity of which increases posteriorly close to the frontoparietal suture. On IGM 3/



126, a short and shallow groove is seen posteriorly along the midline suture, but such a groove is not illustrated for the holotype (Alifanov, 1993b: fig. 3), and the comparable part on the referred specimens is either not preserved (IGM 3/127) or damaged (IGM 3/128). Whether this groove represents a natural condition or an artifact cannot be determined with the available sample. The frontoparietal suture shows a slight undulation, rather than being a simply straight suture.

The parietal table is trapezoidal in shape, having its maximum width at the anterior border, a slightly constricted waist and a narrow posterior width. The lateral border of the table is flanged for the lateral origin of the temporal muscles, and the posterior border is also flanged with a poorly defined median ridge. In dorsal view, the anterior part of the table is ornamented with osteodermal rugosities, but the posterior part of the table is smooth (fig. 17C). The parietal foramen is relatively large in proportion to the table, and it opens anteriorly close to the frontoparietal suture. The supratemporal process is slender and long, having a well-defined dorsal crest. The process posterolaterally contacts the supratemporal bone, posteroventrally contacts the paroccipital process of the occiput, and has no contact with the quadrate.

The maxillae are well preserved on both sides of the specimen. Each element carries 15 teeth to form a complete tooth row (see below). In lateral view, the maxilla is elongate and roughly triangular, having a low nasal process with its apex at the midlevel of the tooth row (fig. 17A, B). The lateral surface of the element is smooth with no osteodermal ornamentation and is penetrated by six lateral superior alveolar foramina (or maxillary foramina) along the ventral border of the bone. The first alveolar foramen is significantly larger than the others on the same specimen. Anteriorly, the premaxillary process overlaps the premaxilla without development of any kind of foramen or aperture at the suture. The anterior palatal process is a well-developed medial extension, but has no midline contact with its opposite element. This process has a concave dorsal surface, forming the floor of the narial opening. The posterior wall of the narial opening is penetrated by a single foramen, representing the

anterior opening of the superior alveolar canal. The foramen is as large as the anterior-most lateral superior alveolar foramen.

The prefrontal is dorsally exposed as a triangular table. It is anteriorly articulated with the dorsal process of the maxilla, medially with the frontals, but has no contact with the nasals. Posteroventral to the maxillary-prefrontal contact, the lacrimal is well developed and forms about the anterior one third of the ventral border of the orbit. Having no posteroventral process, the jugal is shaped like a hockey stick: it has a short "blade" that forms the ventral rim of the orbit together with the lacrimal and a slender and long "handle." The posterodorsal process of the bone has a pointed end that is not extended to contact the squamosal (fig. 17A–C).

The postfrontal is slender, and is clearly sutured to the postorbital laterally. Having slender and elongate anterior and posterior processes, the postfrontal is deeply forked medially to clasp the frontoparietal suture. The postorbital has a triangular base and an extremely slender and long posterior process, which fits in the medial groove of the squamosal and forms the anterior part of the supratemporal arch. The anterior border of the postorbital forms the posterior rim of the orbit, together with the postfrontal. Its posterolateral border, however, has an articular surface for the posterodorsal process of the jugal.

The squamosal is greatly reduced in thickness, with a thin and very lightly built base. It bears a well-defined dorsal process hooked anteriorly, and a notched anterior border forming the posterior rim of the supratemporal fenestra (fig. 17C). The squamosal lacks a lateral process, but the anterior process is slender and elongate, and is medially grooved for the posterior process of the postorbital. The supratemporal bone is quite well developed. It attaches to the lateral side of the supratemporal process of the parietal, as normally seen in other lizards; but it extends more posteriorly than the latter process to contact the cephalic condyle of the quadrate. Therefore, the supratemporal is involved in quadrate suspension together with the squamosal.

The quadrate is completely preserved on

both sides, and is in articulation with the skull and mandibles. The element is slenderly built and relatively straight, lacking the strong arching seen in some other lizards. The anterior surface of the quadrate has a low ridge, running from the cephalic condyle toward the ventral condyle. This vertical ridge separates the narrow tympanic crest from the much wider medial conch, and may served as the origin of the 3a portion of the MAME muscles (Oelrich, 1956; Rieppel, 1980c). Medial to the vertical ridge, the quadrate is strongly widened, concave, and is much posterior in relation to the tympanic crest. The medial border of the quadrate is straight, lacking a pterygoid lappet. The distal condyle is typically saddle-shaped with a shallow ventral notch. Above the notch is a small pocketlike depression, in which opens three small foramina for the anastomotic branch of the anterior tympanic vein and posterior condylar artery (Oelrich, 1956). A single quadrate foramen is the common condition in most lizards, and the presence of three foramina in a small pocket may well be a unique condition for *Gobinatus*.

**PALATAL ELEMENTS:** Preparation of the skull revealed a well preserved palate (fig. 17D). The vomer (left side shown on the specimen) is wide and strongly elongate, with its posterior extension approaching the level of the posterior end of the maxillary tooth row (see discussion below). Concealed by the right dentary, the right side of the vomer cannot be exposed for observation, but it must have a midline suture contact with the left vomer as indicated by the width of the left element. Most of the element is an elongate thin plate with a well-defined posteromedial process that extends between the palatines and contacts the anterior process of the pterygoid. The ventral surface of the vomer is slightly convex and smooth, lacking any trace of vomerine teeth.

The palatine is also wide and toothless. Anteriorly it has an extensive sutural contact with the vomer, and a spikelike lateral process for articulation with the posterior palatal process of the maxilla. Posteriorly, the palatine has a triangular extension, the medial border of which overlaps the lateral border of the anteromedial process of the pterygoid. The tip of this process fits in a V-shaped

notch of the pterygoid. Because of the vomer-ptyergoid contact, the palatine does not form the border of the interptyergoid vacuity (pyriform recess), and the vacuity is extremely narrow as a consequence of the width of the palatal elements.

The pterygoid is not a simple Y-shaped element, differing from most of other scincomorphs except some macrocephalosaurs and some lacertiforms. Besides the palatal and ectopterygoid processes normally seen in other lizards, it has a well-developed antero-lateral process that forms part of the medial rim of the suborbital fenestra. The antero-medial (palatal) process is long and anteriorly abuts the vomer. The lateral (ectopterygoid) process is very short, as commonly seen in other lizards, contacting the ectopterygoid and forming the posterior rim of the suborbital fenestra. Although not completely exposed on the specimen, the posterior (quadrate) process medially has an articular fossa at the base for the basiptyergoid process. Remnant pterygoid teeth are developed in the middle part of the element and extend close to the border of the interptyergoid vacuity.

The ectopterygoid is weakly developed, and it lacks a robust ventral process as seen in some other macrocephalosaurs (e.g., *Adamisaurus*). However, it has a slender anterior process contacting the palatine, and consequently excluding the maxilla from entering the suborbital fenestra. The fenestra itself is greatly reduced to a narrow slit, in keeping with the widening of the palatine and the pterygoid.

**BRAINCASE:** The braincase floor is well exposed in ventral view on IGM 3/126. Unfortunately the lateral wall and occipital aspect of the braincase cannot be observed as preserved. The braincase floor is marked with three distinct depressions (or pits): a single anterior one in the middle part of the basisphenoid and a pair posteriorly on the basioccipital (fig. 17D). Functionally, the development of these depressions probably increases attachment surfaces for the ventral axial musculature (Oelrich, 1956). The basiptyergoid process is wide and platelike. Anteromedially, the parasphenoid process has a slightly widened base, but lacks a well-ossified rostrum. The basisphenoid/basioccipital

suture is medially irregular and laterally diagonal. The basisphenoid symmetrically has on each side a very slender process extending posteriorly to form the anterior part of the spheno-occipital tubercle. The tubercle itself is slender but prominent, and is more ventrally than laterally directed. The occipital condyle is well exposed on the specimen. The basioccipital forms most of the condyle, with the exoccipitals laterally each contributing slightly less than one third of the condyle.

**MANDIBLE:** The mandible is well preserved on both sides, with only the ventral border slightly damaged on the left mandible. The lateral surface of the dentary is smooth, and is penetrated by seven mental foramina. The anterior four foramina are close to one another, but the posterior three are irregularly spaced and are far apart from one another. The last foramen opens at the midlevel of the tooth row. The posterior border of the dentary is clearly notched for the surangular and a small part of the angular bone. Both the posterodorsal and the posteroventral processes are slender and short, terminating roughly at the same level below the coronoid summit.

The surangular bone occupies most of the lateral surface of the postdentary part of the jaw. The ventral border of the surangular bone forms a prominent ridge (adductor crest) for attachment of the external mandibular adductor muscles. This crest extends along the surangular-angular suture, curving up posteriorly to the posterior surangular foramen anterolateral to the craniomandibular joint. The anterior surangular foramen is relatively large and is located posterior to the dentary-surangular suture, below the coronoid apex. Most of the lateral surface of the bone is smooth, but the ventral adductor crest is slightly ornamented with scarlike sculpture for attachment of the adductor muscles.

The angular bone is incompletely preserved on both sides, but clear impressions allow confident interpretation of the shape and extent of this element. Anteriorly in ventral view, the angular is narrowly wedged by the slender posteroventral process of the dentary, so that it is bifurcated as exposed: a small lateral process intervenes between the surangular and the dentary, and a similar process medially intervenes between the dentary

and the splenial. The medial process is penetrated by a small posterior mylohyoid foramen below the posteroventral process of the coronoid. The posterior part of the angular widens slightly and turns dorsolaterally, terminating at the same level, and immediately below, the posterior surangular foramen (fig. 17B). The posterior end of the angular is slightly notched (shown by clear impressions), differing from the strongly bifurcated condition seen in *Tchingisaurus multivagus* (see below). A much stronger extension is seen in *Adamisaurus magnidentatus*, in which the angular terminates at the level of the craniomandibular joint (see above).

The articular and prearticular are entirely fused as in many other lizards. The retroarticular process has a wide base at the level of the articular fossa of the jaw, but narrows posteriorly and ends with a slender tubercle that is strictly posteriorly directed.

In medial view, the subdental shelf is significantly reduced to a very slender structure, and the sulcus dentalis medial to the shelf is entirely lost. The splenial is slender and elongate. It anteriorly extends to a point close to the mandibular symphysis and posteriorly terminates at the level of the posterior mylohyoid foramen, where it may contact the posteroventral process of the coronoid bone. The anterior inferior alveolar foramen is significantly enlarged and located below the fourth tooth position from the back (fig. 17A). The anterior mylohyoid foramen is much smaller and is very close to, and right below, the former foramen.

**DENTITION:** As mentioned above, the premaxillae bear seven teeth counting from the broken bases. The maxillary and dentary teeth are well preserved. These teeth are characteristically thick and bulbous, and the crowns are unicuspid and posteromedially curved. The tooth implantation is subpleurodont, having about one third of the teeth attached to the low lateral parapet of the jaws. The complete maxillary tooth row contains 15 positions as shown on both sides of the upper jaws. The first five teeth are similar in size and are more strongly recurved than other teeth; the sixth tooth is significantly smaller than others, creating a "step" in the tooth row. Those in the middle and posterior

part of the tooth row have their crowns more inwardly curved than posteriorly, but the last four teeth are slightly smaller than those in front of them.

The complete dentary tooth row contains 18 positions. The lower dentition shows a similar pattern to the upper dentition, but increase in tooth size from the middle to the posterior part of the tooth row is more pronounced. Despite the thickened tooth shafts, both the maxillary and dentary tooth rows have teeth that are widely spaced from one another. No teeth show development of replacement pits, and this may reflect suppression of tooth replacement in adult individuals (MacLean, 1974).

**POSTCRANIAL SKELETON:** A partial postcranial skeleton of the same individual is preserved in association with the cranial material. Exposed in ventral view, the preserved part of the skeleton includes eight articulated vertebrae, the right clavicle in articulation with the scapula-coracoid complex, and the right humerus in articulation with the pectoral girdle (fig. 18). The interclavicle is not preserved.

The eight vertebrae include the posterior four or five cervicals, as these bear short and expanded ribs that could not have connected with the sternum. In articulation with these cervicals are the first three or four anterior dorsal vertebrae. All these vertebrae have a procoelous centrum, which is triangular in ventral view. As the vertebrae are exposed in ventral view, the morphology of the neural arch cannot be examined. The centrum of all these vertebrae is ventrally crested, but the sharpness of the crest is reduced posteriorly. The intercentra remain separate from the centrum and are in an intervertebral position.

The clavicle is slightly shifted laterally, and so is in articulation with the anterior border of the scapula blade. The element is angulated, but has no clavicle fenestra. The proximal end is a narrow, slender rod. The main part of the clavicle is a wide blade with a sharp edge that dorsally becomes slender and extends to the dorsal end of the scapula to presumably contact the suprascapula (an unossified element not preserved).

The scapula and the coracoid plate are completely fused, as no suture can be delimited. The scapula is thick and narrow, more

rodlike than bladelike. The anterior border of the scapula is largely covered by the clavicle, but two barlike structures exposed represent the mesoscapular process and the procoracoid process, respectively (fig. 18). The rounded coracoid foramen is located between the glenoid fossa and the notched border of the anterior coracoid emargination. No posterior coracoid emargination is developed.

The right humerus is completely preserved and is exposed in ventral view. It has a slender shaft with expanded proximal and distal ends capped by ossified epiphyses. Proximally, it has an anterior crest for the attachment of *M. subcoracoscapularis*, and posteroventral to the crest is a triangular depression for *M. coracobrachialis brevis* (Romer, 1956). The distal end of the bone is slightly wider than the proximal end. The entepicondyle is more robustly developed than the ectepicondyle, but neither an entepicondylar nor an ectepicondylar foramen can be identified on this specimen. Between the condyles are the capitellum (or radial condyle) and the trochlea (or ulnar condyle) as seen in other lizards. Differing from the common condition seen in most lizards, however, a well-defined triangular fossa is developed above the two condyles, and a foramen opens in the fossa. A similar condition is seen in extant *Tupinambis teguixin* (AMNH 141941), but the actual nature of this similarity needs further investigation.

#### COMPARISON AND DISCUSSION

In tooth morphology and jaw structures, all three referred specimens clearly show diagnostic features of *Gobinatus arenosus*; accordingly, they are referred to this particular species. One specimen (IGM 3/126) represents the best-preserved material known for this lizard, allowing us to revise the diagnosis of the species (see above). Alifanov's (1993b) diagnosis included two other features: trigeminal notch anteriorly closed, and pterygoid strongly bent to the level below the maxillary tooth row; however, the type specimen (PIN No. 3142/308) as figured appears to show that both the braincase and the pterygoid have been distorted (see Alifanov, 1993b: fig. 3c). Therefore, the two features



in question are more likely to be artifacts than to be diagnostic of the species.

The tooth number of this species is individually variable. The holotype was described as having 20 maxillary and 24 dentary teeth (Alifanov, 1993b), while IGM 3/126 and 3/128 both have 15 maxillary teeth, and the former specimen has 18 dentary teeth. Therefore, the variation range is about five or six positions.

The relationships of this scincomorph lizard are uncertain, although it was classified in the Mongolochamopinae (Macrocephalosauridae) by Alifanov (1993b). In light of this uncertainty, it is worthwhile to discuss a few features that may bear on the relationships of this lizard.

(1) The vomer is strongly elongate, with its posterior extension approaching the level of the posterior end of the tooth row. Such a condition of vomer elongation is similar to that in many advanced anguimorphs (see Rieppel, 1980a). However, in *Adamisaurus* the vomer is also extremely wide, as is typical of other scincomorphs. Anguimorphs have an extremely narrow vomer associated with the elongation of the fenestra exchoanalis (Rieppel, 1980a).

(2) As shown on both the holotype (Alifanov, 1993b) and the new specimens, the posterior end of the angular bone in *Gobinatus* is slightly notched. The notch condition differs from the deeply bifurcated condition in *Tchingisaurus multivagus* (see below), and the angular extends to the posterior surangular foramen. Pending the evaluation of this character (i.e., possible homology), the condition in *Gobinatus arenosus* may represent a more plesiomorphic state than that in *Tchingisaurus multivagus*. Our observation of a new specimen of *Pyramicephalosaurus cherminicus* (see below) indicates that the latter species may also share this condition with *Gobinatus arenosus*.

(3) In spite of their significant difference in size (30 mm vs. 50 mm), *Gobinatus arenosus* and *Dzhadochotosaurus giganteus* as figured (compare Alifanov, 1993b: figs. 2, 3) are astonishingly similar to one another in general configuration and several specific features. They both have slender processes of the forked postfrontal, both have the suborbital fenestra reduced to a narrow slit, and

both have bulbous teeth with unicuspid crowns. The structural differences recognized by comparison of the figures are that *Dzhadochotosaurus giganteus* has substantially longer nasals and lacks a posterior notch of the angular. A slender spikelike premaxillary spine is figured for the holotype of the species; however, this morphology is highly doubtful as the same specimen (PIN No. 3143/103) is figured as having a complete premaxilla in dorsal view, but in lateral view it is figured as missing most of this element (Alifanov, 1993b: fig. 2).

Nonetheless, *Gobinatus arenosus* and *Dzhadochotosaurus giganteus* are probably more closely related to one another than to any other scincomorphs, as indicated by their astonishing similarities in skull configuration, jaw structure, and tooth morphology.

#### *Tchingisaurus multivagus* Alifanov, 1993

Figure 19

HOLOTYPE: PIN No. 3142/309, nearly complete left mandible with well-preserved teeth.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Nemegt Basin, Mongolia; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Barun Goyot Formation—Khermeen Tsav (Alifanov, 1993b); Djadokhta Formation—Ukhaa Tolgod (this paper).

REVISED DIAGNOSIS: Polyglyphanodontine differing from other members of the group in having the following derived character states: Parietal foramen greatly reduced to a minute opening on parietal table; marginal teeth have cylindrical basal part of shaft with abruptly expanded and bulbous crowns; cusp-bearing part of crowns laterally compressed and symmetrically tricuspid with higher central cusp and equally developed lateral accessory cuspules; angular bone enlarged and posteriorly bifurcated; prominent adductor crest present on lateral surface of surangular; retroarticular process straight, slender, and pointed.

REFERRED SPECIMEN: IGM 3/129 (MAE 95-92), incomplete skull articulated with mandibles from Ukhaa Tolgod (Camel Humps sublocality).

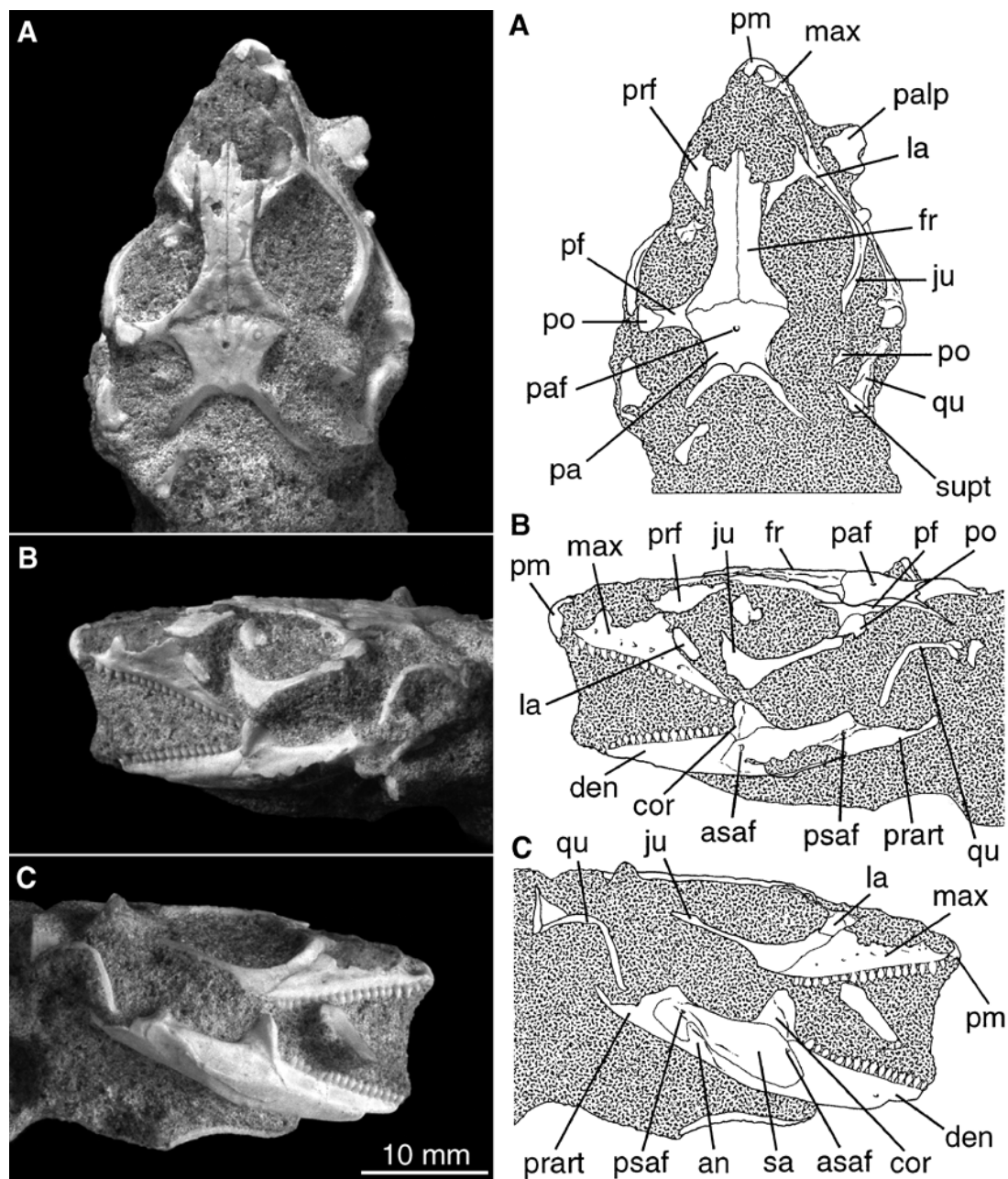


Fig. 19. *Tchingisaurus multivagus*: A–C, IGM 3/129, incomplete skull with mandibles, dorsal, left and right lateral views.

#### DESCRIPTION

This species is previously known from a single mandible only. IGM 3/129 is the first skull material known for this species; there-

fore, it is described in detail. Although fairly complete, the specimen is preserved with an open-jaw position, and this makes it difficult to expose the palatal region without removal of the lower jaws.

**SKULL ROOF:** The skull has a pointed snout with a laterally bulging cheek region, giving it a subtriangular shape anteriorly (fig. 19A). The orbit is large and subcircular comprising a large part of the facial region of the skull. The premaxillae are fused, and bear seven teeth. The anterior surface of this element is smooth, without premaxillary foramina. The spine is broken and largely missing; hence, the length and shape of the spine cannot be determined. The nasals are not preserved, but impressions indicate that they were paired and would laterally contact the dorsal process of the maxilla.

The frontals are paired and slightly constricted between the orbits. These elements are anteriorly broken and their suture pattern with the nasals, and possibly with the maxilla, cannot be identified; however, they laterally have an extensive sutural contact with the prefrontal. The dorsal surfaces of the bones are lightly ornamented with osteodermal rugosities. The posterior borders of the frontals each have a shelf underlying the anterior border of the parietal.

The parietal is short and trapezoidal. Its anterior border slightly overlaps the frontals and has an irregular wavy suture with the frontals. The parietal foramen is greatly reduced as a small, round opening located close to the center of the parietal table. The lateral flange of the table is deep and nearly vertical, indicating a lateral origin of the temporal muscles. The table sharply narrows posteriorly, and the posterior flange of the table is more sloped than the lateral flange (fig. 19A). The supratemporal process of the parietal is slender, and is much longer than the parietal table. The articulation pattern of the supratemporal process with the quadrate is unknown, owing to the lateral dislocation of the quadrate on both sides of the skull.

The maxilla is incompletely preserved on both sides (fig. 19B, C). The dorsal process is high, rising above the anterior two thirds of the tooth row. The lateral surface of the process is smooth, slightly concave, and is ventrally penetrated by a row of small lateral superior alveolar foramina. The premaxillary process is a very short spike, attached to the lateral surface of the premaxillae. The anteromedial process is so strongly developed that it extends medially behind the base of

the premaxilla, nearly contacting the opposite element. No aperture is developed at the premaxillary-maxillary suture. The posterior process of the maxilla is a short triangle. Along the dorsal margin of the process are the well-developed lacrimal and anteroventral processes of the jugal, which together form the ventral border of the large orbit. Like in *Gobinatus arenosus* (see above), the jugal has an extremely slender posterodorsal process and lacks a posteroventral process, but the jugal of this species is more angulated than in the former species. The dorsal process of the jugal contacts the postorbital along a short suture. It can not be determined whether the jugal contacted the squamosal, because of the incomplete preservation of the latter element on the specimen.

The prefrontal is well developed, forming the anterior rim of the orbit. It is laterally articulated with the maxilla, medially with the frontal, but is possibly separated from the nasal by the anterolateral process of the frontal (not preserved). The frontal process of the prefrontal is very short, terminating far anterior to the midlevel of the orbit. The postfrontal and the postorbital are clearly separate elements, and the two together form a short bar separating the orbit from the supratemporal fenestra. The postfrontal is medially well forked to clasp the frontoparietal suture, and is laterally notched to receive a small triangular wedge of the postorbital. The latter element has a very short anterior process (shown on the left side), but the posterior process (preserved on the right side) is slender and long.

Only the right squamosal is partially preserved. It is slightly dislocated vertically and is closely associated with another small splint bone, which is probably the supratemporal. The base of the squamosal is widened slightly, and has a weakly developed dorsal process. The anterior process of the squamosal is slender and is medially grooved for reception of the posterior process of the postorbital.

The quadrate is well preserved on both sides. The element lacks an anterior arching, with a straightly vertical tympanic crest (except for the lateral edge of the cephalic condyle). Anteriorly, the quadrate has an extremely narrow and convex lateral part, but



a much wider and strongly concave medial extension. The medial crest is oblique, running from the medial side of the cephalic condyle to the distal condyle. The crest lacks a pterygoid lappet of the quadrate. The distal condyle is ventrally notched, with a well-defined lateral epicondyle. Above the notch, a single quadrate foramen is present on the anterior surface as seen in most of other lizards generally.

**MANDIBLE:** The mandible is robust, having a strongly convex lateral surface. The posterior border of the dentary is deeply notched to a level slightly anterior to the posterior end of the dentary tooth row (contra Alifanov, 1993b: fig. 7). The coronoid process of the dentary does not extend onto the anterior surface of the coronoid, but on its ventral edge it fully articulates to the surangular bone, leaving no space for the coronoid to wedge in. The dentary-surangular suture in this specimen ends dorsally at the anteroventral tip of the coronoid dorsal process, rather than at the midlevel of the latter process as figured for the holotype (Alifanov, 1993b: fig. 7). The posteroventral process of the dentary has a similar extension, and terminates at the same level as the posterodorsal process.

Anteriorly, the surangular has a blunt process that fits into a notch of the dentary. The anterior surangular foramen is small and close to the surangular-dentary suture, below the anterior tip of the coronoid summit. The posterior surangular foramen is even smaller, and is located posterodorsally, close to the glenoid fossa of the jaw. Running between the two foramina is a ventrally curved adductor ridge on the lateral surface of the surangular. Ventral to this ridge, the angular bone is proportionally wide and has extensive exposure on both the medial and lateral side of the jaw. As in the holotype specimen, the angular is posteriorly bifurcated and terminates anterior to the posterior surangular foramen.

**DENTITION:** The premaxillae are fused into a single bone with seven teeth. The crown pattern of the premaxillary teeth cannot be observed because of erosion. The complete maxillary tooth row contains 18 teeth (shown on both sides of the specimen). The first three maxillary teeth are larger than the rest,

and are caniniform with pointed, unicuspid crowns. The other 15 teeth are conspicuously bulbous and tricuspid; however, the base of the crown is very narrow (see fig. 19B, C). The central cusp is well developed, and far more prominent than the lateral accessory cusps. The lateral cusps are actually not well defined, instead, they are miniature horizontal crests that are not well separated from the main cusp. This crown pattern is different from that in *Pyramicephalosaurus cherminicus* (see below), in which the three cusps are similar in height and the lateral cusps are clearly separated from the main cusp by a well-developed groove.

The dentary tooth row is incompletely preserved on both sides, because the anterior tip of both jaws is missing. The left side has 14 teeth and the right side has 16 teeth preserved. The total number of dentary teeth can be estimated as about 19–20 on comparison with the upper dentition. This estimation is very close to the holotype mandible (PIN No. 3142/309), which is illustrated as having 19 teeth (but described as having 17, see Alifanov, 1993b). All the marginal teeth are subpleurodont, with slightly less than half of the tooth attached to the lateral parapet of the tooth row. This description is different from the figure of the holotype mandible (Alifanov, 1993b: fig. 7), in which the dentary teeth are figured as acrodont (see comments below).

#### COMPARISON AND DISCUSSION

Alifanov (1993b) named *Tchingisaurus multivagus* on the basis of a single left mandible (PIN No. 3142/309) from Khermeen Tsav (Barun Goyot Formation), and referred the species to the Macrocephalosauridae Sulimski, 1975. Because the family Macrocephalosauridae is inadequately diagnosed and the monophyly of the group is highly questionable (Estes, 1983), the referral of *Tchingisaurus multivagus* to the family is problematic. We tentatively classify the taxon in the Teiidae, pending wholesale revision of this and allied taxa.

The new specimen from Ukhaa Tolgod is identical to the holotype of *Tchingisaurus multivagus* in jaw configuration, crown pattern of the marginal teeth, and in having an



angular that is posteriorly bifurcated. On the basis of these similarities, the new specimen is referred to this species. The deceptive differences in number and implantation of the teeth in the two specimens (see above) are probably the result of a descriptive or illustration error in the original description of the holotype specimen. Alifanov (1993b: 89) described the teeth on the holotype as “high above level of upper margin of subdental crest,” but figured them as acrodont (Alifanov, 1993b: fig. 7).

In terms of tooth morphology, the closest similarity of *Tchingisaurus multivagus* is to *Pyramicephalosaurus cherminicus* Alifanov, 1988. The two forms share similarities in having bulbous teeth with strongly constricted crown bases, but are clearly different from one another in detailed crown pattern and the mode of tooth implantation as described above (see also description of *P. cherminicus* below). In addition, these two species (together with *Gobinatus*) differ from the so-called macrocephalosaurs in lacking a prearticular crest medially at the base of the retroarticular process. Such a crest (which differs from the fingerlike process in iguanians) occurs in most lacertids, xantusiids, and teiids (see Estes et al., 1988: character 73). Functionally, the crest is for attachment of the pterygoideus muscle (Rieppel, 1980c), and lack of such a crest in *Tchingisaurus multivagus* may indicate a fundamental difference in muscle attachment from the macrocephalosaurs.

If Alifanov's (1993b) observation is correct, *Pyramicephalosaurus cherminicus* lacks a posterior bifurcation of the angular (but see below) that is characteristic of *Tchingisaurus multivagus*. Other differences that Alifanov (1993b) mentioned are either ambiguous or invalid. For example, *Tchingisaurus multivagus* was described as differing from *Pyramicephalosaurus cherminicus* in having a “larger number of teeth,” but the holotype of the former taxon is ambiguously described as having 17 teeth and figured as having 19. Furthermore, the lower dentition of *Pyramicephalosaurus cherminicus* on the holotype is incomplete (see Alifanov, 1988: fig. 3); thus, the total number of lower teeth on the specimen is, in fact, unknown (a new speci-

men from Khulsan has 16 dentary teeth, see below).

As alluded to above, the new specimen from Ukhaa Tolgod has subpleurodont teeth, differing from the “acrodont” condition of the holotype mandible figured by Alifanov (1993b: fig. 7). This supposed difference is probably not individual variation, but is likely to be observational. The holotype specimen is unavailable for this study, and the uncertainty about its tooth implantation cannot be clarified until the specimen is reexamined.

*Pyramicephalosaurus cherminicus* Alifanov, 1988

[nom. correct. Alifanov, 1993b  
(pro *Pyramicephalosaurus cherminicus*  
Alifanov, 1988)]

Figure 20

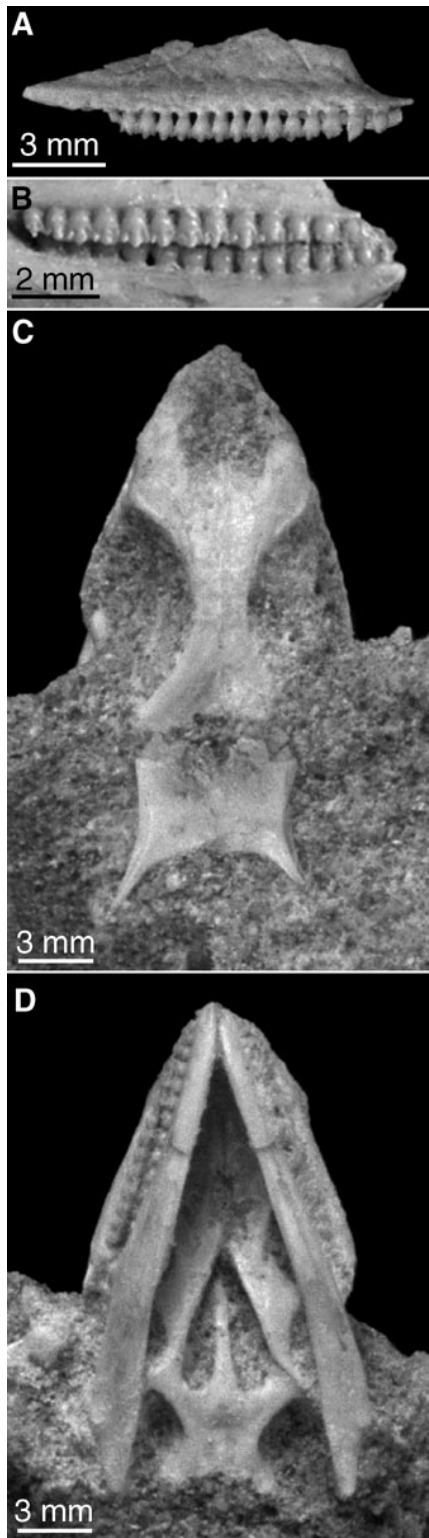
HOLOTYPE: PIN No. 3142/307, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Khermeen Tsav and Khulsan, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

REVISED DIAGNOSIS: Scincomorph lizard distinguished from other members of the group by the following derived character states: skull lightly built, with pointed snout; parietal table rectangular, having relatively straight lateral borders; well-ossified parasphenoid rostrum extending far anteriorly; marginal teeth laterally swollen but having strongly constricted base of crown; cusp-bearing part of crown laterally compressed and conspicuously tricuspid; lateral accessory cusps at same height but well separated from central cusp by well-defined groove; tooth attachment subacrodont, with extremely low parapet of tooth row less than one third of tooth height.

REFERRED SPECIMENS: IGM 3/130 (MAE 91-30), incomplete skull with mandibles; IGM 3/131 (MAE 70/244), incomplete right maxilla with well-preserved teeth; both specimens from Khulsan, Barun Goyot Formation.



## DESCRIPTION

The newly recovered specimen IGM 3/130 is an incomplete skull with mandibles, which provides information on skull features of the species that are unknown from the holotype. As the specimen reveals supplementary information for this poorly known species, a description based on this specimen is given below.

**SKULL ROOF:** Although not preserved, the nasals were probably paired as in the holotype (Alifanov, 1988: fig. 3) as is suggested by the articular surfaces on the anterior part of the frontals. The frontals are paired, with a clear midline suture. The dorsal surface of the bone is smooth, without osteodermal ornamentation. Anterolaterally, the frontal contacts the prefrontal and the dorsal process of the maxilla, and hence, separates the prefrontal from contact with the nasal. The posterior border of the frontals is incomplete, and the actual suture pattern with the parietal and the location of the parietal foramen cannot be determined. The parietal table is also incompletely preserved, but displays a roughly square outline with very short supratemporal processes.

The premaxillae are not preserved, but are known (from the holotype) to be a single unit (Alifanov, 1988: fig. 3). The maxillae are nearly complete on both sides. The dorsal process is located above the anterior part of the tooth row, and an elongated posterior process extends below the jugal. The lateral surface of the maxilla is smooth, but is penetrated by six irregularly spaced lateral superior alveolar foramina along the ventral border of the bone. Anteriorly, the premaxillary process is very short, and this process is separated from the anteromedial process by a small notch. The latter process is so well developed that it closely approaches and

←

Fig. 20. *Pyramicephalosaurus cherminicus*: A, IGM 3/131, incomplete right maxilla with well-preserved teeth from Khulsan, lateral view; B, close-up shot showing crown pattern of IGM 3/130; C, D, IGM 3/130, incomplete skull with mandibles from Khulsan, dorsal and ventral views. Dislocated parietal is digitally placed back to its original position.

nearly contacts its opposite element. At the anterior surface of the nasal process of the maxilla, the anterior interior alveolar foramen is clearly identifiable. It opens slightly above the level of the lateral superior alveolar foramina.

The medial aspect of the maxilla is best shown on IGM 3/131. The supradental shelf is extremely thin but is well developed. The dental gutter, however, is lost in keeping with the development of subacrodonty. Anteriorly above the shelf, and at the level of the third and the fourth teeth, a small pocketlike structure is developed for articulation with the septomaxilla. The posterior interior alveolar foramen is large, located above the sixth tooth position from the rear. The supradental shelf posteriorly lacks a palatal process, instead, a scarlike surface dorsally on the shelf indicates the palatine-maxillary articulation. A short groove is developed posterodorsally on the shelf for articulation with the anteroventral process of the jugal.

The prefrontal is preserved on both sides. It has extensive sutural contact with both the maxilla and the frontal, but is separated from the nasal (not preserved) by the anterolateral process of the frontal. The lacrimal is well developed. It forms the anterior one third of the ventral border of the orbit. The jugal is slender, and is only preserved on the right side of the specimen. The anteroventral process of the jugal forms the posterior two thirds of the ventral rim of the orbit. The base of the jugal is slightly expanded, but lacks a clearly defined posteroventral process. The posterodorsal process is slender, forming a complete bar at the back of the orbit.

The postfrontal and postorbital are not preserved; neither are the squamosal and the supratemporal. These elements are also unknown from the holotype, therefore, the morphologies of the supratemporal fenestra and upper temporal bar remain unknown for this species.

**PALATAL ELEMENTS:** The palatal aspect is unknown on the holotype, but is well preserved on IGM 3/130 (fig. 20D). Anteriorly, the vomers are paired, having a straight sutural contact along the midline. The ventral surface of the element shows no vomerine teeth, but a slanted, transverse ridge is well

developed anteriorly. Medial to this ridge, each side has two vomerine apertures penetrating the vomer. The anterior aperture is significantly larger than the posterior one, and the two are widely separated from one another. Posteriorly, the vomer has a triangular notch that receives the palatine. The vomer has a slender and ventrally ridged posteromedial process, which separates the palatines along the midline but does not contact the pterygoid.

The palatines are very wide, reducing the size of the anterior part of the pyriform recess to a narrow slit. The lateral wing of the element contacts both the maxilla and the ectopterygoid (see below), forming the anterior border of the suborbital fenestra. The palatine forms the anterior half of the medial border of the suborbital fenestra, and it posteriorly has a long triangular process wedging into a small notch of the pterygoid. The concave ventral surface of the bone is smooth, without any trace of palatal teeth.

The pterygoid has a relatively short anteromedial process, which laterally articulates with the palatine and medially forms the border of the pyriform recess. There is a significant gap between it and the posterior tip of the vomer. At the base of the anteromedial process, remains of pterygoid teeth are clearly identifiable along the medial edge of the pterygoid. An even shorter anterolateral process forms the posterior half of the border of the suborbital fenestra. The lateral process of the pterygoid is short and robust, contacting the ectopterygoid and forming part of the posterior border of the suborbital fenestra. The posterior process is slightly shorter than the anterior process, but is laterally compressed as a blade. The medial surface of the process is only slightly concave.

The ectopterygoid is proportionally a small element, with a very weakly developed ventral process. However, a slender anterior extension forms the entire lateral border of the suborbital fenestra and excludes the maxilla from the fenestra by contact with the vomer.

**BRAINCASE:** The supraoccipital and exoccipital parts of the braincase are not preserved, but the ventral and partial lateral aspects of the braincase were exposed with preparation for observation. The basisphe-

noid is proportionally large, forming more than two thirds of the floor of the braincase. It anteriorly has a well-ossified cultriform process, which is slender and extremely elongate, extending to the anterior end of the pyramiform recess and slightly bending dorsally. The basiptyergoid process is short and has a well-defined shaft and slightly expanded distal end articulating with the pterygoid. The recessus vena jugularis is broken on both sides of the basisphenoid, and only part of the prootic is in articulation with the basisphenoid. The basioccipital part of the braincase floor is not preserved.

**MANDIBLE:** The lower jaw is preserved on both sides of the specimen (IGM 3/130), with little damage of the dentaries. The mandible is very slenderly built, and is strongly laterally compressed. The lateral surface is smooth, and is penetrated by a row of small mental foramina, the number of which cannot be determined owing to breakage of the dentary. Posteriorly, the dentary has a well defined coronoid process, which does not cover the lateral surface of the coronoid bone. The anterior surangular foramen opens below this small process. The posteroventral process of the dentary is broken on both sides, and thus its extent cannot be determined on this specimen.

The lateral exposure of the surangular is relatively narrow, as it is ventrally extensively covered by the angular (shown as clear impressions on both sides). The impressions of the angular show that the element extends posterodorsally toward the posterior surangular foramen, which opens anterior to the craniomandibular joint, as normally seen in other forms. The posterior end of the angular is slightly notched, although it is not strongly bifurcated as in *Tchingisaurus multivagus*.

In medial view, the splenial is slender and elongate, closely approaching the mandibular symphysis. The anterior inferior alveolar foramen is twice the size of, and directly above, the anterior mylohyoid foramen; the two foramina are located at the level of the posterior one third of the dentary tooth row. The posterior extension of the splenial terminates below the anteroventral process of the coronoid bone. Above the splenial, the subdental shelf of the dentary is extremely slender and a sulcus dentalis is nearly lost.

The mandibular fossa is wide open posterior to the ventral process of the coronoid. The retroarticular process is slender, straight and directed posteriorly. It bears no medial crest (prearticular crest) or angular process.

**DENTITION:** The marginal teeth of *Pyramicephalosaurus cherminicus* are closely similar to those of *Tchingisaurus multivagus* in being bulbous with a strong constriction at the base of the crowns. However, the teeth of the two species are different in crown patterns and in the mode of attachment to the jaws. Differing from the blunt, low-cuspid crowns of *Tchingisaurus multivagus*, the crowns of *Pyramicephalosaurus cherminicus* are more sharply pointed, and the well-developed lateral cuspules are clearly set off from the central cusp by a vertical groove. Also, the cusp-bearing part of the crowns are strongly laterally compressed and flared. In terms of tooth attachment, the high-crowned marginal teeth of *Pyramicephalosaurus cherminicus* have less than one third of the tooth height attached to the extremely low lateral parapet of the tooth row. This type of tooth attachment is best termed as subacrodont (Gao and Fox, 1991, 1996).

On IGM 3/130, each maxilla has 13 teeth preserved, with probably the one or two anteriormost missing in comparison with the other known specimens. Both the holotype (Alifanov, 1988: fig. 3) and IGM 3/131 have 15 teeth for the complete maxillary tooth row. The first maxillary tooth is always slender and unicuspid, while the second tooth could be the same as the first (IGM 3/131) or weakly tricuspid (as figured for the holotype, see Alifanov, 1988: fig. 3a). The third and following teeth have strongly laterally compressed and flared crowns, and the crowns are pointedly tricuspid.

The dentary tooth row on IGM 3/130 has 14 teeth exposed on the right side, and a total of 16 for the complete tooth row on the left side of the jaw. The first tooth is slender and conical, the second is slightly thicker with an incipient anterior accessory cuspule. Like in the upper dentition, the third through the sixteenth are strongly tricuspid.

#### COMPARISON AND DISCUSSION

The referral of the new specimens from Khulsan to *Pyramicephalosaurus chermini-*



*cus* is primarily based on the diagnostic tooth form of the species (see diagnosis). The species is previously known from a single specimen (holotype: PIN No. 3142/307) from Khermeen Tsav, consisting of a partial skull, jaw material and vertebrae (Alifanov, 1988). The new specimen IGM 3/130 from Khulsan provides more complete skull material for the species, and reveals some taxonomically important features of this poorly known species.

From the skull roof elements, the frontals are paired and each side sends a slender anterolateral process separating the nasal from the prefrontal as in most other scincomorphs. In the palatal aspect, the ectopterygoid anteriorly contacts the palatine excluding the maxilla from entering the suborbital fenestra. The latter feature, together with the development of subacrodonty, indicates a teiid relationship of *Pyramicephalosaurus cherminicus* within the Scincomorpha.

The angular bone is not preserved on IGM 3/130, but clear impressions on both sides indicate that the posterior end of the element is slightly notched, posterodorsally approaching the posterior surangular foramen. This condition of the angular bone is different from the figure of the holotype mandible, which shows a posteriorly nonbifurcated angular bone (Alifanov, 1988: fig. 3). Comparison with the holotype specimen is necessary to clarify this morphology.

#### *Macrocephalosaurus* Gilmore, 1943

TYPE SPECIES: *Macrocephalosaurus ferrugineus* Gilmore, 1943.

KNOWN DISTRIBUTION: Djadokhta and Barun Goyot formations; Mongolian Gobi Desert.

REVISED DIAGNOSIS: Differing from other closely related scincomorphs in having the following derived character states: postorbital elongate, reaching posterior border of supratemporal region; supratemporal lost by fusion with squamosal; parietal short, with parietal foramen near or on frontoparietal suture; suborbital fenestra small or closed; angular process of lower jaw reduced to obtuse angle; teeth high-crowned and slender; crowns flared, laterally compressed, and multicusped.

#### *Macrocephalosaurus* sp.

Figure 21

SPECIMENS: IGM 3/132, partial skull and postcranial skeleton; IGM 3/133 (MAE 51/93-25), disarticulated vertebrae.

LOCALITY AND HORIZON: Ukhaa Tolgod, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

REMARKS: IGM 3/132 consists of well-preserved premaxillae, maxillae, and partial postcranial skeleton. The premaxillae are fused, and carry five pleurodont and unicuspid teeth and vacant spaces for four others. The maxillary teeth are typical of *Macrocephalosaurus*, being high-crowned, and having a flared and multicuspid crown pattern. Although the teeth are similar to those of *Macrocephalosaurus gilmorei*, the specimen cannot be confidently identified to species without reference to other skull morphology.

IGM 3/133 consists of several associated dorsal vertebrae. These are generally macrocephalosaur-type, as the vertebral centrum is strongly elongate and posteriorly narrowed. However, lack of cranial material makes it impossible to refer this material to any known species.

It is worth noting that IGM 3/132 and 3/133 are the only *Macrocephalosaurus* material out of over 1000 specimens that were collected from the Ukhaa Tolgod locality. As this remarkably productive locality has been extensively sampled for several years, this ratio likely reflects the rarity of this particular herbivorous lizard in the Cretaceous vertebrate community at Ukhaa Tolgod. The paucity of this and other herbivorous lizards at this locality may or may not reflect stratigraphic differences from the Khermeen Tsav and Khulsan localities, as large herbivorous species are also known from the classic Bayn Dzak locality (Djadokhta Formation). It is likely that the rarity of large herbivorous lizards at some localities indicates environmental differences between these sites.

#### *Macrocephalosaurus chulsanensis*

Sulimski, 1975

Figure 22

HOLOTYPE: ZPAL MgR-I/14, nearly complete skull with mandibles and postcranial skeleton.

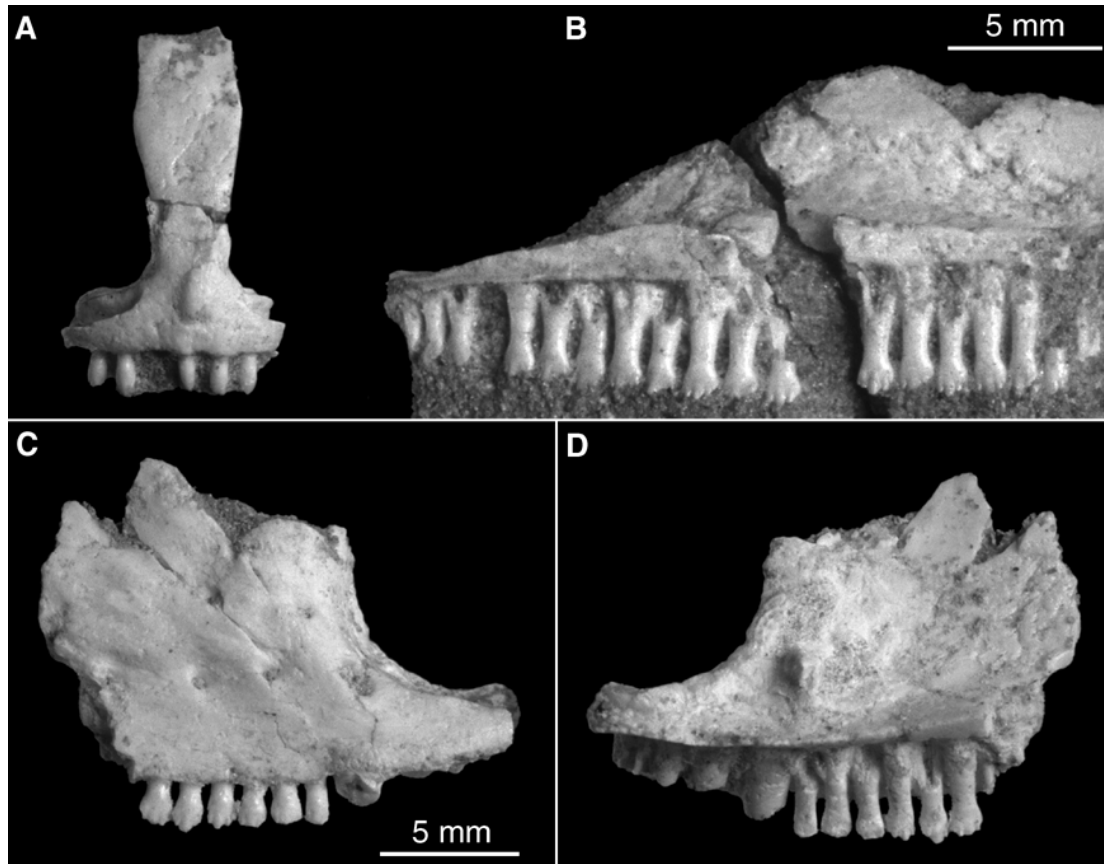


Fig. 21. *Macrocephalosaurus* sp.: IGM 3/132, **A**, fused premaxillae anterior view; **B**, left maxilla medial view; **C**, **D**, right maxilla, lateral and medial views.

**TYPE LOCALITY AND HORIZON:** Khulsan, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

**KNOWN DISTRIBUTION:** Khulsan and Monadnock, Barun Goyot Formation.

**DIAGNOSIS:** “Skull smaller (40-80 mm), more delicate and slender, canine teeth less well developed, tooth shafts projecting farther over parapet of jaw, skull sculpture more symmetrical (forming rosettes) and pectoral girdle more massive than in other species of *Macrocephalosaurus*; differs from *M. gilmorei* in having a more slender lower jaw; differs from *M. ferrugineus* in having lanceolate, polycusate teeth” (Estes, 1983: 83).

**REFERRED SPECIMEN:** IGM 3/134 (MAE 215/92-47), incomplete skull with mandibles from Khulsan.

**REMARKS:** The specimen (IGM 3/134) shows the same skull configuration and tooth

morphology as the holotype of *Macrocephalosaurus chulsanensis* (fig. 22); also, it has the same pattern of osteodermal ornamentation. The parietal foramen is nearly closed and is located at the frontoparietal suture (fig. 22A). On the basis of these similarities, the specimen is referred to *Macrocephalosaurus chulsanensis*.

Among the three recognized *Macrocephalosaurus* species, *Macrocephalosaurus chulsanensis* is distinguished from *Macrocephalosaurus gilmorei* in having the parietal foramen opening at the frontoparietal suture, and having the suborbital fenestra entirely closed. Other aspects of cranial and tooth morphologies of the two species are astonishingly similar, and these two species are not easily distinguished from the type species *Macrocephalosaurus ferrugineus*, except for the significant size differences (see Sulimski,

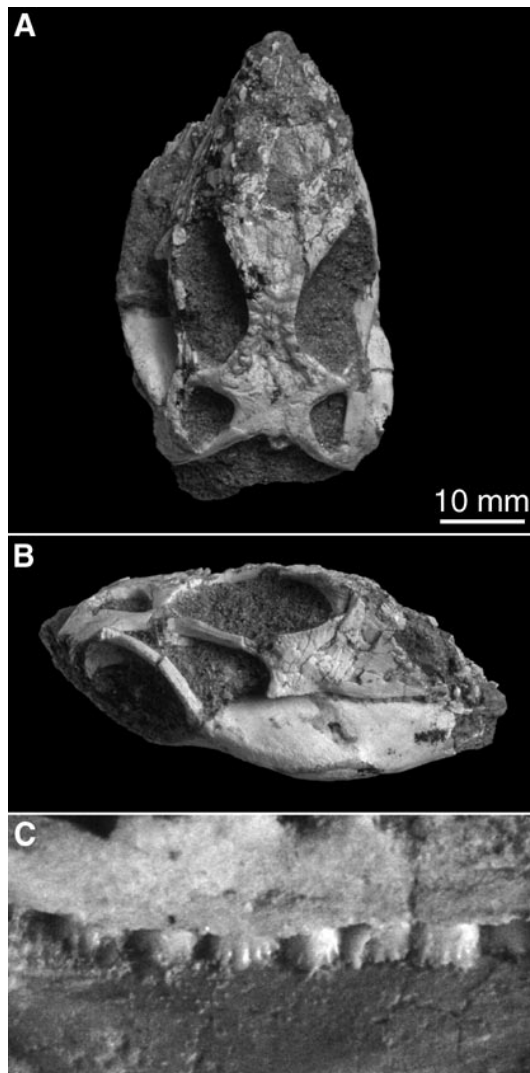


Fig. 22. *Macrocephalosaurus chulsanensis*: IGM 3/134, **A**, **B**, incomplete skull articulated with mandibles from Khulsan, dorsal and lateral views; **C**, close-up shot of right maxillary teeth.

1975; Estes, 1983). The type species is based on the holotype and only known specimen (AMNH 6520) from Bayn Dzak (Gilmore, 1943). Examination of the type specimen (K. Gao, personal obs., 1998) permits clarification of the following points: (1) The marginal teeth are pleurodont (contra Gilmore, 1943: acrodont; Estes, 1983: subpleurodont), as they have at least half of the tooth height attached to the lateral parapet of the tooth row. The pleurodonta is best shown on the

lower dentition on the holotype specimen. (2) Anterior maxillary teeth are enlarged and caninelike, as clearly indicated by the significantly thickened tooth bases. (3) Posterior teeth have widened and laterally compressed crowns, indicating multicuspoid rather than bluntly chisel-like crown pattern (see comments by Estes, 1983).

*Erdenetesaurus robinsonae* Sulimski, 1975

Figure 23A, B

**HOLOTYPE:** ZPAL MgR-III/19, incomplete skull with mandibles.

**TYPE LOCALITY AND HORIZON:** Khermeen Tsav II, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

**KNOWN DISTRIBUTION:** Only known from the type horizon.

**DIAGNOSIS:** "Skull high, well arched. Parieto-occipital region elongated. Maxilla moderately high, slightly inclined medially dorsal. Postfrontal with poorly developed distal processes. Supratemporal fossa small, oval, slit shaped. Supratemporal bone squamous, vestigial. Parietal foramen in parietal. Posterior processes of the parietal diverge at an angle of about 80°. Frontals partially fused, posteriorly widened. Descending thickening of the parietal well developed. Ectopterygoid with a long anterior process. Lower jaw slender with slight posterior backward inclination of coronoid process. Retroarticular process wide and long. Dentition pleurodont, almost homodont. Tooth replacement of iguanid-type. Cheek tooth crowns rounded in outline, mediolaterally compressed with six-seven radially arranged denticles" (from Sulimski, 1975: 78).

**REFERRED SPECIMEN:** IGM 3/135 (MAE 129/92-31), incomplete skull with mandibles from Khermeen Tsav.

**REMARKS:** IGM 3/135 is a small specimen (20 mm long), the size of which is only about half of the holotype of the species (ZPAL MgR-III/19: 55 mm). However, it shows diagnostic features of the species in tooth morphology and jaw structures: the teeth are short crowned, having rounded crowns that are aligned with no more than seven cusps; the mandible is slender, lacking the typical deepening and lateral swelling of the jaws in

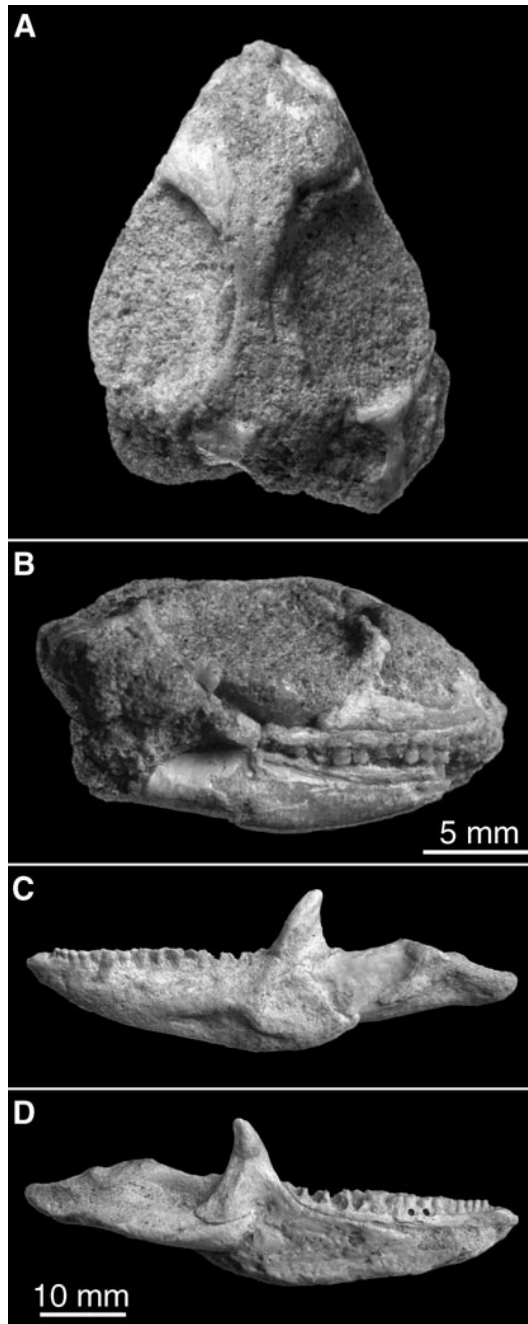


Fig. 23. *Erdennetesaurus robinsonae*: A, B, IGM 3/135, incomplete skull with mandibles from Khermeen Tsav, dorsal and lateral views; *Cherminsauros kozlowskii*: C, D, IGM 3/136, left mandible from Khermeen Tsav, lateral and medial views.

*Macrocephalosaurus* species. On the basis of these features, the specimen IGM 3/135 is referred to *Erdennetesaurus robinsonae*.

Sulimski (1975) noted the close similarities of *Erdennetesaurus robinsonae* with *Cherminsauros kozlowskii*, and placed the two species in the Polyglyphanodontidae. The two species are similar in general configuration of the skull, position of the parietal foramen, reduction of the suborbital fenestra, pattern of the postorbital-squamosal articulation, but are clearly different from one another in proportion of the parietal table and the orientation and cusp pattern of the crowns along the tooth row (see Sulimski, 1975). These two species may be closely related to one another, but their relationships to *Macrocephalosaurus*, *Adamisaurus*, and *Polyglyphanodon* are far from clearly understood.

*Cherminsauros kozlowskii* Sulimski, 1975

Figure 23C, D

HOLOTYPE: ZPAL MgR-III/24, skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Only known from the type locality and horizon.

DIAGNOSIS: Polyglyphanodontine diagnosed by the following characters: "Skull length 65 mm; skull contours relatively unmodified; snout region high, arched, but not widened; jaw robust but not deepened; dentition essentially homodont, subpleurodont; tooth number low (19 dentary teeth); supratemporal and squamosal separate; parietal foramen in parietal; weak sagittal crest on parietal; ectopterygoid with long anterior process; suborbital fenestra open; teeth large, crowns diagonally arranged at about 30° angle to axis of jaw; cutting edges of teeth with 5-6 low, blunt cusps; coronoid and dentary in contact" (from Estes, 1983: 79).

REFERRED SPECIMEN: IGM 3/136 (MAE 256/92-23), incomplete skull with mandibles and partial postcranial skeleton; IGM 3/137 (MAE 267/92-35), partial skull; both specimens from Khermeen Tsav locality, Barun Goyot Formation.



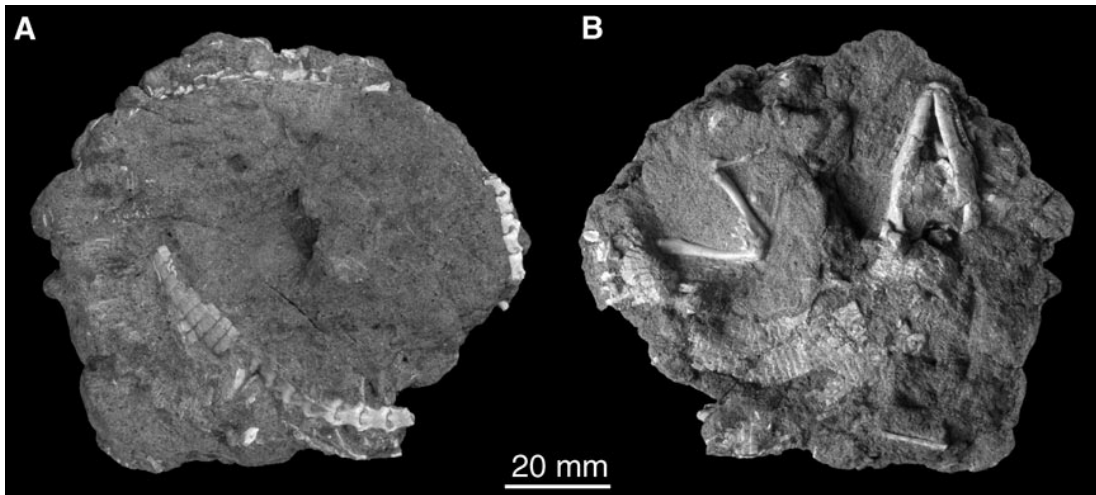


Fig. 24. ?Scincoidea, family incertae sedis, *Parmeosaurus scutatus*, new genus and species: **A**, **B**, IGM 3/138 (holotype), skull with articulated postcranial skeleton from Ukhaa Tolgod, dorsal and ventral views.

REMARKS: As noticed by Sulimski (1975), the most distinctive features of *Cherminsauros kozlowskii* are the oblique arrangement of the marginal teeth along the tooth row and the chisellike crowns with five to six low cusps. The two specimens from Khermeen Tsav clearly show these diagnostic features and they are accordingly referred to this species.

Sulimski (1975) placed *Cherminsauros kozlowskii* together with *Erdenesaurus robinsonae* in the Polyglyphanodontidae. This placement is accepted by Estes (1983) with change of ranking of the familial group as a subfamily (Polyglyphanodontinae). However, the phylogenetic positions of the two taxa in relation to other Gobi taxa (e.g., *Macrocephalosaurus*, *Adamisaurus*) and *Polyglyphanodon* need to be carefully investigated, before a reliable classification scheme can be provided.

?SCINCOIDEA OPPEL, 1811

FAMILY INCERTAE SEDIS

*Parmeosaurus scutatus*,  
new genus and species

Figures 24, 25

ETYMOLOGY: *parme* (Gr.), small light shield; *scutatus* (L.), armored with shield.

HOLOTYPE: IGM 3/138 (MAE 95-30),

well-preserved skull with articulated postcranial skeleton.

TYPE LOCALITY AND HORIZON: Ukhaa Tolgod, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

KNOWN DISTRIBUTION: Known only from the type locality and horizon.

DIAGNOSIS: Sharing with scincoids the following derived character states: presence of both dorsal and ventral body osteoderms; cephalic osteoderms present; palpebral ossification present; lateral coronoid process of dentary large, extending dorsally onto anterolateral surface of coronoid; retroarticular process inflected medially with small flange on medial margin. Differing from other scincoids in having the following autapomorphies: skull narrow and elongate, with laterally compressed snout; parietal table having well-developed lateral flange for dorsal origin of temporal musculature; marginal teeth stout with tricuspid crowns; autotomy fracture present behind caudal ribs.

REFERRED SPECIMENS: IGM 3/139–3/142 (MAE 475/93-152, 96-27, 95-70, 94-16), all incomplete skull with mandibles; IGM 3/143 (MAE 93-53), fragmentary cranial and postcranial skeleton; IGM 3/144 (MAE 94-51), articulated vertebrae with body osteoderms. All the referred specimens are topotypic.

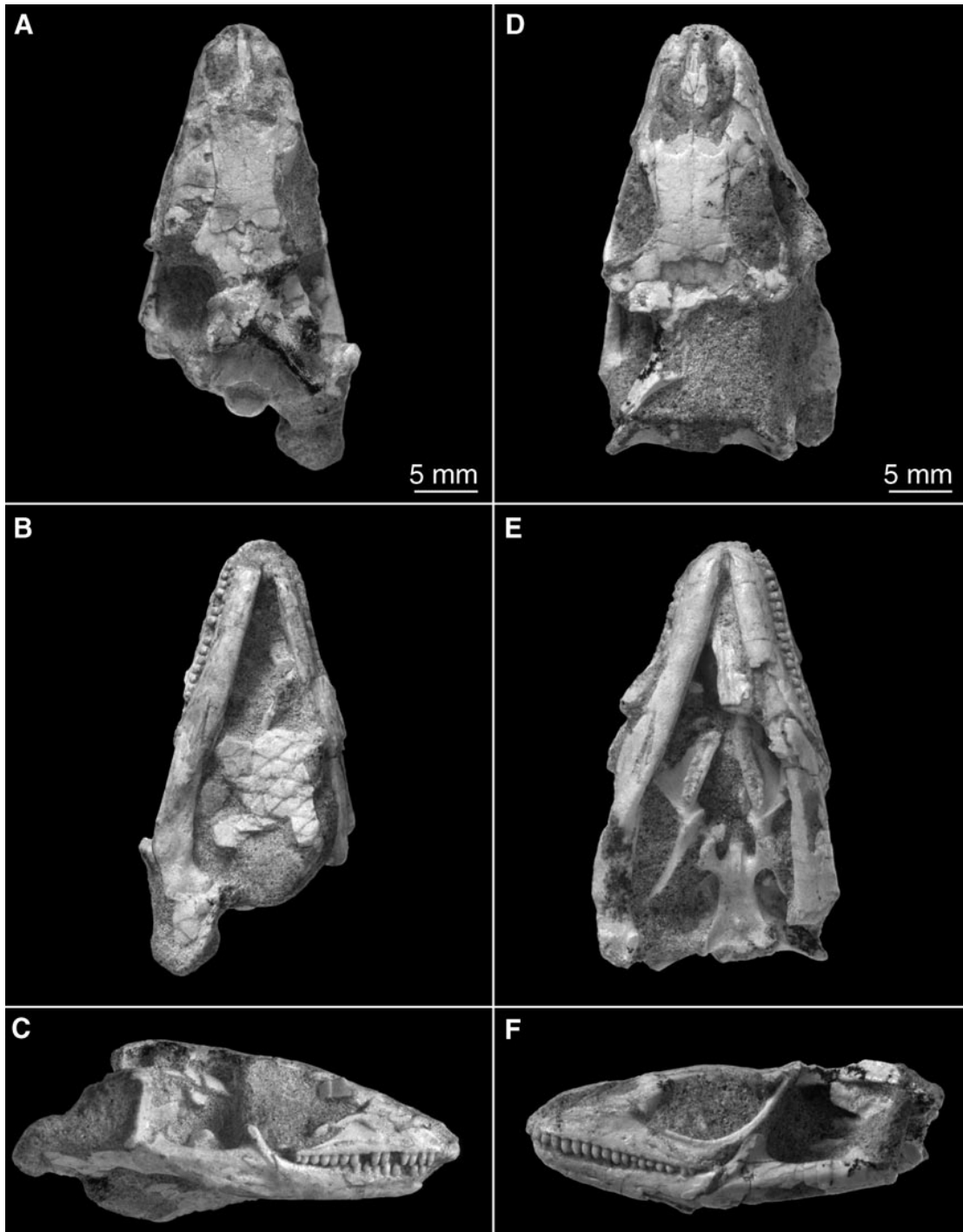


Fig. 25. Skull of *Parmeosaurus scutatus*, new genus and species: **A–C**, IGM 3/139, incomplete skull with mandibles, dorsal, ventral, and right lateral views; **D–F**, IGM 3/140, incomplete skull with mandibles, dorsal, ventral, and left lateral views.

## DESCRIPTION

**SKULL ROOF:** The skull of the holotype specimen is concealed beneath the tail, and is exposed only in ventral view (fig. 24B). However, several other specimens (IGM 3/139–3/142) show that the dorsal aspect of the skull is covered with platelike osteoderms. The skull is elongate and the snout is laterally compressed. Anteriorly, the premaxillae are fused and have a slender dorsal spine that deeply intervenes the paired nasals. The nasals have an anterior extension lateral to the premaxillary spine, and posteriorly end with a thin plate that overlaps the frontal.

The paired frontals anterolaterally contact the dorsal process of the maxilla, and this contact separates the prefrontal from the nasal. Posteriorly, the frontals are overlapped by a squared off parietal tab, so that the frontoparietal suture is not transverse (fig. 25A, D). The frontals have parallel lateral borders, showing no interorbital constriction. Along the lateral borders is developed a palpebral series roofing the medial part of the orbit. The frontals have well-developed subolfactory flanges, but have no midline contact below the olfactory tract. The descending processes extend anteroventrally, but do not contact the palatines to prevent the prefrontal from entering the orbitonasal fenestra.

The parietal table is penetrated by a small parietal foramen, which is located slightly anterior to the center of the table. At the frontoparietal suture, parietal tabs are present as small triangular structures that are interlocked with the frontals. Laterally, the parietal has a well-developed flange, the sloped surface of which indicates a dorsal origin of the temporal musculature. The ventral edge of the flange contacts the prootic bone (best shown on IGM 3/140), but lacks a pointed downgrowth (ventral process of the parietal) that normally contacts the epipterygoid. The supratemporal process of the parietal is elongate, and has an extensive lateral surface for muscle attachment as the extension of the parietal flange. The posterior end of the process reaches the paroccipital process, and apparently has no contact with the quadrate. A small part of the right supratemporal bone is preserved on IGM 3/140.

In lateral view, the maxilla is roughly a triangular bone with the apex of the dorsal process located at the midlevel of the tooth row. The dorsal process contacts the frontal, separating the nasal from the prefrontal. The lateral surface of the maxilla is largely vertical and slightly concave, having six lateral superior alveolar foramina along the ventral border. The posterior maxillary process is dorsally articulated with the well-developed lacrimal and jugal, and the latter two elements form the entire ventral border of the orbit. The jugal forms a complete postorbital bar, although its dorsal process is much more slender than the anteroventral process. The element is generally hockey-stick shaped, having no trace of a posteroventral process (fig. 25F).

The prefrontal is dorsally covered by the palpebral bones (IGM 3/139). When exposed (IGM 3/140), it shows a well-defined frontal process that extends to the midlevel of the orbit along the lateral border of the frontal. The anteroventral process of the prefrontal forms the entire anterior wall of the orbit and ventrally contacts the palatine. This process laterally contacts the lacrimal and borders the single lacrimal foramen. The process medially enters the orbitonasal fenestra, although the well-developed descending process of the frontal forms part of border of the fenestra.

The postfrontal and postorbital are incompletely preserved on IGM 3/140, and are dorsally covered with osteoderms. On IGM 3/142, however, the two elements are exposed and seem to be separate as a suture can be identified. The postfrontal is medially forked to clasp the frontoparietal suture, and the postorbital has a long posterior extension forming large part of the supratemporal arch. The supratemporal fenestra is normally developed, although the squamosal is not preserved.

**PALATAL ELEMENTS:** The vomers are incompletely preserved on several specimens, and are apparently fused with a prominent midline ridge. The posterior vomer extension reaches the level slightly posterior to the midlevel of the tooth row, where the vomers enter the interpterygoid vacuity between the palatines. The palatines are widened and have a strongly concave ventral surface lateral to the vomers. A row of palatal teeth is

developed along the medial border of the bone. The posterior border of the palatine is notched for articulation with the pterygoid.

The pterygoid bears two rows of prominent teeth (best shown on IGM 3/140), which are closely packed along the medial border of the palatal process of the bone (fig. 25E). The anterior process of the pterygoid forms large part of the medial border of the interpterygoid vacuity, and apparently has no contact with the vomer. Medially, a well-defined "mesopterygoid process" functions to enhance the articulation with the basipterygoid process of the basisphenoid. The lateral process of the pterygoid is thin but strongly widened, with its posterior border forming a weak crest for the attachment of the pterygomandibularis muscle. Posteriorly, the quadrate process is medially concave, forming a shallow trough.

The ectopterygoid forms part of the posterior border of the suborbital fenestra and has an interlocking articulation with the pterygoid. It has a robust anterolateral extension to form the lateral border of the suborbital fenestra, but whether the extension contacted the palatine cannot be determined given the condition of preservation of the specimens.

**BRAINCASE:** The braincase floor is elongate, carrying a pit anteriorly and a knob posteriorly, and in the middle of these two structure is a small foramen (best shown on IGM 3/140; see fig. 25E). The basisphenoid and the basioccipital are completely fused, and no suture can be delimited. Anterolaterally, the basipterygoid process is short, and more anteriorly than laterally directed. Between the basipterygoid processes, the rostrum is well ossified and proportionally robust. It extends anteriorly to the same level as the tip of the basipterygoid processes. The braincase floor is posterolaterally expanded, and the speno-occipital tubercles project ventrally.

Dorsolateral to the floor, a troughlike recessus vena jugularis is deep with the well-developed crista prootica forming the lateral wall. Within the recess, the posterior opening of the Vidian canal is located close to the middle of the trough, a short distance from the base of the basipterygoid process. The canal opens at the suture between the fused basisphenoid-basioccipital and the prootic. A

much smaller opening (facial foramen) is more posterodorsally located in the trough. Laterally at the base of the speno-occipital tubercle, the occipital recess is small, oblique, and narrowly elongate. It does not extend onto the lateral surface of the tubercle. The recess is separated by a small ridge from the more dorsally positioned foramen ovale, which is at about the same level as, but directly posterior to the facial foramen.

The lateral wall of the braincase is observed on the left side on IGM 3/140, which also shows the best view of the braincase floor as described above. As in other lizards, the lateral wall of the braincase is mainly formed by the prootic. A well-defined alar process projects anterodorsally contacting the ventral edge of the parietal flange as preserved. Whether the process contacted the epipterygoid cannot be determined, as the latter element is not preserved. Without distortion, the well-developed anterior inferior process of the prootic is anteromedially directed lying in a different vertical plane from the alar process. Between the two processes, the trigeminal notch is narrow and deep, nothing to the level of the anterior ampulla.

**MANDIBLE:** The mandible is massive. The posterior border of the dentary has a single surangular notch. Dorsal to the notch, the dentary displays a prominent coronoid process extending onto the anterior surface of the coronoid. Ventral to the surangular is a posteroventral process of the dentary that extends roughly to the same level as the coronoid eminence. The surangular has a strong anterior process fitting into the corresponding notch on the dentary. The anterior surangular foramen opens far posterior from the surangular-dentary suture and slightly posterior to the coronoid eminence (IGM 3/139 shows double openings, whereas the holotype and IGM 3/140 show only single openings). The posterior surangular foramen is small and is in the typical position close to the jaw joint. The angular is a narrow band, covering the surangular-prearticular suture and forming a large part of the ventral border of the postdentary jaw. It has a slender anterior process that intervenes the surangular and posteroventral process of the dentary.

In medial view, the well-developed splenial extends anteriorly almost to the symphy-



sis. The anterior inferior alveolar foramen and the anterior mylohyoid foramen are located posterior to the midlevel of the tooth row, and are located far apart. The posterior extension of the splenial terminates at the level ventral to the dorsal summit of the coronoid. The prearticular and articular are fused. The retroarticular process is broad, slightly inflected medially, and bears a small tubercle (flange) on the medial margin (best shown on IGM 3/139). The mandibular fossa is elongate, opening between the posterior medial process of the coronoid and the craniomandibular joint. The fossa is not expanded or inflated, a condition differing from that seen in extant lacertiforms (Estes et al., 1988).

**DENTITION:** The marginal teeth are fully pleurodont, having slightly over half of the tooth height attached to the lateral parapet of the tooth row. The premaxillae have as many as nine teeth, and these are unicuspid and are about equal in size. The maxillary tooth row contains 17–18 teeth, and the dentary contains roughly 22 teeth. The first four or five teeth on both maxilla and dentary are relatively slender and unicuspid, those on the middle part of the tooth row have stout crowns and are bicuspid with a small anterior accessory cusplule. The most posterior teeth are short-crowned, very stout, and weakly tricuspid.

**POSTCRANIAL SKELETON:** The postcranial skeleton is best preserved on the holotype. The actual number of its presacral vertebrae cannot be determined, but it appears to have had 26 or more (in keeping with the elongation of the body). The vertebrae are slightly elongate, with procoelous centra and low neural spines. The centra are procoelous. Zygosphenes and zygantra are absent, and therefore, there are no accessory articulations between vertebrae. The caudals are more strongly elongate than the presacrals and have a longitudinal furrow on the ventral surface of the centrum. At least the anterior caudals have a single pair of caudal ribs fused to the centrum. The autotomy fracture is developed right behind the caudal ribs—a condition known for some iguanians and gekkotans (Estes et al., 1988).

The pectoral and pelvic girdles on the holotype cannot be exposed without damaging

the covering sheet of osteoderms, but some long bones can be observed in ventral view. The left forelimb has the radius exposed as a slender element. The right hindlimb is well preserved, having the femur, tibia, and a metatarsal preserved in articulation. The hindlimb is quite robust, and the tibia is slightly shorter than the femur (fig. 24B).

**OSTEODERMS:** One of the notable features of this lizard is the presence of osteoderms covering both dorsal and ventral aspects of the skull and the body. The osteoderms on the skull roof are thin and platelike with essentially no imbrication. Those covering the ventral aspect of the skull are significantly smaller than those on the skull roof, and are more or less rhomboid and imbricated.

The dorsal body osteoderms are rectangular. Having a well-developed gilding surface anteriorly, these are imbricated one another anteroposteriorly but are sutured laterally. The ventral osteoderms are also rectangular, but are even smaller than the dorsal ones. Each individual osteoderm is about half the size of those covering the dorsal side of the body; therefore, there are more ventral rows of osteoderms than dorsal ones. All the osteoderms have smooth surfaces and are not keeled.

#### COMPARISON AND DISCUSSION

The referral of *Parmeosaurus scutatus* to the Scincomorpha is supported by two character states: nasal-prefrontal contact is lost, owing to the presence of a frontal-maxillary contact; and the lateral process of the coronoid is overlapped anteriorly by the dorsal process of the dentary, so that the lateral exposure of the coronoid process is limited to a narrow wedge between the dentary and surangular (see Estes et al., 1988 for evaluation of the characters). Presence of both dorsal and ventral body osteoderms merits further investigation: it occurs in Scincidae and Cordylidae, as well as the Paramacellodidae (Evans and Chure, 1998). The rectangular osteoderms in this Cretaceous lizard are similar to cordylids and paramacellodids, but differ from the cycloid-type in most skinks. This character was not investigated in either Estes et al. (1988) or Presch (1988) and polarity is yet to be established.

Within the Scincomorpha, the new species cannot be reliably classified in a particular subgroup because of conflicting evidence. It shares with the Scincoidea (Scincidae + Cordylidae) several derived character states. These include: cephalic osteoderms present; lateral coronoid process of dentary is large, extending dorsally onto anterolateral surface of coronoid; retroarticular process is inflected medially; medial margin of the retroarticular process has a tubercle or a small flange; retroarticular process is broadened posteriorly (see Estes et al., 1988 for character evaluation). In contrast, at least two character states indicate a possible lacertiform relationship of *Parmeosaurus scutatus*: presence of a pterygoid lappet of the quadrate (best shown on IGM 3/139), and a facial region that is elongate with the snout laterally compressed (see Estes et al., 1988). Another character state, presence of palpebral ossifications, has been interpreted as a separate synapomorphy for the Scincoidea, Lacertidae, and the Anguimorpha (see Estes et al., 1988), but it also occurs in the fossil group Paramacellodidae, which is probably the sister taxon of the Scincoidea (Evans and Chure, 1998). Therefore, this character state should be interpreted as a synapomorphy for a more inclusive group. Alternatively, if the Paramacellodidae represent the basal clade of the Scincomorpha (a hypothesis that needs to be tested), it would be a synapomorphy of Autarchoglossa with secondary loss within the Scincomorpha.

The available evidence seems to support referral of the new species to the Scincoidea, but conflicting evidence, such as having a pterygoid lappet on the quadrate and facial elongation, significantly weakens this referral. Pending wholesale revision of related taxa and the complete description and preparation of additional material, we tentatively refer *Parmeosaurus scutatus* to the Scincoidea.

*Hymenosaurus clarki*,  
new genus and species

Figure 26

ETYMOLOGY: *hymen* (Gr., god of marriage) + *sauros* (Gr., lizard), a present for Jim Clark's wedding; the species epithet is to recognize

Clark's profound contribution in collecting vertebrate fossils, including many lizard specimens, from the Gobi Desert.

HOLOTYPE: IGM 3/53 (MAE 154/93-40), incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Ukhaa Tolgod, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

DIAGNOSIS: Sharing with scincoids character states such as: retroarticular process inflected medially, broadened posteriorly; sharing with scincids presence of jugal-squamosal contact.

Differing from other scincomorphs in having the following derived character states: presence of moderate retraction of narial openings; frontals proportionally wide; presence of prefrontal-postfrontal contact; parietal foramen greatly reduced as minute opening and located close to posterior border of parietal table; occipital condyle formed exclusively by basioccipital; posterior notch of dentary articulates with surangular only, without involvement of angular; retroarticular process posteriorly notched; spheno-occipital tubercle greatly reduced, and shifted anteriorly close to midlevel of braincase floor.

DESCRIPTION

The entire skull and the mandibles are generally well preserved without distortion. However, the dorsal surface of the skull roof was exposed in the field and the elements such as the nasals and the frontals are eroded and incomplete.

SKULL ROOF: The premaxillae are clearly paired, with extremely slender and elongate dorsal spines. The nasals are incompletely preserved on both sides. Although the midline suture is not shown as preserved, there is no indication of fusion of the two bones.

The frontals are clearly separated by a midline suture and are proportionally wide with parallel lateral borders. Although lacking a slender anterolateral process, the frontal contacts the dorsal process of the maxilla, so that the nasals are separated from the prefrontals. The frontals have parallel lateral borders, lacking well-defined interorbital constriction. The lateral border is also ex-

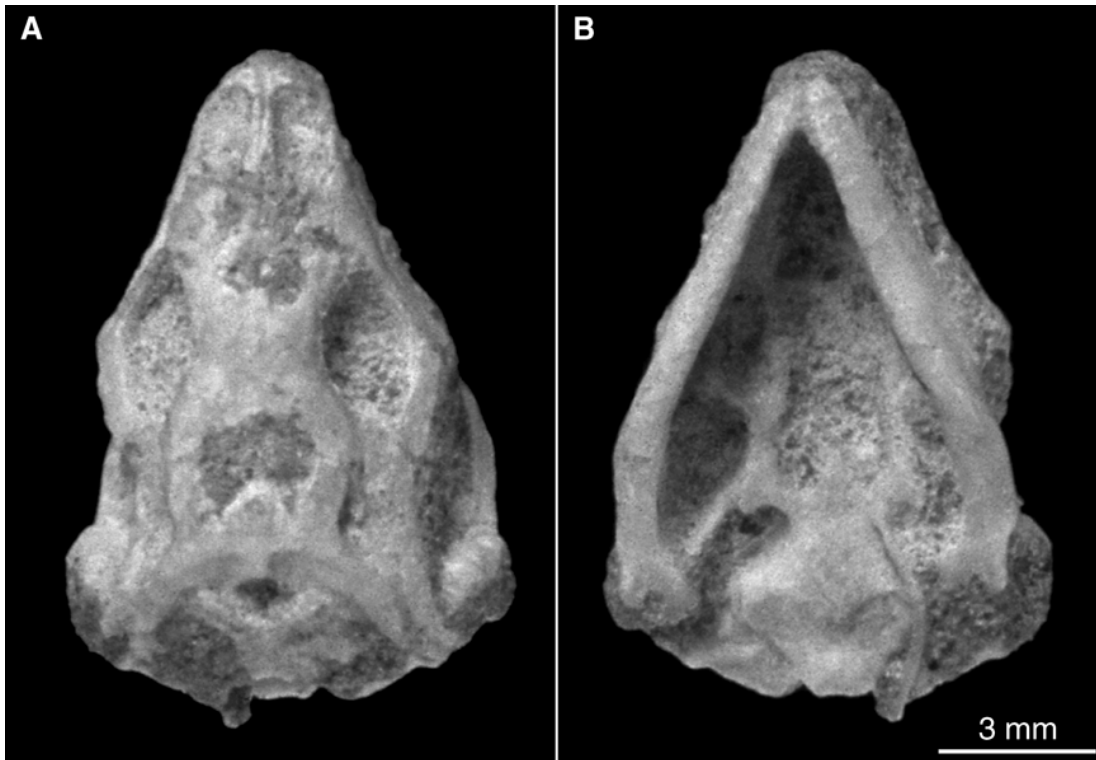


Fig. 26. *Hymenosaurus clarki*, new genus and species: **A**, **B**, IGM 3/53 (holotype), incomplete skull with mandibles from Ukhaa Tolgod, dorsal and ventral views.

cluded from the medial rim of the orbit, because of the abutting contact of the prefrontal with the postfrontal. Ventrally, the subolfactory flange is fairly well developed, but is relatively shallow and has no contact along the midline.

The parietal table is roughly rectangular in shape. It lacks lateral flanges, indicating a ventral origin of the temporal muscles; however, the posterior border of the table has a well-developed flange for attachment of the axial muscles. The parietal foramen is greatly reduced to a minute opening lying close to the posterior border of the parietal table (fig. 26A). Like in many extant skinks, the supratemporal process of the parietal distinctly bends so the basal part of the process extends laterally, then turns more posteriorly. Distally, this process contacts the paroccipital process and is separated from the quadrate by the supratemporal and the squamosal.

The prefrontals have a slender and elongate frontal process extending posteriorly to

contact the anterior process of the postfrontal. This contact excludes the frontals from the medial rim of the orbit. The postfrontal and postorbital are clearly separate elements. The postfrontal is proportionally larger than the postorbital, and is medially forked to clasp the frontoparietal suture. It has an elongate anterior process contacting the prefrontal, and the two bones together form the medial rim of the orbit and exclude the frontal from entering the orbit.

The squamosal is preserved on both sides. The element lacks a dorsal process, but the anterior process is strongly elongated to have an abutting contact with the jugal. The supratemporal is clearly identifiable on the right side of the specimen. It medially attaches to the lateral surface of the paroccipital process and the supratemporal process of the parietal, and laterally contacts the squamosal and the cephalic head of the quadrate. The quadrate is strongly widened as commonly

seen in extant skinks and lacks a pterygoid lappet.

The maxilla is completely preserved on both sides. The lateral surface of the bone is smooth without osteodermal ornamentation. Above the ventral border is a shallow groove, in which opens a horizontal row of lateral superior alveolar foramina. Anteriorly, the premaxillary process is well developed in keeping with the narial retraction. It has a sutural articulation with the premaxilla, leaving no aperture between the two elements. The anteromedial process is short, showing no tendency to develop a midline contact with its opposite element. In keeping with the moderate narial retraction, the dorsal process of the maxilla rises above the middle level of the tooth row. The process is roughly triangular, and bends medially to form a facial "table" together with the nasal and prefrontal. The posterior process forms the lateral part of the ventral border of the orbit, as the jugal contributes to the medial part of the border.

The lacrimal is apparently absent, as it cannot be identified on either side. The jugal is generally boomerang-shaped. At the posteroventral corner it has a blunt, but prominent, process directed ventrally. The posterodorsal process is equilateral along its entire length without the distal narrowing seen generally in other lizards. It has a blunt dorsal tip which contacts both the postorbital and the squamosal. The anteroventral process is attached to the medial side of the posterior process of the maxilla, so that the jugal cannot be seen in lateral view.

**PALATAL ELEMENTS:** The palatal elements are mostly well preserved. The vomers are short and seem to be paired as preserved. The palatal surface of the element is toothless. The palatine is short and wide, but it lacks the characteristic scrolling seen in skinks and has no midline contact with the opposite side of the element. The palatine has a posterior process, which contacts the pterygoid and forms most of the medial border of the suborbital fenestra. No palatal teeth are developed on the ventral surface of the element.

The pterygoid is a typical Y-shaped bone, with short anterior processes and a longer posterior process. The anteromedial process

is slender, but small denticles are identifiable on the ventral surface. The anterolateral process forms the entire posterior rim of the suborbital fenestra, and contacts the ectopterygoid to form a very weak ventral process (pterygoid process). The ectopterygoid is small, and its short anterior process forms the posterior half of the lateral border of the suborbital fenestra. Thus, the maxilla contributes to the anterior half of the border of the suborbital fenestra.

**BRAINCASE:** The braincase floor is well preserved, and is slightly convex ventrally. The basioccipital and the basisphenoid are fused, as no suture can be delimited between the two elements. Like in many extant scincoids, the floor is narrow at the base of the basiptyergoid processes, strongly widened at the level of the spheno-occipital tubercles, and narrow posteriorly at the base of the occipital condyle (fig. 26B). The basiptyergoid process is short and laterally directed. The cultriform process has a short but well-ossified base. The spheno-occipital tubercle is greatly reduced as an extremely small knob, and is shifted anteriorly close to the midlevel of the braincase floor. The occipital recess is a fissurelike structure and is strongly oblique anteroventral-posterodorsally. The occipital condyle is small, and is formed entirely by the basioccipital, with essentially no contribution from the exoccipitals. The articulation of the exoccipital with the basioccipital is marked by a ridge, indicating possible fusion of the two bones.

The recessus vena jugularis is greatly reduced as an extremely shallow groove. The crista prootica is a low crest, in keeping with the reduction of the recessus vena jugularis. The posterior opening of the Vidian canal is very small and is located at the base of the basiptyergoid process. Posteriorly within the recessus, the facial foramen opens on the medial wall of the groove and just anterior to the knoblike spheno-occipital tubercle. The foramen ovale is slightly elongate and is located right above the oblique occipital recess.

In dorsal view, the entire braincase is shifted posteriorly and well exposed posterior to the parietal margin (perhaps a burrowing adaptation, see Rieppel, 1981). In occipital view, the paroccipital process is short and is proportionally robust. It is horizontal in pos-



terior view, but is anterolaterally directed in dorsal view, differing from the normal condition in which the process is posterolaterally oriented. This feature of the paroccipital process, seen in many extant skinks, is correlated with the posterior shifting of the braincase as a burrowing adaptation.

**MANDIBLE:** The mandible is extremely slender. In lateral view, the dentary is penetrated by five extremely small mental foramina. The posterior border of the dentary is slightly notched for the blunt anterior process of the surangular. The surangular is the only element that fits in the dentary notch, and the anterior part is separated from the angular bone by a slender posterior ventral process of the dentary. This condition is similar to that seen in typical burrowing skinks (e.g., AMNH 2245: *Scincus officinalis*; AMNH 48509: *Acontias gigracilicauda*), but differs from other scincomorphs in which normally both the surangular and angular fit in the dentary notch.

In medial view, the subdental shelf is slender but clearly defined, unlike the sloped tooth-bearing border in advanced anguimorphs (Anguidae and Platynota). The Meckelian canal is narrow and largely covered by the splenial. The splenial is narrowly elongate, with its anterior extension terminating close to the mandibular symphysis and its posterior extension terminating below the posteroventral process of the coronoid bone. The anterior inferior alveolar foramen and the anterior mylohyoid foramen cannot be properly identified as a matter of preservation.

The retroarticular process is medially inflected and posteriorly widened. The most distinctive feature of the lower jaw is the posterior notch of the retroarticular process. This notch may be functionally related to attachment of the mandibular depressor muscles, but its actual role is unclear. To our knowledge, no other lizard known has developed this type of notch.

**DENTITION:** Marginal teeth are preserved on both sides of the upper and lower jaws, but neither side of the jaws shows a complete tooth row. The teeth are slenderly cylindrical, and closely spaced from one another along the tooth row. Tooth implantation is pleurodont, as about half of the tooth height atta-

ches to the relatively high lateral parapet of the tooth row. The crowns are poorly preserved, the cusp pattern cannot be clearly viewed on the specimen.

#### COMPARISON AND DISCUSSION

The new taxon is possibly referable to the Scincoidea on the basis of the feature retroarticular process inflected medially and broadened posteriorly. Within the Scincoidea, it shares with scincids the presence of a jugal-squamosal contact and expansion of the postfrontal, but lacks any tendency toward developing a secondary palate (see Estes et al., 1988 for character evaluation).

A notable feature of the skull is that the prefrontal contacts the postfrontal above the orbit and along the lateral border of the frontal. Such a contact occurs homoplastically in several groups of lizards, including chamaeleonids, some skinks, and some anguimorphs (Estes et al., 1988). Whether such a condition seen in the new taxon is homologous to the similar condition in those skinks cannot be determined, because of the uncertain relationships of the new taxon within the Scincomorpha.

Generally, the characters discussed above indicate a possible scincoid relationship of this new lizard; however, lack of other character support (see Estes et al., 1988) prevents us from placing it in any of the two extant familial groups of the Scincoidea (Scincidae and Cordylidae). Also, further work needs to be done to resolve its relationships with other scincomorphs such as *Parameosaurus*, *Sla-voia*, *Globaura*, and *Eoxanta*.

#### SCINCOMORPHA INCERTAE SEDIS

##### FAMILY INCERTAE SEDIS

##### New genus and species (unnamed)

Figure 27

**SPECIMEN:** IGM 3/54 (MAE 29/93-192), incomplete skull articulated with mandibles.

**LOCALITY AND HORIZON:** Ukhaa Tolgod, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation.

#### DESCRIPTION

The specimen IGM 3/54 is an incomplete skull articulated with mandibles. The speci-

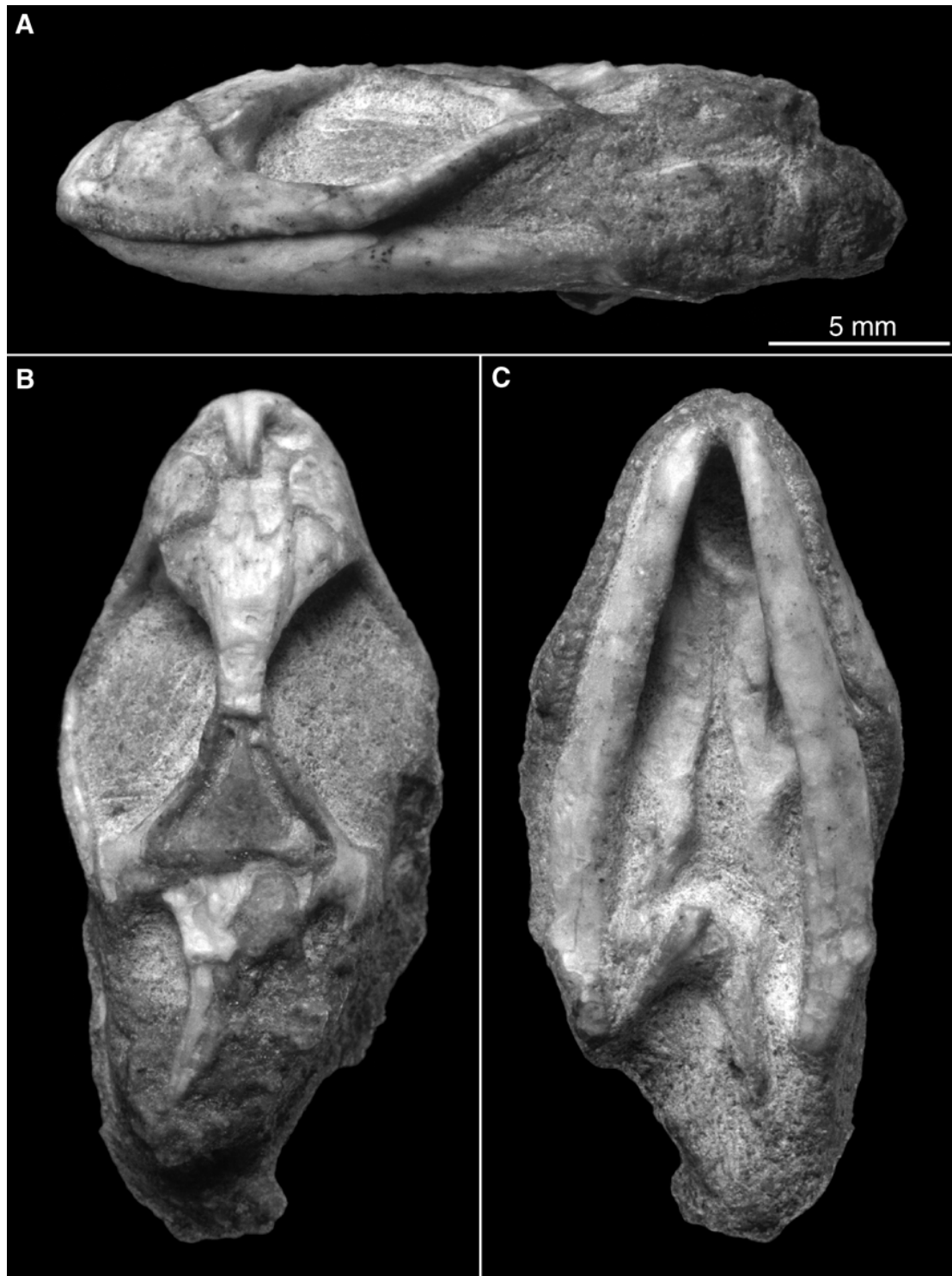


Fig. 27. Scincomorpha, family incertae sedis, new genus and species (unnamed): A–C, IGM 3/54, incomplete skull with mandibles, lateral, dorsal and ventral views.

men was collected from the Gilvent Wash sublocality at Ukhaa Tolgod, and is preserved in well-cemented sandstone concretion. This type of preservation is different from most of the other lizard specimens from Ukhaa Tolgod, which are often preserved in poorly cemented sandstones.

**SKULL ROOF:** The premaxillae are paired with a clear midline suture. The anterior surface of the premaxilla is smooth, and has no anterodorsal premaxillary foramina. The nasals are also paired, and each element laterally contacts the dorsal process of the maxilla, but is separated from the prefrontal by a frontal process (fig. 27B). The frontals are fused and strongly narrowed between the orbits. The subolfactory processes of the frontals are not exposed, but the impressions of the posterior part of the frontals show the processes are well developed and may well have a midline contact below the olfactory tract.

The parietal is incompletely preserved. It appears to have had a short and rectangular table, and proportionally long supratemporal processes. Although the table is incomplete, impressions show a parietal foramen is present at the center of the table. The lateral border of the parietal table is not flanged, indicating a ventral origin of the temporal muscles.

The prefrontal anteriorly sutures with the posterior border of the dorsal process of the maxilla. Medially, the bone contacts the frontal only and is separated from the nasal by a frontal-maxilla contact. The postfrontal and the postorbital are completely fused as a single element (i.e., postorbitofrontal). Such fusion occurs in six extant groups (see Estes et al., 1988 for discussion), and its phylogenetic significance is equivocal among squamate taxa. On IGM 3/54, the posterior process of the postorbitofrontal is very short, and thus the upper temporal bar may be largely formed by a strongly elongated squamosal (not preserved on both sides).

The maxilla is well preserved on both sides. The nasal process of the maxilla is primitively located above the anterior part of the tooth row, and the lateral surface of the process appears to be ornamented with light dermal rugosities (fig. 27A). The maxilla forms a large part of the ventral border of the

orbit, and obscures the greatly reduced lacrimal, which is confined to the inner side of the orbital corner. The lacrimal borders a small lacrimal foramen with the prefrontal, without involvement of the maxilla. Anteriorly, the premaxillary process of the maxilla is short and slightly overlaps the lateral side of the premaxilla. No premaxillary aperture is developed at the notched suture with the premaxilla. Posteriorly, the maxilla has a slender process extending to the midlevel of the large and slightly elongate orbit. The posterior end of this process ends with a small notch, which articulates with the jugal (fig. 27A). Such an articulation occurs in some skinks (e.g., AMNH 140794: *Corucia zebra-ta*; AMNH 27296: *Tropidophorus queen-slandae*), but is highly variable in other skinks (e.g., AMNH 57864: *Eumeces schnei-deri*; AMNH 99684: *Tiliqua nigrolutea*).

The jugal is a lightly built element without a posteroventral process. It has an elongate anteroventral process, which extends along the medial side of the posterior process of the maxilla and hence is not exposed in lateral view. The posterodorsal process is extremely slender but forms a complete post-orbital bar. As the squamosal is not preserved on both sides it can not be determined whether a jugal-squamosal contact was present.

**PALATAL ELEMENTS:** Some palatal elements can be identified in ventral view. The vomers are poorly preserved, and whether the two sides are fused or separate cannot be determined. The palatines are short and wide, and are toothless. The two sides are very close to the midline, and together with the pterygoids strongly restrain the interpterygoid vacuity as a narrow recess. The pterygoids have an oblique suture articulation with the palatine at the midlevel of the suborbital fenestra, and form part of the posterior border of the fenestra together with the ectopterygoid. Like the palatines, the pterygoids are also toothless (fig. 27C).

**MANDIBLE:** The mandibles are completely preserved on both sides (fig. 27C). The lower jaw is relatively heavily built in relation to the skull. The lateral surface of the dentary is smooth, without any trace of ornamentation. Sutures between the dentary and coronoid can be identified, but the dentary-sur-angular suture cannot be delimited because

of fusion. The posterodorsal part of the dentary seems to have a small notch for the anterior process of the surangular bone. The coronoid bone is small, and its weakly developed dorsal process is anteriorly overlapped by the coronoid process of the dentary bone. The coronoid is laterally exposed as a small wedge between the dentary and the surangular as in most other scincomorphs (see Estes et al., 1988 for evaluation). The anterior surangular foramen is small and located on the surangular behind the base of the coronoid dorsal process. The posterior surangular foramen is barely identifiable and probably located anteroventral to the craniomandibular joint. The surangular-prearticular suture is recognizable on the posterior part but anteriorly blurred because of fusion. The retroarticular process is slender and straight, nondeflected, and medially carries no angular process or prearticular crest.

Medially, the splenial is reduced to cover the posterior two thirds of the Meckelian canal. The anterior one third of the canal tends to be closed, but remains open as a narrow and medially faced fissure. The posterior extension of the splenial reaches at least the level of the posteroventral process of the coronoid bone, but its actual extent cannot be identified because of fusion with the prearticular. The anterior inferior alveolar foramen and the anterior mylohyoid foramen are close to one another, and both lie at a level about two thirds of the way back along the tooth row. The anterior part of the angular can be delimited as a very slender splint, but it is posteriorly fused with the prearticular and the surangular.

**DENTITION:** The paired premaxillae carry a total of nine fine teeth (the right side has five and the left side four). The left maxilla carries about 22 teeth, and the tooth row posteriorly extends to the midlevel of the orbit. The teeth are extremely tiny, simple and peg-like, and closely spaced from one another. This type of dentition, in keeping with the relative small size of the skull, indicates the lizard may have fed largely on ants. The lower dentition cannot be exposed for observation; however, the number of dentary teeth can be estimated at 22-24, as the dentary normally carries a few more teeth than the maxilla. All the marginal teeth are presumably

pleurodont, although they are not exposed in medial view.

#### COMPARISON AND DISCUSSION

Morphologically, the specimen (IGM 3/54) shows a unique mosaic of characters. Presence of frontal fusion and interorbital constriction seems to indicate an iguanian affinity, but many other character states such as presence of the parietal foramen near the center of the parietal table and a ventral origin of the temporal musculature indicate that the above-mentioned character states are homoplastic relative to similar conditions in iguanians. On the other hand, fusion of the frontals with descending processes in contact below the olfactory tract suggests a gekkotan affinity of this lizard; however, this possible affinity is disproved by other character states (see below).

Despite the above-mentioned uncertainties, the unnamed new taxon is referred to the Scincomorpha based on a combination of the following features: the nasal and prefrontal are separated by an anterolateral process of the frontal; origin of the adductor muscle is on the ventral aspect of the parietal; and the coronoid is laterally exposed as a small wedge between the dentary and the surangular. Within the Scincomorpha, two character states (paired premaxillae, and nearly closed Meckelian canal by dentary with strong reduction of the splenial) seem to indicate a possible affinity of the new taxon to the Scincoidea; however, a slender and straight retroarticular process disproves this affinity.

The species is known from a single and relatively poorly preserved specimen, and there is still much to learn about this lizard before a confident taxonomic assignment can be made. For this reason, we leave the genus and species unnamed, and hence, no type designation and diagnosis are provided. However, the following character states are potential autapomorphies of this species: fused frontals are extremely narrow; marginal teeth are extremely fine and closely arranged along the tooth row; postdentary bones are partially fused in the lower jaw.



*Slavoia darevskii* Sulimski, 1984

Figure 28

HOLOTYPE: ZPAL MgR-I/8, skull with mandibles and postcranial skeleton.

TYPE LOCALITY AND HORIZON: Khulsan, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Djadokhta Formation—Ukhaa Tolgod locality; Barun Goyot Formation—Khulsan and Khermeen Tsav localities (Sulimski, 1984; this paper).

REVISED DIAGNOSIS: Scincomorph lizard differing from other members of the group in having the following derived character states: skull very short and wide; nasal-prefrontal contact lost owing to widening of frontals; significantly wide frontals; great reduction of orbit into narrow teardrop-shaped opening; parietal foramen rudimentary or entirely closed; prefrontal-postfrontal contact forming medial rim of orbit; anteroventral process of jugal nearly lost; strong reduction in number of marginal teeth, with short entirely antorbital maxillary tooth row; suborbital fenestra strongly reduced; ectopterygoid contacts palatine anteriorly and posteriorly, excluding both maxilla and pterygoid from entering suborbital fenestra.

REFERRED SPECIMENS: Ukhaa Tolgod—IGM 3/145 (MAE 96-1), nearly complete skull with mandibles and partial postcranial skeleton (fig. 28C); IGM 3/146, incomplete skull with mandibles and articulated postcranial skeleton (fig. 28D); 3/147–3/153 (MAE 178/92-21, 160/93-40, 95-7, 94-66-1, 94-66-2, 94-66-3, 94-66-4), all incomplete skull with mandibles (total: 9 specimens from Ukhaa Tolgod). Khulsan—IGM 3/154 (MAE 63), nearly complete skull with mandibles and partial postcranial skeleton (fig. 28A, B); Khermeen Tsav—IGM 3/155–3/159 (MAE 175/92-21, 176/92-21, 181/92-21, 185/92-21, 198/92-25), all incomplete skulls with mandibles (total: 5).

REMARKS: Although Sulimski (1984) suggested that a relationship of *Slavoia darevskii* with the gymnophthalmine teiids “seems to be more probable,” he made no formal familial assignment of this taxon. Borsuk-Bialynicka (1991a: 10) ambiguously stated that “*Eoxanta*, and possibly *Slavoia darevskii*, become sister groups of both Xantusiidae

and Scincidae.” We interpret that this statement implies a possible *Slavoia darevskii*-Scincidae sister group relationship. More recently, Alifanov (1993a) without explanation listed *Slavoia darevskii* under the Acontiidae, which is commonly treated as a subfamily in the Scincidae (Greer, 1970; Estes, 1983; Estes et al., 1988).

In terms of skull morphology, *Slavoia darevskii* shares a single palatal character state with the acontine skinks (ectopterygoid contacts palatine anteriorly and posteriorly, excluding maxilla and pterygoid from entering the suborbital fenestra), but lacks many derived character states of the latter group (e.g., loss of limbs, loss of supratemporal arch, prefrontal and squamosal reduced, and Meckelian canal closed with fusion). Presence of palatine scrolling indicates that the taxon may be scincid related, but lack of other features (such as the jugal-squamosal contact) may prevent classifying *Slavoia darevskii* in the Scincidae. The relationships and classification of *Slavoia darevskii* within the Scincomorpha remain ambiguous, pending thorough phylogenetic study of this highly specialized form and its likely relatives.

*Globaura venusta* Borsuk-Bialynicka, 1988

Figure 29

HOLOTYPE: ZPAL MgR-III/40, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Barun Goyot Formation—Khermeen Tsav and Khulsan localities (Borsuk-Bialynicka, 1988; this paper); Djadokhta Formation—Bayn Dzak and Ukhaa Tolgod (this paper).

DIAGNOSIS: “Small non-teioid lacertoid with paired premaxillae, and frontals fused and constricted. Ratio of minimum frontal width/sagittal length 0.16-0.19. Postfrontal posterior extension subject to variability. No osteoderms. Snout/skull length ratio 0.3-0.33. Ratio of length of tooth row underlying orbit/orbit length 0.18-0.27” (generic diagnosis of Borsuk-Bialynicka, 1988: 214).

“Skull length 14-25 mm. Modal skull length of 21.5 mm, as in holotype. Postfrontal rarely extends posteriorly more than half

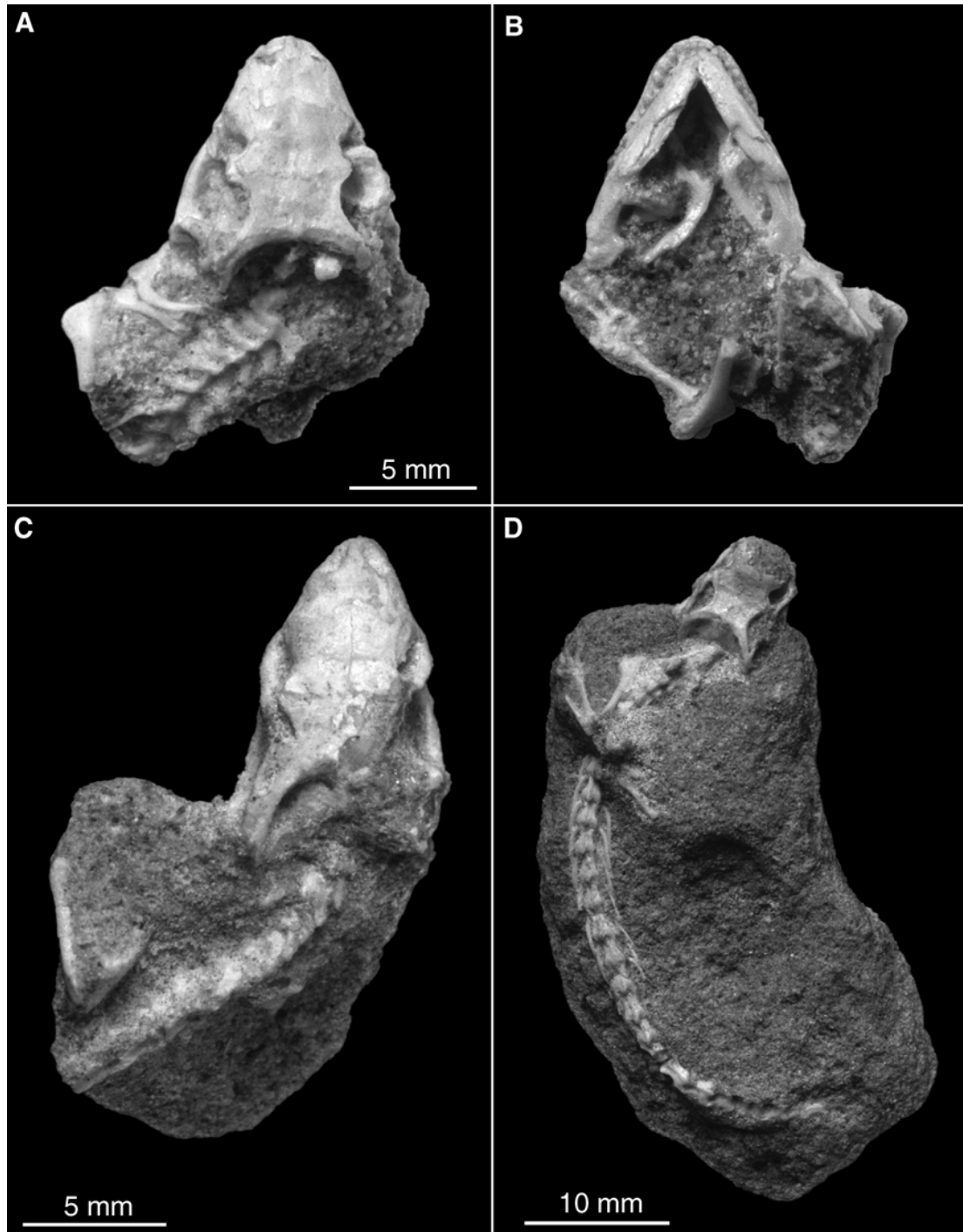


Fig. 28. Scincomorpha, family incertae sedis, *Slavoia darevskii*: **A**, **B**, IGM 3/154, incomplete skull with mandible and partial postcranial skeleton from Khulsan, dorsal and ventral views; **C**, IGM 3/145, nearly complete skull with mandibles and partial postcranial skeleton from Ukhaa Tolgod, dorsal view; **D**, IGM 3/146, incomplete skull with mandibles and articulated postcranial skeleton from Ukhaa Tolgod, dorsal view.

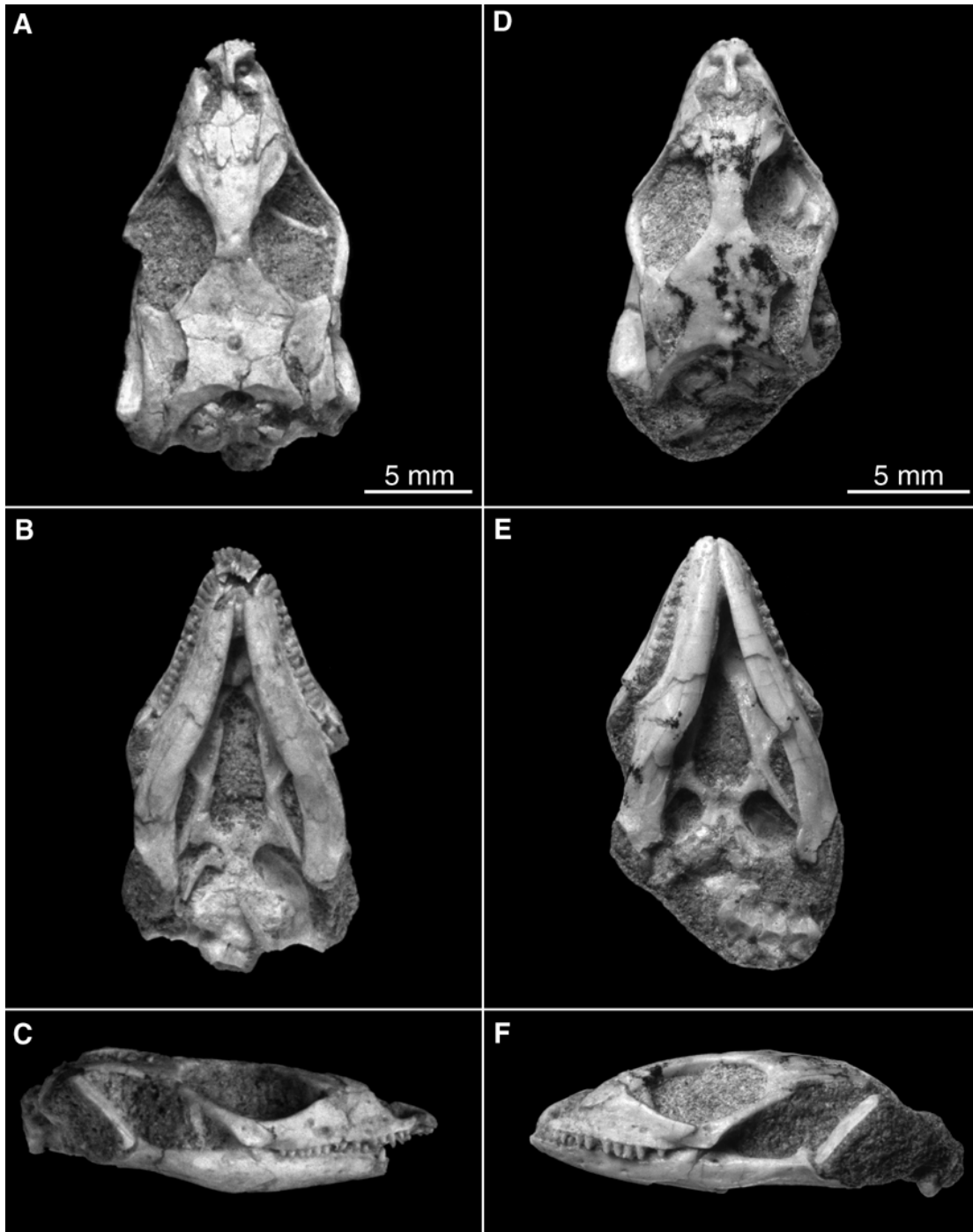


Fig. 29. *Globaura venusta*: A–C, IGM 3/164, nearly complete skull with mandibles from Khulsan, dorsal, ventral, and right lateral views; D–F, IGM 3/160, nearly complete skull with mandibles from Ukhua Tolgod, dorsal, ventral, and left lateral views.

the length of the parietal table. Otic regions of the brain case globose” (specific diagnosis of Borsuk-Bialynicka, 1988: 215).

REFERRED SPECIMENS: Ukhaa Tolgod—IGM 3/160 (MAE 95-89), nearly complete skull with mandibles; IGM 3/161–3/163 (MAE 21/93-176, 95-24, 95-40), all incomplete skulls with mandibles. Khulsan—IGM 3/164 (MAE 217/92-61), nearly complete skull with mandibles. Khermeen Tsav—IGM 3/165–3/167 (MAE 173/92-21, 172/92-21, 183/92-21), all incomplete skulls with mandibles.

REMARKS: Borsuk-Bialynicka (1988) described *Globaura venusta* and classified it in the Lacertoidea. Later, Alifanov (1993a) listed this species under the Xenosauridae without explanation. There is little doubt about its affiliation with the Scincomorpha, but the relationships of *Globaura venusta* to other scincomorphs are far from clear. Presence of interdigitation of the frontoparietal suture (fig. 29A, D) is the single character state supporting the referral of *Globaura venusta* to the Lacertiformes, based on the phylogenetic framework provided by Estes et al. (1988). Two other character states (pyriform recess narrow throughout most of its length, and facial region elongated and snout region laterally compressed) are incorrectly described for this species (fig. 29). Lack of a pterygoid lappet of the quadrate and a noninflated mandibular fossa are two other features that disprove the close relationship of *Globaura venusta* with the Lacertiformes. The enlarged postfrontal can be interpreted as either a lacertid or scincid feature, while fused and constricted frontals, and the presence of a jugal-squamosal contact ambiguously suggest possible relationships with either the Teiidae or the Scincidae. Because of conflicting evidence, we tentatively place *Globaura venusta* in the Scincomorpha without further referral to any subgroup.

*Eoxanta lacertifrons* Borsuk-Bialynicka,  
1988

HOLOTYPE: ZPAL MgR-III/37, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Ukhaa Tolgod and Khermeen Tsav localities; Djadokhta and Barun Goyot formations.

DIAGNOSIS: “Small xantusiid-like lacertoid with paired premaxillae; parietal not extended to cover dorsal aspect of the braincase; frontals fusing late in ontogeny, provided with ventral sagittal crest partly separating olfactory tracts. Ratio of minimum frontal width/sagittal length 0.38. Ectopterygoid massive, shifted anteriorly to parallel the palatine borders the slit-like suborbital fenestra. Postfrontal extending posteriorly to close the supratemporal fenestra. Postorbital and squamosal dorsoventrally flattened, bandlike. Osteoderms present in some specimens. Snout/skull length ratio 0.23-0.26. Ratio of length of tooth row underlying orbit/orbit length almost 0” (Borsuk-Bialynicka, 1988: 222).

REFERRED SPECIMEN: IGM 3/168 (MAE 95-90), incomplete skull with mandibles, from Ukhaa Tolgod (sublocality Camel Humps).

REMARKS: The general proportions of the skull (IGM 3/168) are identical to the holotype of *Eoxanta lacertifrons* (ZPAL MgR-III/37). The two specimens are similar in several respects: the snout is short and wide; the frontals are paired and have parallel lateral borders anteriorly; and the parietal table is roughly square (Borsuk-Bialynicka: subquadrangular) with a small parietal foramen in the center. On the basis of these similarities, the new specimen can be referred to *Eoxanta lacertifrons*. However, the new specimen shows a different frontoparietal suture pattern than the holotype. The suture on the holotype is described as “straight as a whole but finely interdigitating with a slight suggestion of frontal tabs” (Borsuk-Bialynicka, 1988: 223). IGM 3/168 shows a non-interdigitating zigzag suture, with well-defined parietal tabs. Whether the difference is the result of individual variation or specimen preservation cannot be determined due to the small sample size. Also, the postfrontals of the holotype are enlarged tending to enclose the supratemporal fenestra, whereas the new specimen from Ukhaa Tolgod has only a small part of the element preserved on both sides. These uncertainties make the referral of the new specimen to *Eoxanta lacertifrons* tentative.



ANGUIMORPHA FÜRBRINGER, 1900  
 CARUSIOIDEA GAO AND NORELL,  
 1998  
 CARUSIIDAE BORSUK-BIALYNICKA,  
 1987

Carolinidae Borsuk-Bialynicka, 1985: 153

*Carusia intermedia* Borsuk-Bialynicka, 1987,  
 nom. subst.

[pro *Carolina* Borsuk-Bialynicka, 1985  
 (non Thomson, 1880)]

Figure 30

HOLOTYPE: ZPAL MgR-III/34, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Djadokhta Formation—Bayn Dzak, Bayan Mandahu, Ukhaa Tolgod localities (Gao and Hou, 1996; this paper); Barun Goyot Formation—Khermeen Tsav and Khulsan (Borsuk-Bialynicka, 1985).

DIAGNOSIS: Sharing with extant xenosaurids the following derived character states: frontals fused and constricted between orbits; presence of jugal-squamosal contact; presence of dermal vermiculate rugosities on skull roof elements; postorbital branch of jugal ornamented.

Distinguished from all other closely related taxa including *Xenosaurus* and *Shinisaurus* by the following autapomorphies: lacrimal absent, with anteroventral process of jugal contacting prefrontal; caudoventral process of jugal ventrally directed; fenestra exochoanalis distinctively short and elliptic; presence of midline contact of palatines anteriorly; palatine rectangular and strongly widened, suppressing suborbital fenestra into narrow and elongate opening; presence of vertical crest anteriorly on quadrate; condyle-fossa articulation for both squamosal and supratemporal with cephalic condyle of quad-

rate; descending process of parietal subrectangular and laterally compressed; epipterygoid strongly oblique posterodorsally; marginal process of supraoccipital prominent and well ossified; presence of strong adductor crest dorsolaterally on surangular; marginal teeth extremely fine, large in number, and having comblike arrangement; strong posterior extension of neural spine of axis over entire third cervical (see Gao and Norell, 1998).

REFERRED SPECIMENS: IGM 3/16–3/23 (MAE 95-5, 95-52, 94-38, 40/93-90, 94-26, 96-9, 96-122, 96-191), all nearly complete skulls with mandibles; IGM 3/24–3/47 (MAE 35/93-167, 115/93-93, 241/93-130, 104/93-158, 33/93-167, 470/93-134, 92/93-104, 231/93-99, 414/93-111, 311/93-127, 36/93-129, 314/93-127, 37/93-129, 94-27, 94-49-1, 94-101, 95-72, 96-17, 96-40, 96-50, 96-52, 96-65, 96-109, 96-196), all incomplete skulls with mandibles; IGM 3/48–3/50 (MAE 94-49-2, 95-51, 61/93-130), all incomplete mandibles. The above-enumerated specimens (total: 35) are all from Ukhaa Tolgod and adjacent localities.

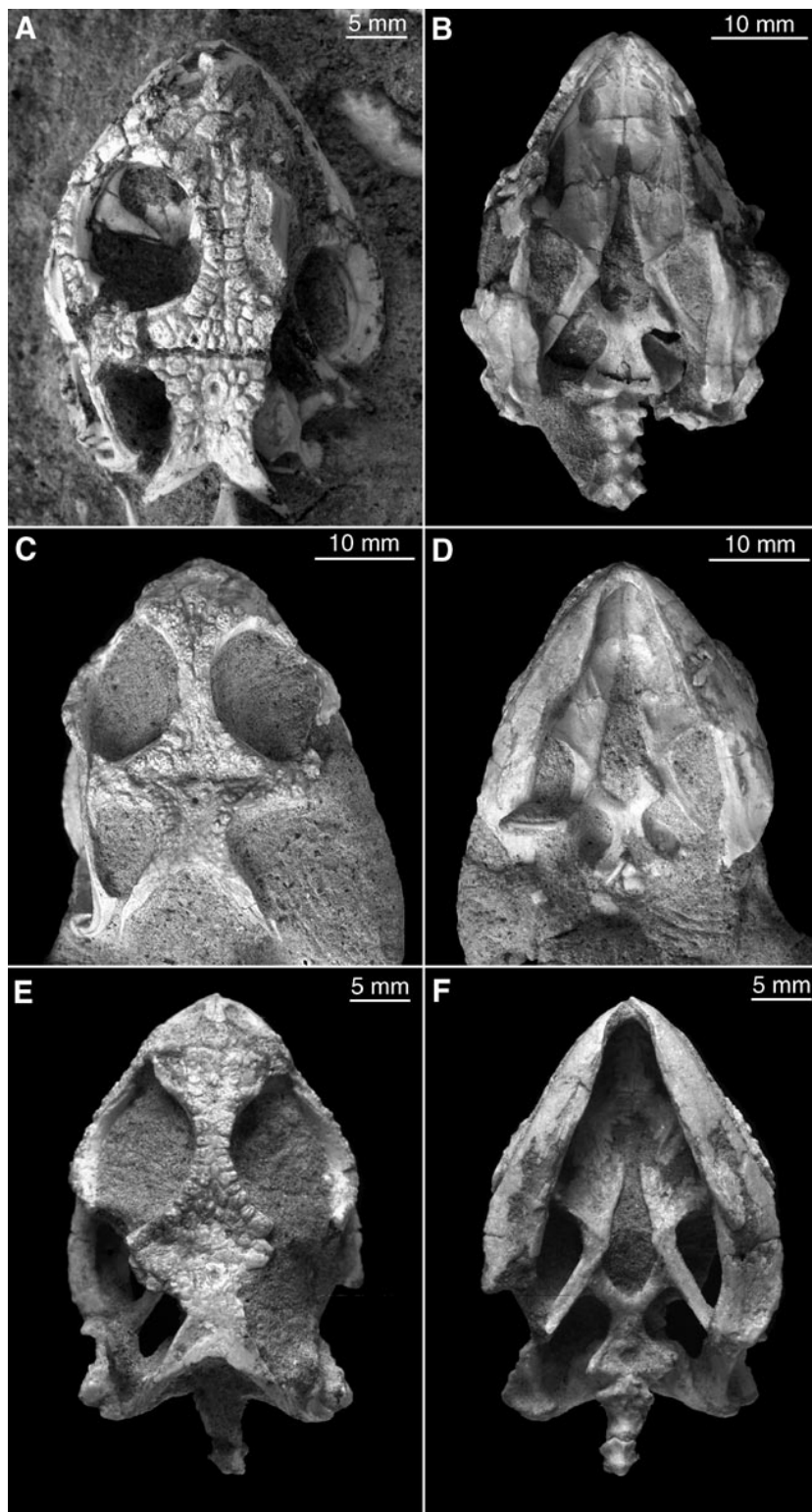
In addition, two incomplete skulls with mandibles IGM 3/51 and 3/52 (MAE 67, 71) represent the only specimens of *Carusia intermedia* from the classic Bayn Dzak (Flaming Cliffs) locality.

REMARKS: Although noticing some similarities shared by *Carusia intermedia* with the xenosaurids, Borsuk-Bialynicka (1985) originally classified the Gobi lizard in the Carusiidae and referred it to the family ?Scincomorpha. Later, the same author (Borsuk-Bialynicka, 1991a) regarded the family as “either a sister-group of the Xenosauridae or an autarchoglossan taxon convergent to this family.”

Recently, new specimens of this phylogenetically significant lizard species were collected from Bayan Mandahu (Gao and Hou, 1996), and from Ukhaa Tolgod and adjacent localities (Gao and Norell, 1998). The large

→

Fig. 30. Anguimorpha, Carusiidae, *Carusia intermedia*: **A**, IGM 3/16, skull with mandibles in dorsal view; **B**, IGM 3/25, palatal view; **C**, **D**, IGM 3/17, skull with mandibles, dorsal and ventral views; **E**, **F**, IGM 3/18, skull with mandibles, dorsal and ventral views.



number of exquisitely preserved specimens (fig. 30) from Ukhaa Tolgod provided important material for a thorough taxonomic revision and re-appraisal of the phylogenetic relationships of *Carusia intermedia*; and results of previous analysis place *Carusia intermedia* as the basal member of the Carusoidea, which in turn occupies the most basal position within the Anguimorpha (see Gao and Norell, 1998).

#### PLATYNOTA CAMP, 1923

**DEFINITION:** The taxon Platynota refers to a clade that includes the most recent common ancestor of Monstersauria and Varanidae, and all its descendants (see Gao and Norell, 1998).

**DIAGNOSIS:** The clade Platynota is diagnosed by an array of derived characters including: presence of plicidentine infolding at marginal tooth bases (McDowell and Bogert, 1954); marginal teeth widely spaced with expanded tooth bases (McDowell and Bogert, 1954); replacement teeth developed posteriorly without presence of resorption pits (Rieppel, 1978); maxillary tooth row entirely antorbital or slightly suborbital by no more than three tooth positions (McDowell and Bogert, 1954; Gao and Norell, 1998); vomer strongly elongate approaching level of posterior end of tooth row (Pregill et al., 1986); palatal shelf of vomer narrow (Pregill et al., 1986); palatine equally wide as long (Rieppel, 1980a); ectopterygoid in palatal view contacting palatine and excluding maxilla from entering suborbital fenestra (Rieppel, 1980a; Estes et al., 1988); development of intermandibular hinge (McDowell and Bogert, 1954); surangular blunt anteriorly in lateral view (Rieppel, 1980a; Pregill et al., 1986); posterior extension of splenial terminates anterior to or below the coronoid eminence (Estes et al., 1988); splenial-dentary suture loose, with much connective tissue between the two bones (Pregill et al., 1986); anterior process of coronoid elongated and extensively exposed dorsally (Estes et al., 1988); medial exposure of angular extensive, vertically suturing with splenial (McDowell and Bogert, 1954); cervical intercentrum sutures to posterior part of preceding centrum (Rieppel, 1980a, 1980b); autotomy on caudal

vertebrae absent (Hoffstetter and Gasc, 1969).

**REMARKS:** Camp (1923) included Varanoidea and Mosasauroidea in his Platynota. McDowell and Bogert (1954) used the term Platynota as an alternate name for Varanoidea, and a similar usage is seen in other publications (e.g., Rieppel, 1980a, 1988; Estes, 1983; Borsuk-Bialynicka, 1984). Lee (1997: 78) provided a stem-based definition of the Platynota: “*Heloderma*, *Lanthanotus* and *Varanus*, and all taxa more closely related to these forms than to other anguimorphs.” On the basis of a recent analysis of 105 characters across 30 ingroup and three outgroup taxa, Gao and Norell (1998) redefined the group as the most recent common ancestor of Monstersauria and Varanidae, and all its descendants. This definition is close to Camp’s (1923) original usage. The monophyly of the Platynota is supported by a long list of derived characters.

#### MONSTERSAURIA NORELL AND GAO, 1997

**DEFINITION:** A clade that includes the last common ancestor of *Gobiderma* and *Heloderma*, and all its descendants (see Norell and Gao, 1997).

**DIAGNOSIS:** This robust platynotan clade is diagnosed by the following derived character states: anterior extension of supratemporal reaches level of apex of parietal notch (equivocal); pterygoid lappet of quadrate present (unequivocal, Estes et al., 1988); anterolateral process of pterygoid extends dorsally on ectopterygoid to contact jugal (unequivocal); cephalic osteoderms fragmented and thickened as subconical mounds (unequivocal, McDowell and Bogert, 1954); dermal rugosities present with conspicuously pitted surfaces (McDowell and Bogert, 1954; equivocal); neural spines narrow and tall (Pregill et al., 1986; Norell and Gao, 1997; unequivocal); foramen ovale located anterior to the spheno-occipital tubercle (Norell and Gao, 1997).

**REMARKS:** The taxonomic treatment and the phylogenetic relationships of this important platynotan clade was discussed by Norell and Gao (1997). The Monstersauria, including the crown group Helodermatidae and

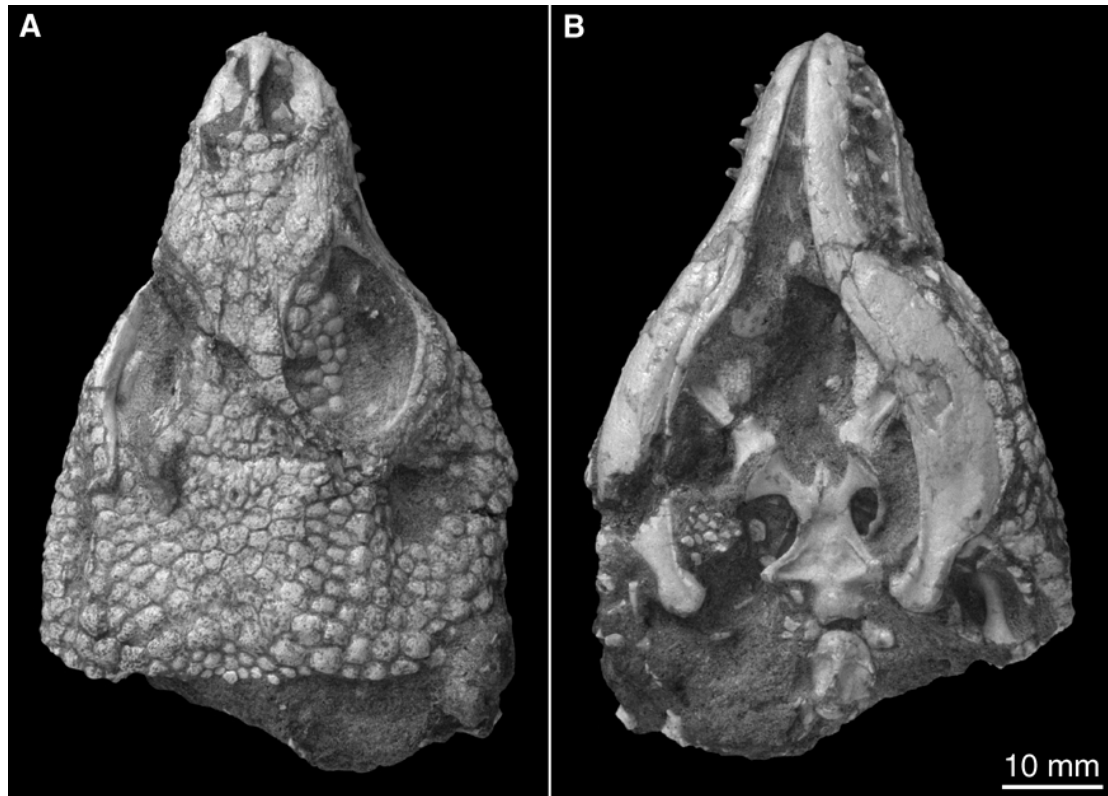


Fig. 31. Anguimorpha, Monstersauria, *Gobiderma pulchrum*: **A**, **B**, IGM 3/55, nearly complete skull with mandibles from Udan Sayr, dorsal and ventral views.

its closely related fossil taxa, forms the most basal platynotan clade (see Gao and Norell, 1998); and the monophyly of the group is well supported (see above).

*Gobiderma pulchrum* Borsuk-Bialynicka,  
1984

Figure 31

HOLOTYPE: ZPAL MgR-III/64, incomplete skull with mandibles.

TYPE LOCALITY AND HORIZON: Khermeen Tsav II, Upper Cretaceous Barun Goyot Formation, Mongolian Gobi Desert.

KNOWN DISTRIBUTION: Khermeen Tsav II (Borsuk-Bialynicka, 1984), Udan Sayr and Ukhaa Tolgod (this paper) localities; Barun Goyot and Djadokhta formations. Undescribed material is also known from Bayan Mandahu (K. Gao, personal obs.).

DIAGNOSIS: "Skull subpentagonal in outline, its larger part posterior. Frontal paired

but sometimes fusing with individual age. Posterolateral extensions of parietal close an angle of about  $130^\circ$ . An angle between paroccipital processes is only slightly less than this. Position of lacrimal foramen changing from prefrontolacrimal suture to lacrimal surface. Number of tooth positions is 11 on maxilla, 4 on premaxilla, 10 on dentary. Osteodermal skull covering of small-plate type or variable (anterior to the orbit)" (Borsuk-Bialynicka, 1984: 41).

REFERRED SPECIMENS: Udan Sayr—IGM 3/55 (MAE 96-162), nearly complete skull with mandibles from Udan Sayr; Ukhaa Tolgod—IGM 3/56–3/58 (MAE 68/93-45, 220/93-248, and 95-29), all incomplete skulls with mandibles; Khermeen Tsav—IGM 3/59 (MAE 254/92-33), partial skull with postcranial skeleton; Khulsan—IGM 3/60 (MAE 96-149), incomplete skull with mandibles.

REMARKS: Borsuk-Bialynicka (1984)





Fig. 32. Anguimorpha, *Estesia mongoliensis*: IGM 3/14 (holotype), nearly complete skull with mandibles from Khulsan (courtesy of L. Meeker and C. Tarka).

named and described *Gobiderma pulchrum* (original spelling: *Gobiderma pulchra*; nom. correct. in Norell et al., 1992), and classified it as “Necrosaurian grade” within the Platynta (family uncertain). Alifanov (1993a) listed *Gobiderma* in Necrosauridae without explanation. Lee (1997) grouped *Gobiderma* with *Parviderma* in the Gobidermatidae. A recent phylogenetic analysis, however, showed that *Gobiderma* is the basal taxon of the Monstersauria (Norell and Gao, 1997). This hypothesis is supported by results from our more recent analyses using additional data and a more sophisticated outgroup analysis (Gao and Norell, 1998).

New specimens collected by the Mongolian Academy of Sciences–American Museum of Natural History Expeditions include material not only from the type Khermeen Tsav area (IGM 3/59) but from Ukhaa Tolgod and adjacent localities. IGM 3/55 (fig. 31) from Udan Sayr represents the best specimen known for this taxon, and provides valuable information for understanding the skull morphology and relationships of this Gobi lizard taxon (see Gao and Norell, 1998). Complete redescription of the skull of

this taxon, and a revised diagnosis, will be presented elsewhere.

*Estesia mongoliensis* Norell et al., 1992

Figure 32

HOLOTYPE: IGM 3/14, a well-preserved skull with mandible.

TYPE LOCALITY AND HORIZON: Lizard Hill, Khulsan, (43°29'19"N, 101°08'44"E); Upper Cretaceous Barun Goyot Formation, Mongolian Gobi Desert.

KNOWN DISTRIBUTION: Khulsan, Khermeen Tsav, Ukhaa Tolgod, and Bayn Dzak localities (Norell et al., 1992; Norell and Gao, 1997; this paper); Djadokhta and Barun Goyot formations.

DIAGNOSIS: Distinguished from *Heloderma* and its fossil relatives by the following autapomorphies: presence of a distinct single, median palatal trough formed by vomers; long median contact of vomers; presence of extensive convex surface medial to posterior ridge on posterior surface of quadrate; no distinct articular; foramen ovale located far anterior to spheno-occipital tubercle; spheno-occipital tubercle strongly elongate and posterolaterally oriented (for characters shared

with its closely related taxa see discussion in Norell and Gao, 1997).

REFERRED SPECIMENS: IGM 3/15, partial skeleton with well-preserved braincase from Khermeen Tsav; IGM 3/169 (MAE 17/93-184), incomplete mandibles with teeth from Ukhaa Tolgod; additional specimens have been collected from Bayn Dzak, Djadokhta Formation (Norell and Gao, 1997).

REMARKS: On the basis of a nearly complete skull with mandibles from Khulsan (fig. 32), Norell et al. (1992) named and described *Estesia mongoliensis*, and provided alternative hypotheses in which *Estesia mongoliensis* could be grouped with either the Varanidae or the Helodermatidae (see also Lee, 1997). Additional specimens were later recovered from Khermeen Tsav and Ukhaa Tolgod, including a well-preserved braincase with partial postcranial skeleton (IGM 3/15), and incomplete mandibles with teeth (IGM 3/169). Discovery of the braincase (IGM 3/15) revealed pivotal evidence for clarifying the phylogenetic position of *Estesia mongoliensis*. Recent analyses using a different data set and different outgroup rooting indicate that the taxon is the sister group to the Helodermatidae in a clade named the Monstersauria (see Norell and Gao, 1997; Gao and Norell, 1998).

#### VARANOIDEA CAMP, 1923

DEFINITION: The most recent common ancestor of *Telmasaurus* and Varanidae, and all its descendants. The term Varanoidea as defined by Gao and Norell (1998) differs from the usage of previous authors (e.g., McDowell and Bogert, 1954; Rieppel, 1980a; Estes, 1983; Pregill et al., 1986; Estes et al., 1988), who in most cases used Varanoidea as alternative name for Platynta (see also Lee, 1997).

DIAGNOSIS: The Varanoidea as defined above can be unambiguously diagnosed by the following derived character states: subolfactory processes of frontals closely approach or contact posteromedially (McDowell and Bogert, 1954); entocarotid fossa within recessus vena jugularis absent (McDowell and Bogert, 1954); posterior lacrimal foramen double (Pregill et al., 1986); precondy-

lar constriction of vertebrae present (Estes et al., 1988).

REMARKS: The Varanoidea include the extant familial group Varanidae (*Varanus* and *Lanthanotus*) and three fossil taxa (*Cherminotus*, *Saniwa*, and *Telmasaurus*). Another fossil taxon, *Palaeosaniwa*, known from fragmentary jaws and vertebrae, shares with the group at least one character state: precondylar constriction of vertebrae; and hence, could well be a member of the group (see discussion in Gao and Norell, 1998).

#### *Cherminotus longifrons* Borsuk-Bialynicka, 1984 Figure 33

HOLOTYPE: ZPAL MgR-III/59, incomplete skull with mandibles missing.

TYPE LOCALITY AND HORIZON: Khermeen Tsav, Gobi Desert; Upper Cretaceous Barun Goyot Formation.

KNOWN DISTRIBUTION: Barun Goyot Formation—Khermeen Tsav (Borsuk-Bialynicka, 1984; Alifanov, 1993a); Djadokhta Formation—Ukhaa Tolgod and Tugrugen Shireh localities (this paper).

DIAGNOSIS: "A small-sized lanthanotid not attaining 3 cm of skull length with relatively long and slender snout and non-elongated parietal. Parietal foramen present. Vomers relatively long and slender. Teeth number very low. Basal fluting present but not very complicated" (Borsuk-Bialynicka, 1984: 60; see below for comments).

REFERRED SPECIMEN: IGM 3/170 (MAE 24/93-26), incomplete skull with mandibles and partial postcranial skeleton, from Tugrugen Shireh.

REMARKS: Although known from several specimens from the Gobi, the skull morphology of *Cherminotus longifrons* is poorly understood. Consequently, published diagnoses are inadequate. Besides the generic diagnosis (see above), Borsuk-Bialynicka (1984: 61) provided a species diagnosis as follows: "frontal to parietal length ratio is about 1.5 in sagittal axis. Five widely spaced conical teeth in the maxilla." However, none of these characters are diagnostic of the taxon and this diagnosis needs to be revised. For example, the holotype specimen is described as having an extra anterior surangular foramen.

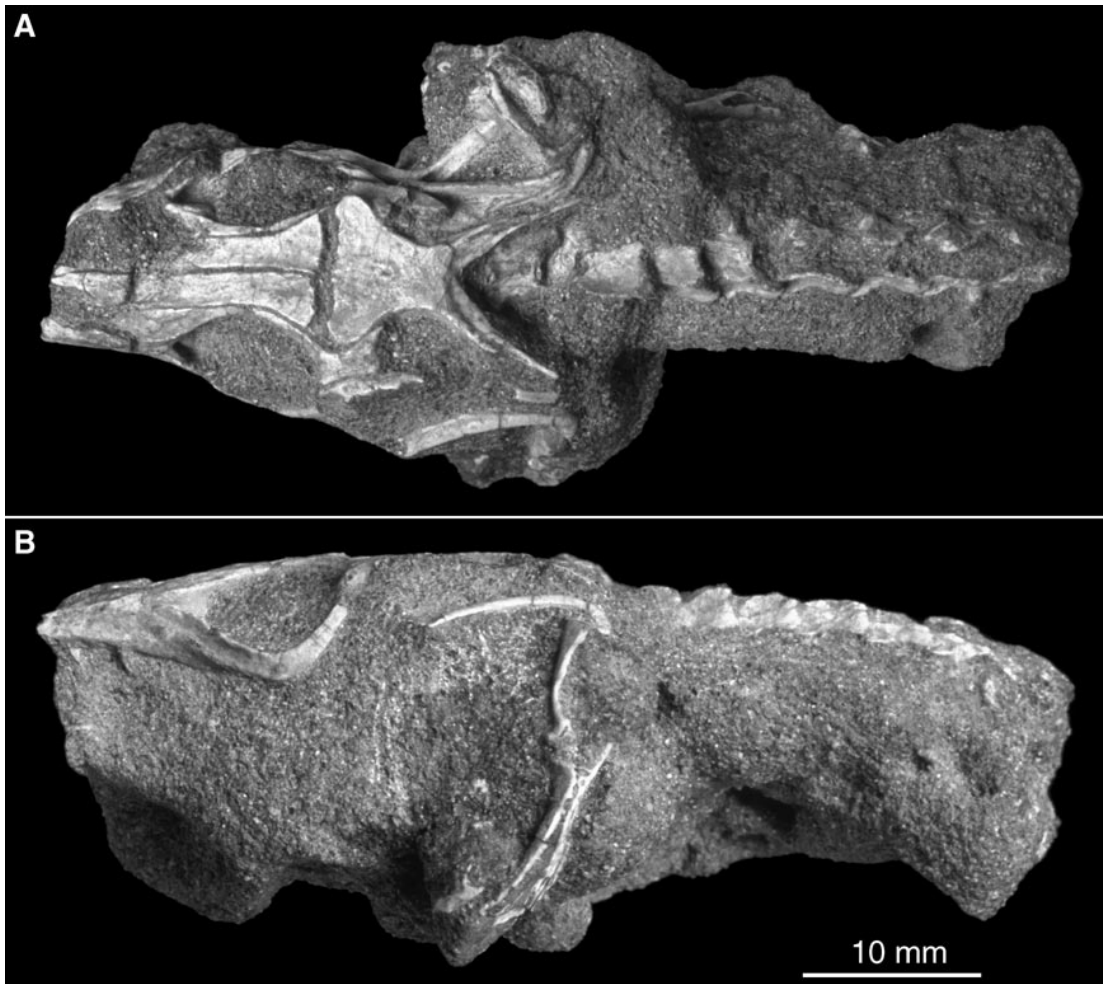


Fig. 33. Anguimorpha, Varanoidea, *Cherminotus longifrons*: **A**, **B**, IGM 3/170, incomplete skull with mandibles and cervical vertebrae from Tugrugeen Shireh, dorsal and lateral views.

men below the coronoid (Borsuk-Bialynicka, 1984: 66); if the observation is justified, this unique feature should be included in the diagnosis.

Phylogenetically, *Cherminotus longifrons* was grouped with *Lanthanotus* within the Varanidae (Borsuk-Bialynicka, 1984; Gao and Norell, 1998). The new material from Tugrugeen Shireh, however, provides significant data that may well challenge this interpretation. One phylogenetically significant feature concerns the supratemporal arch, which is not preserved on the holotype, yet was suggested to be incomplete. The new specimen (IGM 3/170) clearly shows that the

arch is complete, having a slender and elongated squamosal that extends far anterior to contact the postorbital (contra Borsuk-Bialynicka, 1984: fig. 17). Another important feature concerns the number of lacrimal foramina (see discussion below), but like the supratemporal arch, the actual condition is uncertain from previously known specimens. As shown on the new specimen (see fig. 33), *Cherminotus longifrons* has a single lacrimal foramen. Also, contrary to the original description of the teeth as conical, well-preserved teeth on the new specimen are trenchant, laterally compressed, and recurved. A complete redescription of this taxon based on



this material, which will result in a determination of its phylogenetic position, will be presented elsewhere. All that will be added here is that grouping *Cherminotus* with *Lanthanotus* is unsupported by any character evidence.

***Aiolosaurus oriens*, new genus and species**

Figure 34

ETYMOLOGY: *aiolos* (Gr.), god of the winds; *oriens* (L.), east.

HOLOTYPE: IGM 3/171 (MAE 283/93-108), incomplete skull with mandibles and partial postcranial skeleton.

TYPE LOCALITY AND HORIZON: Ukhaa Tolgod (between Xanadu and First Strike), Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation (Loope et al., 1998).

KNOWN DISTRIBUTION: Only known from the type locality and horizon.

DIAGNOSIS: Distinguished from *Cherminotus longifrons* and other closely related varanoids by the following character states: nasals paired; presence of aperture between premaxilla and maxilla; anteromedial process of maxilla separating premaxilla from septomaxilla; dorsal septomaxillary foramen strongly reduced and close to midline; anterior surangular foramen opening in distinct groove ventral to apex of coronoid process.

**DESCRIPTION**

The type and only known specimen IGM 3/171 (MAE 283/93-108) consists of a partial skull with both mandibles and partial postcranial skeleton. The preserved skull elements include the premaxillae, septomaxilla, right nasal, right maxilla with teeth, right frontal and prefrontal, right lacrimal, quadrate, squamosal, and supratemporal. The skull shows a strong narial retraction, as seen in other varanoids. Both left and right mandibles are preserved.

**SKULL ELEMENTS:** The premaxillae are fused as a single unit. It has a slender and elongate spine that slightly intervenes the anterior part of the nasals. The anterior surface of the premaxilla is smooth, and has no anterior dorsal premaxillary foramina (as opposed to *Varanus*, see Bahl, 1937; personal obs. of AMNH-DVP-CA 1201, 2994). How-

ever, a pair of posterior premaxillary foramina are developed laterally at the base of the premaxillary spine (fig. 34). The nasals are paired, as indicated by the clear midline suture anteriorly and the articular surface at the midline on the posterior part of the right element.

In ventral view, the premaxillae have a pair of short vomeromaxillary processes, which are separated from one another along the midline. The process posteriorly underlies the vomer. Anteriorly at the base of the processes, the incisive process of the premaxillae is well developed and is only slightly bipartite posteriorly by a small groove. No ventral premaxillary foramen can be identified, but a notch on the lateral border of the vomeromaxillary process forms the medial rim of the aperture between the premaxillae and the maxilla. The vomers are strongly elongate as a narrow band, and have a straight midline sutural contact. As seen in other varanoids, the vomer extension reaches to the level of the posterior end of the maxillary tooth row. A single vomerine aperture is developed anteromedially behind the premaxilla-vomer articulation and close to the midline suture of the vomers.

The prefrontal is preserved on the right side of the skull. It has an extensive sutural contact with the frontal medially, but anteromedially is separated from the anterior process of the frontal and the nasal by a narrow gap, as seen in other platynotans. The prefrontal has an elongate posterior extension, which at least extends to the midlevel of the orbit. However, whether the prefrontal contacted the postfrontal cannot be determined. The anteroventral process of the prefrontal laterally sutures with the well-developed lacrimal, which forms the anteroventral border of the orbit. A single lacrimal foramen opens at the suture between the two bones. However, the contribution of the prefrontal to the orbitonasal fenestra is unknown because of breakage in the specimen.

The right maxilla is completely preserved. It has a low nasal process, and is roughly triangular in lateral view, despite the strong narial retraction. Anteriorly, the bone has a slender but well-developed premaxillary process and anteromedial process; between these two processes opens a premaxillary aperture



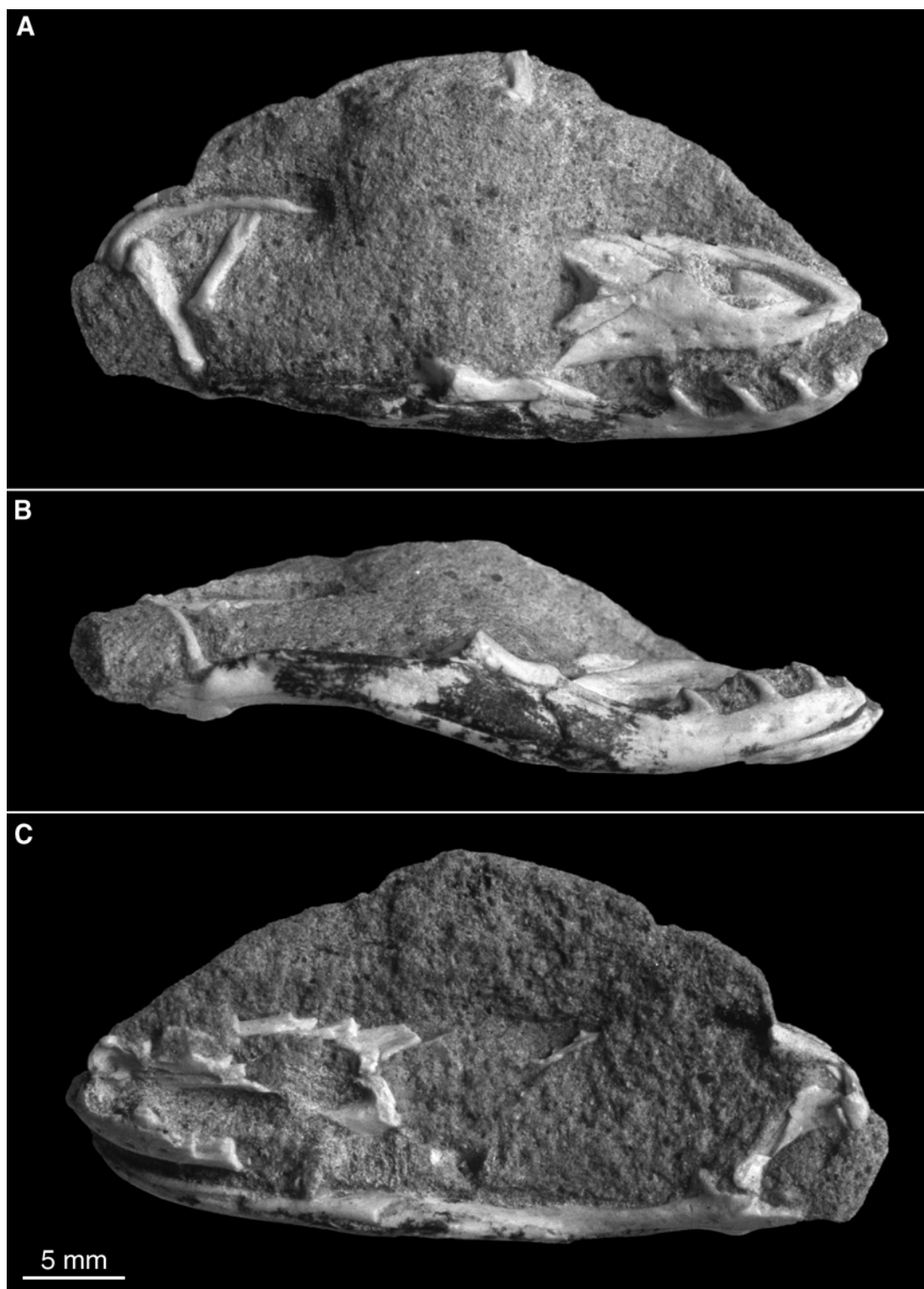


Fig. 34. Anguimorpha, Varanoidea, *Aiolosaurus oriens*, new genus and species: A–C, IGM 3/171, incomplete skull with mandibles from Ukhaa Tolgod, dorsolateral, lateral and ventral views.

(fig. 34). The anteromedial process is so well developed that it extends behind the premaxilla to a point where it must have contacted the opposite element (not preserved). In dorsal view, the dorsal maxillary foramen (anterior opening of the superior alveolar canal) opens anteromedial to the nasal process of the bone and is close to the maxillary-septomaxillary suture. The lateral surface of the maxilla is smooth, and is penetrated by a horizontal row of six irregularly spaced lateral superior alveolar foramina.

As in extant *Varanus*, the septomaxillae are exposed in dorsal view. The paired elements contact one another along the midline, and laterally suture with the inner border of the maxilla. The dorsal surface of the bone is convex, and the dorsal septomaxillary foramen is strongly reduced as a minute opening close to the midline.

**MANDIBLES:** The right mandible is nearly complete, whereas most of the left side is missing (only the anterior part of the dentary is preserved). The mandible is very slender, greatly elongate, and sigmoid in lateral view with a strongly curved ventral border of the dentary and elevated border of the postdentary region. The dentary-surangular articulation of the jaw is typical platynotan type, with the blunt anterior extension of the surangular terminating at the same level as the anterior extension of the coronoid.

The coronoid is proportionally a robust element. It has a strong anterodorsal process, which rests on top of the surangular horizontally and anteriorly clasps the dentary. Lateroventral to the summit of the coronoid, the surangular develops a distinct narrow groove in which opens the anterior surangular foramen. The location of the anterior surangular foramen is similar to other platynotans (*Varanus*, *Heloderma*), but the groove is probably unique for this taxon among platynotans. The posterior surangular foramen is a much smaller opening, which is located shortly anterior to the craniomandibular joint.

The prearticular is slender and long, and dorsally has a horizontal suture with the surangular following the contour of the jaw. The anterior half of the prearticular is ventrally covered by the angular bone, and thus, the anterior part of the prearticular-surangular suture is not exposed in lateral view. The lat-

eral exposure of the angular is more extensive than its medial side, and this is probably a primitive condition in comparison with extant platynotans.

In medial view, the subdental shelf is greatly reduced as a slope of tooth-bearing border, as seen in other platynotans and anguids as well. The Meckelian canal is strongly reduced and open ventrally as a narrow groove below the anterior half of the tooth row. The splenial is retracted to the midpoint of the tooth row, but it posteriorly has a short tonguelike extension that overlaps the angular (nonvertical posterior border). The splenial is dorsally separated from the dentary by a narrow gap, which is for connective tissue to form a mobile articulation. The anterior inferior alveolar foramen and the anterior mylohyoid foramen are closely located to one another, and both the foramina are roughly below the last dentary tooth.

The retroarticular process of the mandible is broken, but the preserved part clearly shows that the process is deflected medially as in other anguimorphs.

**DENTITION:** Marginal teeth are well preserved on the premaxillae and the right side of the jaws (both the upper and lower teeth). The premaxillae bear four teeth, and spaces for three others. The right maxilla has six teeth and spaces for three to four others, and the maxillary tooth row is entirely anterior to the orbit, as in many other platynotans. The right mandible has five teeth preserved, with the last tooth slightly removed from its original position. The teeth are widely spaced from one another, and the crowns are sharply pointed and recurved. Tooth bases are widened, and have weakly developed plicidentine infolding. The total number of dentary teeth is estimated as no more than nine, and this lower number is similar to the condition in *Cherminotus* (see above).

#### COMPARISON AND DISCUSSION

The new specimen (IGM 3/171) from the Ukhaa Tolgod locality is substantially smaller than any of the known specimens of *Telmasaurus grangeri* (see Gilmore, 1943; Borsuk-Bialynicka, 1984). It represents a new taxon that is referable to the Platynota on the basis of the following character states: pres-

ence of plicidentine infolding at the marginal tooth bases; marginal teeth widely spaced with expanded tooth bases; maxillary tooth row greatly shortened with no more than 13 positions, and the tooth row is entirely antorbital; vomer strongly elongated approaching the level of the posterior end of the tooth row; and palatal shelf of the vomer is narrow (see Gao and Norell, 1998).

Within the Platynota, the new taxon is comparable to *Cherminotus longifrons* in size and number of teeth, but differs from the latter in having a nonvertical posterior border of the splenial and a distinct groove for the anterior surangular foramen, and in lacking an extra opening of the anterior surangular foramen below the coronoid process (see Borsuk-Bialynicka, 1984). It is referable to the Varanoidea on the basis of a single character state: presence of precondylar constriction of vertebrae; two other characters about the subolfactory process of the frontal and entocarotid fossa within the recessus vena jugularis are unknown for this taxon.

The presence of double lacrimal foramina occurs in *Varanus* and *Lanthanotus* (McDowell and Bogert, 1954; Rieppel, 1980a), and in the fossil taxa *Telmasaurus grangeri* and *Saniwa* (Borsuk-Bialynicka, 1984; Gilmore, 1928). This morphology was recognized as a varanid synapomorphy (e.g., Estes, 1983; Pregill et al., 1986; but see also Gao and Norell, 1998). However, the specimen (IGM 3/171) clearly has a single lacrimal foramen and a similar condition is con-

firmed for *Cherminotus longifrons* (see above); and as far as this feature is concerned, the latter two taxa may well occupy more basal positions than those mentioned above within the Varanoidea.

Varanoidea, genus and species undetermined

Figure 35

SPECIMEN: IGM 3/172 (MAE 105/93-42), maxillary fragment and associated vertebrae.

LOCALITY AND HORIZON: Ukhaa Tolgod, Nemegt Basin, Mongolian Gobi Desert; Upper Cretaceous Djadokhta Formation.

REMARKS: The fragmentary maxilla and disarticulated vertebrae (see fig. 35) are apparently from the same individual, as they were collected in association. The left maxillary fragment has a fairly complete dorsal process, which is low and dorsally curved towards the midline. It has two incomplete teeth preserved, showing widely spaced, strongly expanded tooth bases with plicidentine infolding. The jaw fragment is similar to *Estesia mongoliensis* in size and configuration, but the teeth show no indication of a venom groove although they are incomplete. Also, the three nearly complete vertebrae show that the condyle is well ossified, expanded, and has a strong precondylar constriction. The condylar cup faces ventrally for articulation with a dorsally oriented condyle. These are typical varanoid features, indicating presence of a large varanoid of a size comparable to that of *Estesia mongoliensis* at Ukhaa Tolgod.

## TAXONOMIC DIVERSITY, PHYLOGENETIC SIGNIFICANCE, AND STRATIGRAPHIC DISTRIBUTION OF THE LIZARD ASSEMBLAGE

TAXONOMIC DIVERSITY: The lizard specimens collected from Ukhaa Tolgod and other Gobi localities document an important Late Cretaceous lizard assemblage, which shows considerable taxonomic diversity. In a preliminary survey of the collection amassed during the 1993–1997 field seasons, approximately 1000 specimens represent at least 30 species, including seven new species described in this paper (see table 1; appendix 1). The collection represents more than half

of the total number of lizard specimens ever collected and about half of the total number of species known from the Gobi Desert. The 30 species are classified in four higher taxonomic groups: Iguania, Gekkota, Scincomorpha, and Anguimorpha. The Iguania are documented by three new and five known species. This rich fossil record reflects an important Late Cretaceous radiation of the group in the Gobi Desert. The Scincomorpha are the most diverse group, represented by as

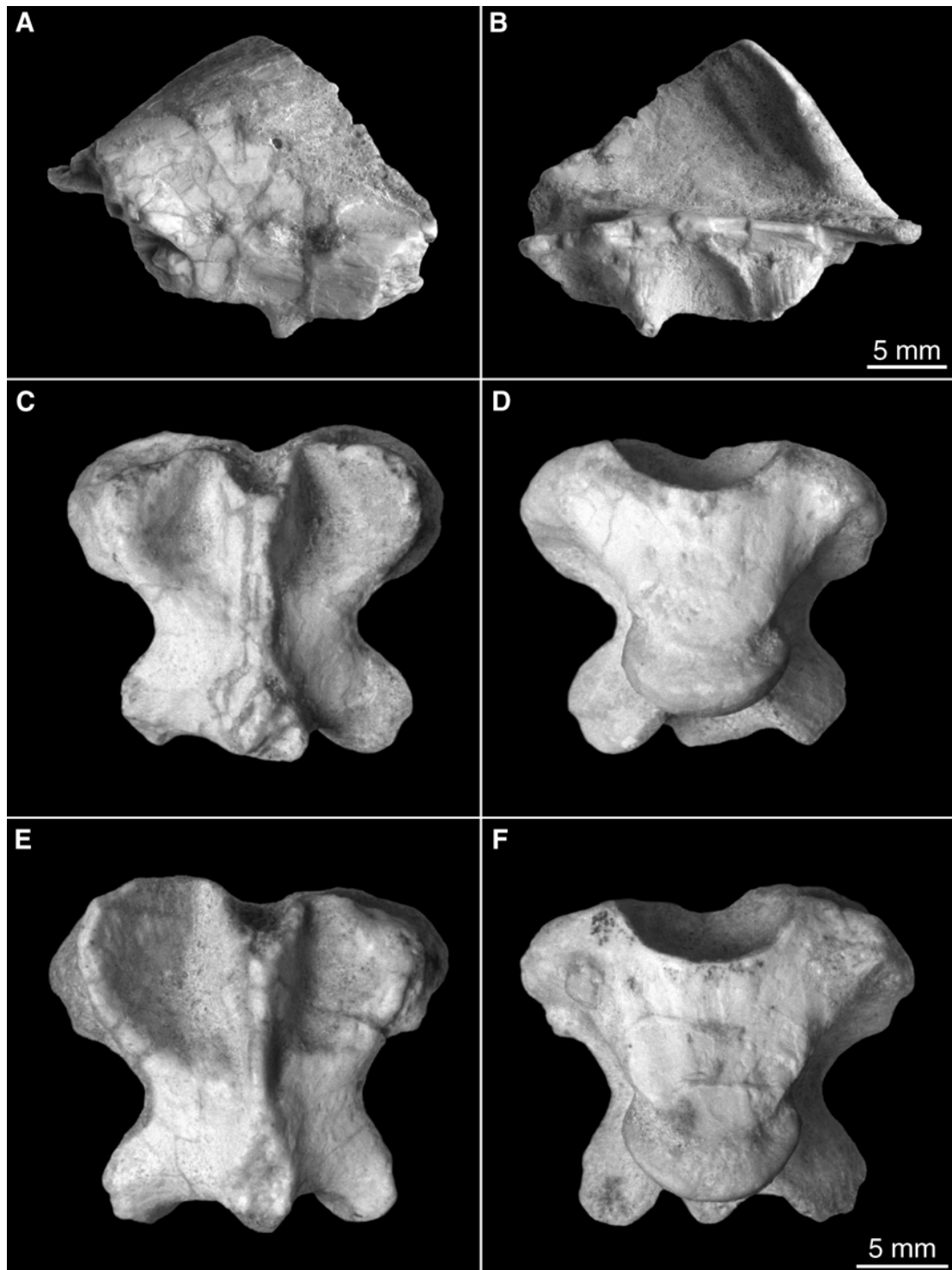


Fig. 35. Varanoidea, undetermined genus and species: **A, B**, IGM 3/172, left maxillary fragment lateral and medial views; **C–F**, associated vertebrae in dorsal and ventral views.



TABLE 1  
Distribution Patterns of Selected Lizard Taxa across Localities

See text for discussion. Taxa shown in boldface are found in both the Djadokhta and the Barun Goyot beds.

Taxon	Djadokhta				Barun Goyot	
	Bayn Dzak	Bayan Mandahu	Ukhaa Tolgod	Tugrugeen Shireh	Khermeen Tsav	Khulsan
<i>Mimeosaurus</i>	x	x	x	x		
<b><i>Priscagama</i></b>	x	x	x		x	x
<i>Isodontosaurus</i>	x	x	x	x		
<i>Anchaurosaurus</i>		x				
<i>Xihaina</i>		x				
<i>Zapsosaurus</i>				x		
<i>Ctenomastax</i>						x
<i>Temujinia</i>			x	x		
<b><i>Phrynosomimus</i></b>			x		x	x
<i>Igua</i>						x
<i>Potrussia</i>						x
<i>Flaviagama</i>				x		
<i>Myrmecodaptia</i>			x			
<b><i>Macrocephalosaurus</i></b>	x		x		x	x
<i>Conicodontosaurus</i>	x	x				
<b><i>Adamisaurus</i></b>	x	x	x	x	x	x
<i>Altanteius</i>					x	
<i>Pyramicephalosaurus</i>					x	x
<b><i>Gobinatus</i></b>			x		x	x
<i>Parameiva</i>					x	
<i>Prodenteia</i>					x	
<b><i>Tchingisaurus</i></b>			x		x	
<i>Parmeosaurus</i>			x			
<i>Hymenosaurus</i>			x			
<b><i>Globaura</i></b>	x	x	x		x	x
<b><i>Eoxanta</i></b>			x		x	x
<i>Darchansaurus</i>					x	
<i>Erdenesaurus</i>					x	
<i>Cherminisaurus</i>					x	
<b><i>Slavoia</i></b>			x		x	x
<i>Dzhadochthosaurus</i>				x		
<b><i>Gurvansaurus</i></b>				x		x
<i>Barungoia</i>						x
<b><i>Telmasaurus</i></b>	x					x
<i>Paravaranus</i>						x
<i>Proplatynotia</i>						x
<i>Parviderma</i>						x
<i>Saniwides</i>						x
<i>Bainguis</i>	x					
<b><i>Carusia</i></b>	x	x	x		x	x
<b><i>Cherminotus</i></b>				x	x	
<b><i>Estesia</i></b>	x		x		x	x
<b><i>Gobiderma</i></b>		x	x		x	x
<i>Aiolosaurus</i>			x			

many as 14 species including three new and 11 previously known species. The Anguimorpha are nearly as diverse as the Iguania, while the Gekkota is the least diverse group with a single species documented in the assemblage.

In terms of taxonomic diversity, lizards constitute an extremely conspicuous element of the vertebrate faunas of the desert systems today (Pianka, 1986). For instance, one of the desert regions with a large number of species (the vast interior deserts of Australia)

was referred to as “a land of lizards” (Finlayson, 1943). Many extant lizard clades may have evolved in response to a desert environments, as 11 of the 15 recognized extant familial groups occur in these systems (Pianka, 1986; Mattison, 1989). Among several studied areas with sand dune environments, North American desert sites support from as few as 4 to 10 species, whereas the Kalahari Desert in Africa supports 11–17 species. The richest lizard fauna today lives in the Great Victoria Desert of Australia, where as many as 40 species have a sympatric distribution (Pianka, 1986). Compared to the desert systems today, the Late Cretaceous Gobi Desert probably sustained one of the most taxonomically diverse lizard faunas yet reported. Since the 1920s, some 2000 specimens have been collected from the Gobi, and more than 60 species have been recognized. Study of these fossil lizards gives important insight into the taxonomic diversity of the Late Cretaceous lizard fauna in the Gobi Desert, and thus permits more accurate estimation of the phylogenetic diversity (Nixon and Wheeler, 1992) of the major squamate clades.

**PHYLOGENETIC SIGNIFICANCE:** The lizard sample from Ukhaa Tolgod and adjacent localities includes phylogenetically important basal taxa of various well-established clades. For example, the most extensive collection of *Carusia intermedia* is documented by some 40 exquisitely preserved skulls with mandibles from this area. A recent study showed that *Carusia intermedia* is a basal member of the Carusioidea, which in turn represent the most basal anguimorph clade (Gao and Norell, 1998). Recognition of the Carusioidea as an anguimorph basal clade is phylogenetically significant, as it helps to resolve an Anguinae/Xenosauridae/Varanoidea polytomy (see e.g., Estes et al., 1988). Other important basal taxa documented in the collection include: *Gobiderma* (basal taxon of the Monstersauria, see Norell and Gao, 1997), and *Myrmecodaptria* (possible basal taxon of Gekkota, this paper).

Current understanding of the phylogeny of the extant lizard clades is primarily based on results of the phylogenetic analysis by Estes et al. (1988). However, recent discoveries of fossil lizards from Late Cretaceous deposits in the Gobi Desert furnish important material

for a better understanding of character transformation among lizard groups, and will allow us to test the current phylogenetic hypothesis through the addition of both characters and taxa. For example, the presence of a forked postfrontal that clasps the frontoparietal suture has been interpreted as a scleroglossan synapomorphy (Estes et al., 1988) because it is absent in extant iguanians. Surprisingly, definite presence of the forked condition in some Late Cretaceous iguanians as described in this paper suggests an alternative interpretation: it may well be a primitive condition for squamates generally, and is later lost in crown-group iguanians. Another example concerns the anteromedial process of the maxilla. Modern acrodontans have well-developed processes that meet anteromedially below the palatal extension of the premaxillae (Cope, 1864). Estes et al. (1988) interpreted this condition as a potential synapomorphy of Acrodonta, although they noted variation in agamids and its occurrence in some gekkonids (recognized by Rieppel, 1984). However, new fossils described in this paper show definite occurrences of this morphology in several fossil iguanians (e.g., *Ctenomastax parva*, *Temujinia ellisoni*, *Phrynosomimus asper*) and some scincos (e.g., *Tchingisaurus multivagus*). Explanation of these occurrences requires reevaluation of this character state in squamate evolution. As many of these Late Cretaceous lizards appear to be basal taxa of their related extant clades, incorporation of these fossil taxa in a comprehensive analysis will have important effects on reconstruction of the phylogenetic history of the major lizard clades.

**STRATIGRAPHIC DISTRIBUTION:** A survey of the known fossil record shows that certain lizard species occur only in Djadokhta beds, while others only in Barun Goyot beds; there are also those species that have a relatively long range, occurring in both horizons. To compile data concerning the stratigraphic distribution of lizard taxa in the Gobi series, we constructed a chart to show the geological range of the selected taxa (see table 1). Sources of data were from various publications, including Gilmore (1943), Sulimski (1972, 1975, 1984), Borsuk-Bialynicka (1984, 1985, 1988), Alifanov (1993a, 1993b,

1996), Gao and Hou (1996), Norell et al. (1992), and this paper. It is obvious from this chart that lizards provide little evidence for temporally ordering or subdividing Barun Goyot and Djadokhta localities, since 15 of the 19 (78.9%) lizard species that occur at more than one locality are found in both the Barun Goyot and Djadokhta localities.

**Iguanians**—Among the iguanians, *Mimeosaurus crassus* and *Isodontosaurus gracilis* appear to be typical “Djadokhta-type” of lizards. Both have been known since the 1940s (Gilmore, 1943), but have never been reported from horizons other than the Djadokhta Formation. Several other iguanian species are also restricted to Djadokhta beds. These include *Anchaurosaurus gilmorei*, *Zapsosaurus sceliphros*, and *Temujinia ellisoni*. As discussed elsewhere in this paper, *Anchaurosaurus gilmorei* from Bayan Mandahu and *Zapsosaurus sceliphros* from Tugrugen Shireh are probably more closely related to one another than to any other lizard. The two forms occur in the same horizon (Djadokhta), but not at the same locality. The species *Polrussia mongoliensis* seems to be confined in the Barun Goyot Formation, whereas three others (*Ctenomastax parva*, *Priscagama gobiensis*, *Phrynosomimus asper*) are known from both Djadokhta and Barun Goyot horizons.

**Gekkotans**—As mentioned elsewhere in this paper, the fossil record indicates that the gekkotans are the least diverse group of lizards in the Cretaceous Gobi Desert. There are only two taxa known from the Djadokhta Formation: *Gobekko cretacicus* from the Bayn Dzak locality (Borsuk-Bialynicka, 1990), and *Myrmecodaptria microphagosa* from Ukhaa Tolgod (this paper). Another Central Asian record of the group is from the Early Cretaceous deposits exposed at Khoobur (Hobur) (Alifanov, 1989b).

**Scincomorphs**—Two new taxa (*Parmeosaurus scutatus* and *Hymenosaurus clarki*) described in this paper are among the few

scincomorphs that are confined to the Djadokhta Formation or its equivalents. On the other hand, several other scincomorphs are only known from the Barun Goyot or younger horizons. These include: *Cherminisaurus kozlowskii*, *Erdenetesaurus robinsonae*, *Macrocephalosaurus chulsanensis*, *Pyramicephalosaurus cherminicus*, and *Darchansaurus estesi*.

A large number of scincomorph species are known from both Djadokhta and Barun Goyot horizons: *Adamisaurus magnidentatus*, *Gobinatus arenosus*, *Tchingisaurus multivagus*, *Eoxanta lacertifrons*, *Slavoia darevskii*, and *Globaura venusta*. Interestingly, specimens of *Slavoia darevskii* are quite abundant at Ukhaa Tolgod (Djadokhta) and Khermeen Tsav (Barun Goyot), but are unknown from another Djadokhta-type locality (Bayan Mandahu) that was extensively sampled. This may be related to the different type of facies at these localities: both Ukhaa Tolgod and Khermeen Tsav have deposits that were formed under mesic environments, whereas Bayan Mandahu reflects an eolian depositional system (Jerzykiewicz et al., 1993; Loope et al., 1998).

**Anguimorphs**—Only a few anguimorphs seem to have a distribution confined to the Djadokhta beds. These include: *Bainguis parvus*, and the two forms (*Aiolosaurus oriens* and *Varanoidea*, genus and species undetermined) described in this paper. Three other anguimorphs (*Proplatynotia longirostrata*, *Parviderma inexacta*, *Saniwides mongoliensis*) are known only from the Barun Goyot horizon to date. The taxa mentioned above are relatively poorly known and are more or less problematic taxonomically. Well-established anguimorph taxa include: *Carusia intermedia*, *Gobiderma pulchrum*, *Estesia mongoliensis*, *Cherminotus longifrons*, *Telmasaurus grangeri*. All these species are known from both the Djadokhta and Barun Goyot horizons.

## PALEOECOLOGY AND MODE OF SPECIMEN PRESERVATION

The general ecosystem of the Late Cretaceous Gobi Desert was compared with the present-day Okavango Oasis, Kalahari Desert in East Africa (Jerzykiewicz, 1998). Although the Upper Cretaceous Djadokhta Formation deposits were interpreted to be predominantly formed in arid or semi-arid, alluvial to eolian environments (Gradzinski and Jerzykiewicz, 1974a; Jerzykiewicz et al., 1993; Eberth, 1993), lizard specimens are often preserved in association with different facies (or microenvironments), as reflected by different modes of preservation. For example, specimens from Bayan Mandahu are preserved in association with three different facies (Jerzykiewicz et al., 1993):

(1) Articulated lizard skeletons were collected, in association with in situ articulated dinosaurs, from structureless sandstones, which have been interpreted as sandstorm deposits containing autochthonous faunal components.

(2) Surface-worn specimens of isolated skulls with mandibles are often preserved in caliche nodules, in association with extraformational granules, pebbles, or cobbles. This type of sediment has been interpreted as alluvial deposits containing allochthonous faunal components.

(3) A large number of lizard specimens are preserved in calcite-cemented toesets of eolian dune deposits. The nature of this type of deposit is not well understood, but could reflect a habitat preference for a moist substrate or diagenetic control on the preservation of the fossils (Jerzykiewicz et al., 1993).

A similar three-facies setting has been recognized at Ukhaa Tolgod, where the redbeds are inferred in association with two eolian facies (Facies E-1-2 of Loope et al., 1998) and one alluvial fan facies (Facies F of Loope et al., 1998). In contrast to the Bayan Mandahu locality, however, the alluvial fan (Facies F, structureless sandstones lacking oriented concretions) is the only facies containing lizard and other vertebrate fossils at Ukhaa Tolgod (Loope et al., 1998). Loope et al. (1998) interpreted the structureless sandstones accompanying in situ burial of animal skeletons as likely to occur on sand fans during rain storms within a stabilized dune field

(contra Jerzykiewicz et al., 1993). Regardless of differing interpretations, we provide here a brief discussion of the mode of lizard fossil preservation in relation to the paleoenvironment (facies) at Ukhaa Tolgod.

Compared to other fossil localities within the Gobi Desert, the fossils from Ukhaa Tolgod are characterized by exceptional preservation and concentration. As mentioned above, all the lizard specimens were collected from fine-grained and structureless sandstones, and the surfaces of the bones show essentially no sand abrasion. Not only are complete or nearly complete skulls with unworn teeth commonly found, they often preserve delicate parts (e.g., braincase, semicircular canals; see fig. 36C). This type of preservation is indicative of quick burial without significant fluvial transport, and fossilization in a relatively moist environment with very low energy water involved in the taphonomic process. Such environment is more likely to occur in a stabilized rather than active dune field.

Many fossil taxa recorded in the collection apparently represent burrowing lizards. These include two forms (*Phrynosomimus asper* and *Slavoia darevskii*) that probably shared the same microenvironment, as the specimens of these two taxa are often preserved in the same kind of loose sand deposits. *Phrynosomimus asper* is an acrodontan iguanian that in skull morphology shows a striking similarity to the North American "horned lizard" (*Phrynosoma*). Although having an acrodont dentition, the marginal teeth of this lizard are reduced in size paralleling those of the "horned lizard," which specialize on a diet of ants in desert environments. *Slavoia darevskii* (scincomorph), commonly known from Khulsan and Khermeen Tsav of the Barun Goyot Formation (Sulimski, 1984), is now known from Ukhaa Tolgod. It shows convergent similarities to southern African acontine skinks (see discussion above), which spend a large proportion of their lives below ground, feeding on worms and other soft-bodied small invertebrates (Mattison, 1989).

Known from both Djadokhta (Bayn Dzak and Ukhaa Tolgod) and Barun Goyot (Kher-



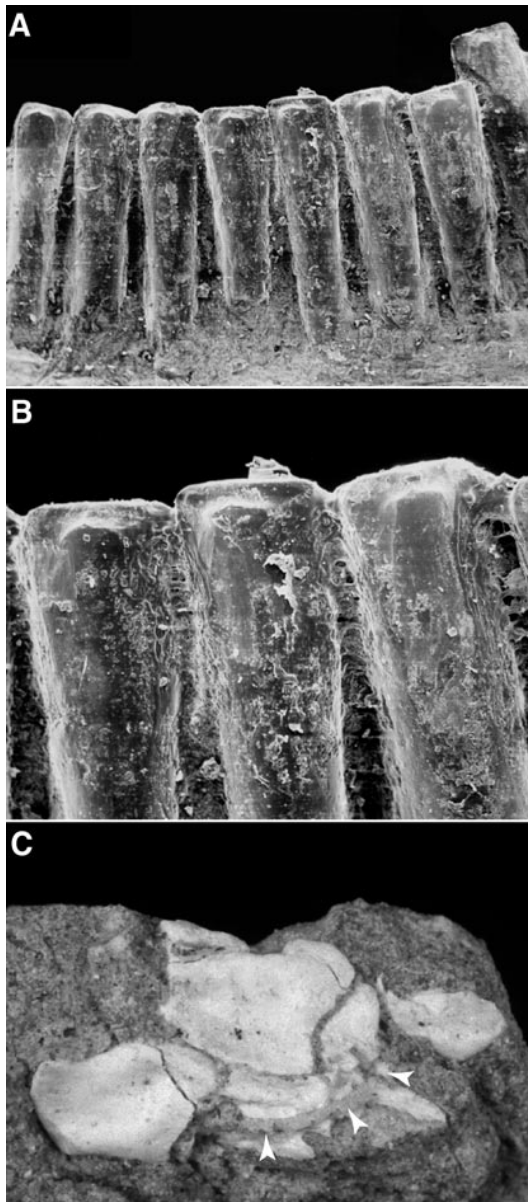


Fig. 36. Exceptional preservation of lizard specimens at Ukhaa Tolgod: **A**, SEM photograph of unworn dentary teeth of IGM 3/50 (*Carusia intermedia*),  $\times 20$ ; **B**, higher magnification of three posterior teeth in lingual view,  $\times 50$ ; **C**, undistorted braincase of a possible iguanian, arrows pointing to lateral semicircular canal.

meen Tsav and Khulsan) localities, *Globaura venusta* is obviously another lizard that was highly adapted to a burrowing life-style. It has a pointed snout and an enlarged braincase exposed posterior to the parietal (Rieppel, 1981). The skull morphology, in keeping with its preservation in poorly cemented sandstone, suggests that the species may represent a Late Cretaceous “ecological equivalent” of extant sandfish in North African, Middle Eastern, and North American deserts (e.g., Mattison, 1989).

Exceptional preservation of virtually complete and undistorted articulated lizard skeletons at Ukhaa Tolgod deserves special attention. Some of these skeletons apparently represent burrowing lizards that died underground and are preserved in burrows. For example, some specimens of *Parmeosaurus scutatus* are preserved in a unique curled body position, with the head hidden underneath the tail (fig. 24). These skeletons are preserved in sandstone concretion blocks, which are better cemented than, and are separated from, the surrounding sediment. This interpretation (skeletons preserved in burrows) is supported by the skull morphology of this lizard, as the pointed snout and enlarged braincase exposed posterior to the parietal are obviously related to burrowing (see Rieppel, 1981). Mesozoic examples of lizard skeletons preserved in burrows are rarely known. The lizard fossils mentioned above may represent one of the earliest known examples of lizard skeletons preserved in burrows.

Another type of preservation of virtually complete skeletons is depicted by an iguanian specimen (fig. 37). The skeleton is remarkably complete with only parts of the right limbs missing. The completeness of the skeleton gives clear indication of quick burial during rapid deposition, and the “struggling” position of the skeleton preserved in fine-grained sandstones seems to indicate a muddy sand fan formed during a major rainstorm (see Loope et al., 1998).

Besides different modes of specimen preservation, another line of evidence for paleoenvironmental inference comes from dentition of lizards. As evidenced from tooth morphology (crown pattern, in particular), the lizards from Ukhaa Tolgod are predomi-

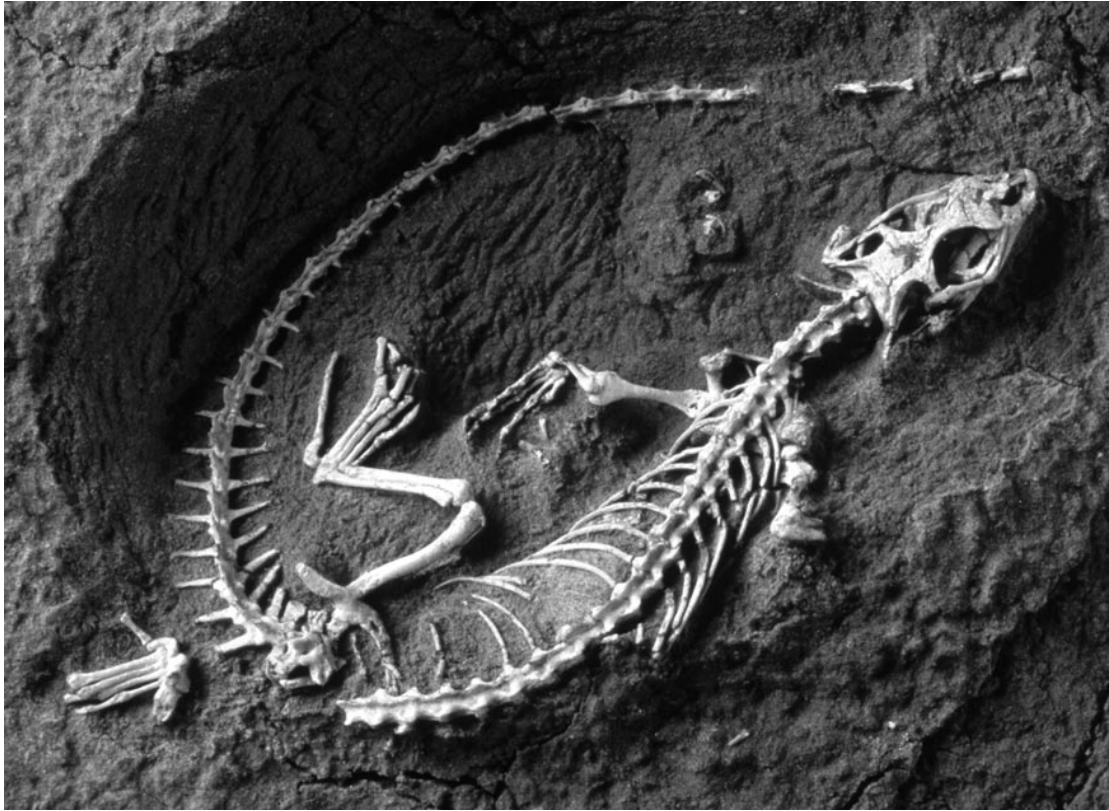


Fig. 37. Virtually complete lizard skeleton from Ukhaa Tolgod, dorsal view (courtesy of Amy Davidson).

nantly predatory (carnivorous and insectivorous), like those from the Bayan Mandahu locality of Inner Mongolia (see Gao and Hou, 1996). True herbivores are extremely rare, in contrast to other localities such as Khermeen Tsav and Khulsan, where large herbivores (e.g., *Macrocephalosaurus*, *Cherminisaurus*) with polycuspid teeth are common (see Sulimski, 1975). Since Ukhaa Tolgod has been extensively sampled for years, we interpret the paucity of true herbivorous lizards as a natural phenomenon of the assemblage, not a taphonomic artifact. Among the insectivores, further ecological categori-

zation can be made based on different types of dentition (Greene, 1982): those with tricuspid crowns in different higher taxonomic groups (Iguania and Scincomorpha) are highly adapted for crushing soft- to hard-shelled insects (e.g., Hotton, 1955), whereas others with peglike teeth are highly adapted for a myrmecophagous diet. These feeding adaptations provide an important source of information for the ecological characterization of lizard species, and for understanding the paleoenvironment in which these species inhabited.

## CONCLUSIONS

A taxonomically diverse lizard assemblage from Ukhaa Tolgod and adjacent localities includes at least 30 species in four higher

groups (Iguania, Gekkota, Scincomorpha, and Anguimorpha). Iguanians are represented by eight species, and are relatively abun-

dant in terms of number of taxa and individuals. The Scincomorpha are the most diverse group, represented by as many as 14 species. The Anguimorpha are nearly as diverse as the Iguania, whereas the Gekkota are the least diverse group with a single species documented in the assemblage.

Several new taxa are named and described based on well-preserved skulls or skeletons. Recognition of these new taxa provides important insights into the taxonomic diversity of the lizard assemblage and the phylogenetic diversity of the relevant lizard clades. These include phylogenetically significant basal taxa of various well-established clades, and hence, description of the morphological details of these taxa lay the foundation for future comprehensive cladistic analyses of the relevant lizard groups.

The paleoecological significance of these lizards cannot be overlooked. Lizard speci-

mens are often preserved in association with different facies that reflect different types of microenvironments in the Gobi. Many taxa are obviously desert dwellers, showing adaptations to a burrowing life-style as interpreted from their cranial morphology and possible analogies of extant species. Some specimens apparently represent lizards that died underground and were preserved in burrows. Virtually complete skeletons preserved in poorly cemented fine-grained sandstones at Ukhaa Tolgod seems to reflect quick burial in muddy sand fans that formed during major rainstorms. As evidenced from tooth morphology, lizards from Ukhaa Tolgod are predominantly predatory, whereas true herbivores are extremely rare. Further study of the feeding adaptations of these lizards is significant for understanding the paleoenvironmental details of the Late Cretaceous Gobi Desert.

## ACKNOWLEDGMENTS

This paper is based on significant field discoveries from the Mongolian Gobi Desert by members of the Mongolian Academy of Sciences–American Museum of Natural History joint expeditions of the 1990s. We thank all those involved. We thank Darrel Frost and Linda Ford (Department of Herpetology, American Museum of Natural History) for providing skeletal specimens of the extant species for comparison, and Demberelyin Dashzeveg for translation of literature in Russian. Extensive discussion with Susan E. Evans (University College London) helped to clarify some taxonomic uncertainties. We thank Mick Ellison for skillful preparation of photographs and drawings. IGM 3/15 and 3/16 were prepared by M. Fox, IGM 3/53 and 3/61 by Amy Davidson, who also prepared

and photographed the complete skeleton in figure 37 (all other specimens were prepared by the first author). Adrine MacDonald helped in preparation of some drawings (figures 7, 14, and 19). We thank the two anonymous reviewers for their helpful comments. The research was supported by the Frick Laboratory Endowment, the Department of Vertebrate Paleontology, American Museum of Natural History, the National Science Foundation (NSF DEB 9300770), the IREX Foundation for International Research, the National Geographic Society, the Philip McKenna Foundation, and Richard, Lynette and Byron Jaffe. Gao's work was supported by a Frick Research Fellowship of the American Museum of Natural History and by the National Science Foundation (NSF DEB-9806811).

## REFERENCES

- Alifanov, V. R.  
1988. New lizards (Lacertilia, Teiidae) from the Upper Cretaceous of Mongolia. *Trans. Soviet-Mongolian Palaeontol. Exped.* 34: 90–100.  
1989a. New priscagamids (Lacertilia) from the Upper Cretaceous of Mongolia and their systematic position among Iguania. *Paleontol. J.* 1989: 68–80.  
1989b. Earliest gekko (Lacertilia: Gekkonidae) from the Early Cretaceous of Mongolia. *Ibid.* 1: 124–126.



- 1993a. Some peculiarities [sic] of the Cretaceous and Palaeogene lizard faunas of the Mongolian People's Republic. *Kaupia* 3: 9–13.
- 1993b. New lizards of the family Macrocephalosauridae (Sauria) from the Upper Cretaceous of Mongolia, critical remarks on the systematics of the Teiidae (sensu Estes, 1983). *Paleontol. J.* 27: 70–90.
1996. Lizards of the families Priscagamidae and Hoplocercidae (Sauria, Iguania): phylogenetic position and new representatives from the Late Cretaceous of Mongolia. *Ibid.* 30: 466–483.
- Andrews, R. C.  
1932. The new conquest of Central Asiatic. A narrative of the Central Asiatic Expeditions in Mongolia and China 1921–1930. New York: Am. Mus. Nat. Hist., 678 pp.
- Averianov, A. O.  
1997. New Late Cretaceous mammals of southern Kazakhstan. *Acta Palaeontol. Pol.* 42 (2): 243–256.
- Averianov, A. O., and L. A. Nessov  
1995. A new Cretaceous mammal from the Campanian of Kazakhstan. *Neues Jahrb. Geol. Paläontol., Monatsh.* 2: 65–74.
- Bahl, K. N.  
1937. Skull of *Varanus monitor* (Linn.). *Rec. Indian Mus.* 39: 133–174.
- Beddard, F. E.  
1905. Some notes on the cranial osteology of the Mastigure lizard, *Uromastix*. *Proc. Zool. Soc. London* 1905: 2–9.
- Bellairs, A. d'A., and A. M. Kamal  
1981. The condrocranium and the development of the skull in recent reptiles. In C. Gans and T. S. Parsons (eds.), *Biology of the Reptilia*, 11: 1–263. London: Academic Press.
- Berkey, C. P., and F. K. Morris  
1927. *Geology of Mongolia, natural history of Central Asia*, Vol. II. New York: Am. Mus. Nat. Hist., 475 pp.
- Blanc, C-P.  
1977. Reptiles Sauriens Iguanidae. Faune de Madagascar: Publiée sous les auspices du Gouvernement de la République Malgache 45.
- Bohlin, B.  
1953. Fossil reptiles from Mongolia and Kansu. Report from the scientific expedition to the northwestern provinces of China under the leadership of Dr. Sven Hedin. *The Sino-Swed. Exped., Publ.* 37, IV. *Vertebr. Paleontol.* Stockholm: Statens Etnogr. Mus., 113 pp.
- Borsuk-Bialynicka, M.  
1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert. *Palaeontol. Pol.* 46: 5–105.
1985. Carolinidae, a new family of xenosaurid-like lizards from the Upper Cretaceous of Mongolia. *Acta Palaeontol. Pol.* 30: 151–176.
1987. *Carusia intermedia*, a new name for the Later Cretaceous lizard *Carolina* Borsuk-Bialynicka, 1985. *Ibid.* 32: 153.
1988. *Globaura venusta* gen. et sp. n. and *Eoxanta lacertifrons* gen. et sp. n.—non-teiid lacertoids from the Late Cretaceous of Mongolia. *Ibid.* 33: 211–248.
1990. *Gobekko cretacicus* gen. et sp. n., a new gekkonid lizard from the Cretaceous of the Gobi Desert. *Ibid.* 35: 67–76.
- 1991a. Questions and controversies about saurian phylogeny, Mongolian perspective. *Univ. Oslo, Contrib. Paleontol. Mus.* 364: 9–10.
- 1991b. Cretaceous lizard occurrences in Mongolia. *Cretaceous Res.* (1991) 12: 607–608.
- Borsuk-Bialynicka, M., and V. R. Alifanov  
1991. The first Asiatic iguanid' lizards in the Late Cretaceous of Mongolia. *Acta Palaeontol. Pol.* 36: 325–342.
- Borsuk-Bialynicka, M., and S. M. Moody  
1984. Priscagaminae, a new subfamily of the Agamidae (Sauria) from the Late Cretaceous Gobi Desert. *Acta Palaeontol. Pol.* 29: 51–81.
- Brinkman, D. B., and J. H. Peng  
1993. A new species of *Zangerlia* (Testudines: Nanhsiungchelyidae) from the Upper Cretaceous redbeds at Bayan Mandahu, Inner Mongolia, and the relationship of the genus. *Can. J. Earth Sci.* 30: 526–540.
- Camp, C.  
1923. Classification of the lizards. *Bull. Am. Mus. Nat. Hist.* 48: 289–481.
- Chiappe, L. M., M. A. Norell, and J. M. Clark  
1998. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. In F. A. Novas and R. E. Molnar (eds.), *Proc. Gondwanan Dinosaur Symp.* *Mem. Queensland Mus.* 39: 557–582.
- Cope, E. D.  
1864. On the characters of the higher groups of Reptilia, Squamata and especially of



- the diploglossa. *Proc. Acad. Nat. Sci. Philadelphia* 1864: 224–231.
- Currie, P. J.  
1993. Preface. *Can. J. Earth Sci.* 30: iii–iv.
- Cuvier, G.  
1817. Le règne animal distribué d'après son organisation, pour servir de base d'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Vol. 2, Les reptiles, les poissons, les mollusques, et les aniélides. Paris: Deterville.
- Dashzeveg, D., M. J. Novacek, M. A. Norell, J. M. Clark, L. M. Chiappe, A. Davidson, M. C. McKenna, L. Dingus, C. Swisher, and P. Altangerel  
1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. *Nature* 374: 446–449.
- de Queiroz, K.  
1987. Phylogenetic systematics of iguanine lizards: a comparative osteological study. *Univ. California Publ. Zool.* 118: 1–203.
- Dong, Z. M.  
1993. The field activities of the Sino-Canadian Dinosaur Project in China, 1987–1990. *Can. J. Earth Sci.* 30: 1997–2001.
- Eberth, D. A.  
1993. Depositional environments and facies transitions of dinosaur-bearing Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China). *Can. J. Earth Sci.* 30: 2196–2213.
- El-Toubi, M. R.  
1945. Notes on the cranial osteology of *Uromastyx aegyptia* (Forskål). Fouad I Univ. (Cairo) *Bull. Fac. Sci.* 25: 1–10.
- Elzanowski, A.  
1977. Skulls of *Gobipteryx* (Aves) from the Upper Cretaceous of Mongolia. *Palaeontol. Pol.* 37: 153–165.  
1981. Embryonic bird skeletons from the Late Cretaceous of Mongolia. *Ibid.* 42: 147–179.
- Estes, R.  
1983. Sauria Terrestria, Amphisbaenia. *Handbuch der Paläoherpétologie*, Pt. 10A. Stuttgart: Gustav Fischer, 249 pp.
- Estes, R., K. de Queiroz, and J. Gauthier  
1988. Phylogenetic relationships within squamata. In R. Estes and G. Pregill (eds.), *Phylogenetic relationships of the lizard families*: 119–282. Stanford: Stanford Univ. Press.
- Etheridge, R.  
1964. The skeletal morphology and systematic relationships of sceloporine lizards. *Copeia* 1964: 610–631.  
1967. Lizard caudal vertebrae. *Ibid.* 1967: 699–721.
- Etheridge, R., and K. de Queiroz  
1988. A phylogeny of Iguanidae. In R. Estes and G. Pregill (eds.), *Phylogenetic relationships of the lizard families*: 283–367. Stanford: Stanford Univ. Press.
- Evans, S. E.  
1993. Jurassic lizard assemblage. *Rev. Paléobiol.*, vol. spéc. 7: 55–65.  
1994. The Solnhofen (Jurassic: Tithonian) lizard genus *Bavarisaurus*: new skull material and a reinterpretation. *Neues Jahrb. Geol. Paläontol.* 192: 37–52.
- Evans, S. E., and D. C. Chure  
1998. Paramacellogid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *J. Vertebr. Paleontol.* 18: 99–114.
- Fastovsky, D. E., D. Badamgarav, H. Ishimoto, M. Watabe, and D. B. Weishampel  
1997. The paleoenvironments of Tugrikin-Shireh (Gobi Desert, Mongolia) and aspects of the taphonomy and paleoecology of *Protoceratops* (Dinosauria: Ornithischia). *Palaos* 1997 (12): 59–70.
- Finlayson, H. H.  
1943. The red centre. Sydney: Angus and Robertson.
- Fox, R. C.  
1978. Upper Cretaceous terrestrial vertebrate stratigraphy of the Gobi Desert (Mongolian People's Republic) and western North America. In C. R. Stelck and B. D. E. Chatterton (eds.), *Western and Arctic Canadian biostratigraphy*. *Geol. Assoc. Can. Spec. Pap.* 18: 577–594.
- Frost, D. R., and R. Etheridge  
1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 81: 1–65.
- Fürbringer, M.  
1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Z.* 34: 215–718.
- Gao, K., and R. C. Fox  
1991. New teiid lizards from the Upper Cretaceous Oldman Formation (Judithian) of southeastern Alberta, Canada, with a review of the Cretaceous record of teiids. *Ann. Carnegie Mus.* 60: 145–162.  
1996. Taxonomy and evolution of Late Cretaceous lizards from western Canada.

- Bull. Carnegie Mus. Nat. Hist. 33: 1–107.
- Gao, K., and L. Hou  
 1995. Iguanians from the Upper Cretaceous Djadokhta Formation, Gobi Desert, China. *J. Vertebr. Paleontol.* 15: 57–78.  
 1996. Systematics and taxonomic diversity of squamates from the Upper Cretaceous Djadokhta Formation, Bayan Mandahu, Gobi Desert, People's Republic of China. *Can. J. Earth Sci.* 33: 578–598.
- Gao, K., and M. A. Norell  
 1996. A rich lizard assemblage from Ukhaa Tolgod, Gobi Desert, Mongolia. *J. Vertebr. Paleontol.* 16 (3): 36A.  
 1998. Taxonomic revision of *Carusia intermedia* (Reptilia: Squamata) from the Upper Cretaceous of Gobi Desert and phylogenetic relationships of anguimorphian lizards. *Am. Mus. Novitates* 3230: 51 pp.
- Gauthier, J., R. Estes, and K. de Queiroz  
 1988. A phylogenetic analysis of Lepidosauriformes. In R. Estes and G. Pregill (eds.), *Phylogenetic relationships of the lizard families*: 15–98. Stanford: Stanford Univ. Press.
- Gilmore, C. W.  
 1928. Fossil lizards of North America. *Mem. Natl. Acad. Sci.* 22: 1–201.  
 1931. Fossil turtles of Mongolia. *Bull. Am. Mus. Nat. Hist.* 59: 213–257.  
 1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming, pt. II. lizards. *Proc. Am. Philos. Soc.* 85: 159–167.  
 1943. Fossil lizards of Mongolia. *Bull. Am. Mus. Nat. Hist.* 81: 361–384.
- Gradzinski, R., and T. Jerzykiewicz  
 1972. Additional geographical and geological data from the Polish-Mongolian palaeontological expeditions. *Palaeontol. Pol.* 27: 17–32.  
 1974a. Dinosaur- and mammal-bearing aeolian and associated deposits of the Upper Cretaceous in the Gobi Desert (Mongolia). *Sediment. Geol.* 12: 249–278.  
 1974b. Sedimentation of the Barun Goyot Formation. *Paleontol. Pol.* 30: 111–146.
- Gradzinski, R., J. Kazmierczak, and J. Lefeld  
 1968. Geographical and geological data from the Polish-Mongolian palaeontological expeditions. *Palaeontol. Pol.* 19: 3–82.
- Gradzinski, R., Z. Kielan-Jaworowska, and T. Maryanska  
 1977. Upper Cretaceous Djadokhta, Barun Goyot and Nemegt formations of Mongolia, including remarks on previous subdivisions. *Acta Geol. Pol.* 27: 281–318.
- Gray, J.  
 1827. A synopsis of the genera of saurian reptiles, in which some new genera are indicated and the others reviewed by actual examination. *Ann. Philos.* 2: 54–58.
- Greene, H.  
 1982. Dietary and phenotypic diversity in lizards: why are some organisms specialized? In D. Mossakowski and G. Roth (eds.), *Environmental adaptation and evolution*: 107–128. Stuttgart: Gustav Fischer.
- Greer, A.  
 1970. A subfamilial classification of scincid lizards. *Harvard Univ., Bull. Mus. Comp. Zool.* 139: 151–184.
- Grismer, L. L.  
 1988. Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. In R. Estes and G. Pregill (eds.), *Phylogenetic relationships of the lizard families*: 369–469. Stanford: Stanford Univ. Press.
- Haas, G.  
 1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In C. Gans and T. S. Parsons (eds.), *Biology of the Reptilia*: 285–490. London: Academic Press.
- Hoffstetter, R.  
 1964. Les Sauria du Jurassique supérieur et spécialement les Gekkota de Bavière et de Mandchourie. *Senckenb. Biol.* 45: 281–324.  
 1966. A propos des genres *Ardeosaurus* et *Eichstaettisaurus* (Reptilia, Sauria, Gekkonoidea) du Jurassique supérieur de Franconie. *Bull. Soc. Géol. Fr.* 8: 529–595.
- Hoffstetter, R., and J-P. Gasc  
 1969. Vertebrae and ribs of modern reptiles. In C. Gans, A. d'A. Bellairs, and T. Parsons (eds.), *Biology of the Reptilia*, vol. 1: morphology A: 201–310. New York: Academic Press.
- Hotton, N. III.  
 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. *Am. Midl. Nat.* 53: 88–114.
- Hutchinson, M. N.  
 1997. The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. *Mem. Queensland Mus.* 41: 355–366.

- Jerzykiewicz, T.  
1995. Cretaceous vertebrate-bearing strata of the Gobi and Ordos basins—a demise of the Central Asian lacustrine dinosaur habitat. *Proc. 15th Int. Symp. Kyungpook Natl. Univ.* 1995: 233–256.  
1998. Okavango Oasis, Kalahari Desert: a contemporary analogue for the Late Cretaceous vertebrate habitat of the Gobi Basin, Mongolia. *Geosci. Canada* 25: 15–26.
- Jerzykiewicz, T., and D. A. Russell  
1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Res.* 1991 (12): 345–377.
- Jerzykiewicz, T., P. J. Currie, D. A. Eberth, P. A. Johnston, E. H. Koster, and J. J. Zheng  
1993. Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. *Can. J. Earth Sci.* 30: 2180–2195.
- Jollie, M.  
1960. The head skeleton of the lizard. *Acta Zool.* 41: 1–64.
- Kemp, T. S.  
1988. Haemothermia or Archosauria?: the interrelationships of mammals, birds and crocodiles. *Zool. J. Linn. Soc.* 92: 67–104.
- Kielan-Jaworowska, Z.  
1969. *Hunting for dinosaurs*. Cambridge: MIT Press, 177 pp.  
1974. Multituberculate succession in the Late Cretaceous of the Gobi Desert (Mongolia). *Palaeontol. Pol.* 30: 23–44.
- Kluge, A.  
1967. Higher taxonomic categories of gekkonid lizards and their evolution. *Misc. Publ. Mus. Zool. Univ. Michigan* 147: 1–221.  
1987. Cladistic relationships among the Gekkonoidea. *Ibid.* 173: 1–54.
- Kurzanov, S. M.  
1992. A gigantic protoceratopsid from the Upper Cretaceous of Mongolia. *Paleontol. Zh.* 1992 (3): 81–93.
- Lakjer, T.  
1926. *Studien über die trigeminus-versorgte kaumuskulatur der Sauropsiden*. Copenhagen: C. A. Rietzel.
- Lavas, J. R.  
1993. *Dragons from the dunes. The search for dinosaurs in the Gobi Desert*. Published by the author. 193 pp.
- Lee, M. S. Y.  
1997. The phylogeny of varanoid lizards and the affinities of snakes. *Phil. Trans. R. Soc. London B* (1997) 352: 53–91.  
1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol. J. Linn. Soc.* 65: 369–453.
- Lefeld, J.  
1971. Geology of the Djadokhta Formation at Bayn Dzak (Mongolia). *Palaeontol. Pol.* 25: 101–127.
- Lillegraven, J. A., and M. C. McKenna  
1986. Fossil mammals from the “Mesaverde” Formation (Late Cretaceous, Judithian) of the Big Horn and Wind River basins, with definitions of the Late Cretaceous Land Mammal “Ages.” *Am. Mus. Novitates* 2840: 68 pp.
- Loope, D. B., L. Dingus, C. C. Swisher, III., and C. Minjin  
1998. Life and death in a Late Cretaceous dune field, Nemegt Basin, Mongolia. *Geology* 26 (1): 27–30.
- Macey, J. R., A. Larson, N. B. Ananjeva, and T. J. Papenfuss  
1997. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *J. Mol. Evol.* 44: 660–674.
- MacLean, W. P.  
1974. Feeding and locomotion mechanisms of teiid lizards; functional morphology and evolution. *Pap. Avulsos Zool.* 27: 179–213.
- Mateer, N. J.  
1982. Osteology of the Jurassic lizard *Ardeosaurus brevipes* (Meyer). *Palaeontol.* 25: 461–469.
- Mattison, C.  
1989. *Lizards of the world*. New York: Facts on File, Inc.
- McDowell, S. B., and C. M. Bogert  
1954. The systematic position of *Lanthanotus* and the affinities of anguimorphophan lizards. *Bull. Am. Mus. Nat. Hist.* 105: 1–141.
- Nixon, K. C., and Q. D. Wheeler  
1992. Measures of phylogenetic diversity. *In* M. J. Novacek and Q. D. Wheeler (eds.), *Extinction and phylogeny*: 216–234. New York: Columbia Univ. Press.
- Norell, M. A.  
1997a. Central Asiatic Expeditions. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of dinosaurs*: 100–105. San Diego, CA: Academic Press.

- 1997b. Ukhaa Tolgod. In P. J. Currie and K. Padian (eds.), *Encyclopedia of dinosaurs*: 769–770. San Diego, CA: Academic Press.
- Norell, M. A., and K. Gao  
1997. Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Upper Cretaceous, Gobi Desert and the recognition of a new clade of lizards. *Am. Mus. Novitates* 3211: 25 pp.
- Norell, M. A., and P. Makovicky  
1997. Important features of the dromaeosaur skeleton: information from a new specimen. *Am. Mus. Novitates* 3215: 28 pp.  
1999. Important features of the dromaeosaur skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *Am. Mus. Novitates* 3282: 45 pp.
- Norell, M. A., M. C. McKenna, and M. J. Novacek  
1992. *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. *Am. Mus. Novitates* 3045: 24 pp.
- Norell, M. A., L. M. Chiappe, and J. M. Clark  
1993. New limb on the avian family tree. *Nat. Hist.* 93 (9): 38–43.
- Norell, M. A., J. M. Clark, D. Dashzeveg, R. Barsbold, L. M. Chiappe, A. R. Davidson, M. C. McKenna, P. Altangerel, and M. J. Novacek  
1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266: 779–782.
- Norell, M. A., J. M. Clark, L. M. Chiappe, and D. Dashzeveg  
1995. A nesting dinosaur. *Nature* 378 (6559): 774–776.
- Norell, M. A., J. M. Clark, and L. M. Chiappe  
1996. Djadokhta series theropods: a summary review. In D. L. Wolberg and E. Stump (eds.), *Dinofest international abstracts*: 86. Tempe: Arizona State Univ.
- Novacek, M. J.  
1996. *Dinosaurs of the Flaming Cliffs*. New York: Anchor Books.
- Novacek, M. J., M. A. Norell, M. C. McKenna, and J. Clark  
1994. Fossils of the Flaming Cliffs. *Sci. Am.* 12/94: 60–69.
- Oelrich, T. M.  
1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Publ. Mus. Zool. Univ. Michigan* 94: 1–122.
- Oppel, M.  
1811. *Die Ordnungen, Familien, und Gattungen der Reptilien*. Munchen, 87 pp.
- Osmólska, H.  
1972. Preliminary note on a crocodilian from the Upper Cretaceous of Mongolia. *Palaentol. Pol.* 27: 43–47.
1980. The Late Cretaceous vertebrate assemblages of the Gobi Desert, Mongolia. *Mem. Soc. Geol. Fr.* 59: 145–150.
1993. Were the Mongolian “fighting dinosaurs” really fighting? *Rev. Paleobiol. spec. vol.*: 161–192.
- Pianka, E. R.  
1986. *Ecology and natural history of desert lizards*. Princeton, NJ: Princeton Univ. Press.
- Pregill, G.  
1984. An extinct species of *Leiocephalus* from Haiti (Sauria: Iguanidae). *Proc. Biol. Soc. Washington* 97: 827–833.
- Pregill, G., J. Gauthier, and H. Greene  
1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Trans. San Diego Soc. Nat. Hist.* 21: 167–202.
- Presch, W.  
1988. Phylogenetic relationships of the “Scincomorpha”. In R. Estes and G. Pregill (eds.), *Phylogenetic relationships of the lizard families*: 471–492. Stanford: Stanford Univ. Press.
- Rieppel, O.  
1978. Tooth replacement in anguimorph lizards. *Zoomorphol.* 91: 77–90.
- 1980a. The phylogeny of anguimorph lizards. *Denkschr. Schweiz. Naturforsch. Ges.* 94: 1–86.
- 1980b. The postcranial skeleton of *Lanthanotus borneensis* (Reptilia, Lacertilia). *Amphibia-Reptilia* 1: 95–112.
- 1980c. The trigeminal jaw adductor musculature of *Tupinambis*, with comments on the phylogenetic relationships of the Teiidae (Reptilia, Lacertilia). *Zool. J. Linn. Soc.* 69: 1–29.
1981. The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *J. Zool. (Lond.)* 195: 493–528.
1984. The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zool. J. Linn. Soc.* (1984) 82: 291–318.
1988. The classification of the Squamata. In M. J. Benton (ed.), *The phylogeny and classification of the tetrapods*, Vol. 1: amphibians, reptiles, birds. *Syst. Assoc.*



- Spec. Vol. 35A: 261–293. Oxford: Clarendon Press.
- Romer, A.  
1956. Osteology of the reptiles. Chicago: Univ. Chicago Press, 772 pp.
- Saksena, R. D.  
1942. The bony palate of *Uromastix*. Merrem. Proc. Indian Acad. Sci. 16: 107–119.
- Säve-söderbergh, G.  
1947. Notes on the brain-case in *Sphenodon* and certain Lacertilia. Zool. Bidr. Upps. 25: 489–516.
- Spock, L. E.  
1930. New Mesozoic and Cenozoic formations encountered by the Central Asiatic Expeditions in 1928. Am. Mus. Novitates 407: 8 pp.
- Sukhanov, V.  
1961. Some problems of the phylogeny and systematics of Lacertilia. Zool. Zh. 40: 73–83.
- Sulimski, A.  
1972. *Adamisaurus magnidentatus* n. gen., n. sp. (Sauria) from the Upper Cretaceous of Mongolia. Palaeontol. Pol. 27: 33–40.
1975. Macrocephalosauridae and Polyglyphanodontidae (Sauria) from the Late Cretaceous of Mongolia. Ibid. 33: 25–102.
1978. New data on the genus *Adamisaurus* Sulimski 1972 (Sauria) from the Upper Cretaceous of Mongolia. Ibid. 38: 43–56.
1984. A new Cretaceous scincomorph lizard from Mongolia. Ibid. 46: 143–155.
- Wiens, J. J., and T. W. Reeder  
1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herpetol. Monogr. 11: 1–101.
- Willard, W. A.  
1915. The cranial nerves of *Anolis carolinensis*. Bull. Mus. Comp. Zool. 59: 17–116.

## APPENDIX 1

## Catalog of Lizards Collected during the MAS-AMNH Expeditions Considered in This Study

IGM number <sup>a</sup>	MAE field number	Year collected	Taxon	Material	Locality
IGM 3/16	MAE 95-5	1995	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/17	MAE 95-52	1995	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/18	MAE 94-38	1994	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/19	MAE 40/93-90	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/20	MAE 94-26	1994	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/21	MAE 96-9	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/22	MAE 96-122	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/23	MAE 96-191	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/24	MAE 35/93-167	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/25	MAE 115/93-93	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/26	MAE 241/93-130	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/27	MAE 104/93-158	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/28	MAE 33/93-167	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/29	MAE 470/93-134	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/30	MAE 92/93-104	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/31	MAE 231/93-99	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/32	MAE 414/93-111	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/33	MAE 311/93-127	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/34	MAE 36/93-129	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/35	MAE 314/93-127	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/36	MAE 37/93-129	1993	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/37	MAE 94-27	1994	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/38	MAE 94-49-1	1994	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/39	MAE 94-101	1994	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/40	MAE 95-72	1995	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/41	MAE 96-17	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/42	MAE 96-40	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/43	MAE 96-50	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/44	MAE 96-52	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/45	MAE 96-65	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/46	MAE 96-109	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/47	MAE 96-196	1996	<i>Carusia intermedia</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/48	MAE 94/49-2	1994	<i>Carusia intermedia</i>	incomplete mandible	Ukhaa Tolgod
IGM 3/49	MAE 95-51	1995	<i>Carusia intermedia</i>	incomplete mandible	Ukhaa Tolgod
IGM 3/50	MAE 61/93-130	1993	<i>Carusia intermedia</i>	incomplete mandible	Ukhaa Tolgod
IGM 3/51	MAE 67	1990	<i>Carusia intermedia</i>	skull with mandibles	Bayn Dzak
IGM 3/52	MAE 71	1990	<i>Carusia intermedia</i>	skull with mandibles	Bayn Dzak
IGM 3/53 [1]	MAE 154/93-40	1993	<i>Hymenosaurus clarki</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/54	MAE 29/93-192	1993	unnamed new taxon	skull with mandibles	Ukhaa Tolgod
IGM 3/55	MAE 96-162	1996	<i>Gobiderma pulchrum</i>	skull with mandibles	Udan Sayr
IGM 3/56	MAE 68/93-45	1993	<i>Gobiderma pulchrum</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/57	MAE 220/93-248	1993	<i>Gobiderma pulchrum</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/58	MAE 95-29	1995	<i>Gobiderma pulchrum</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/59	MAE 254/92-33	1992	<i>Gobiderma pulchrum</i>	skull with mandibles	Khermeen Tsav
IGM 3/60	MAE 96-149	1996	<i>Gobiderma pulchrum</i>	skull with mandibles	Khulsan
IGM 3/61 [2]	MAE 89/93-70	1993	<i>Ctenomastax parva</i>	skull with mandibles	Zos
IGM 3/62 [3]	MAE 131		<i>Ctenomastax parva</i>	skull with mandibles	Khulsan
IGM 3/63 [4]	MAE 121/93-93	1993	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/64	MAE 145/94-40	1994	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/65	MAE 75/93-89	1993	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/66	MAE 235/93-130	1993	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/67	MAE 319/93-147	1993	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod

APPENDIX 1  
Continued

IGM number <sup>a</sup>	MAE field number	Year collected	Taxon	Material	Locality
IGM 3/68	MAE 39/93-90	1993	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/69	MAE 94-37	1994	<i>Temujinia ellisoni</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/70	MAE 19/93-6	1993	<i>Temujinia ellisoni</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/71 [5]	MAE 255/92-10	1992	<i>Zapsosaurus sceliphros</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/72	MAE 20/93-15	1993	<i>Zapsosaurus sceliphros</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/73	MAE 219/92-45	1992	<i>Polrussia mongoliensis</i>	skull with mandibles	Khulsan
IGM 3/74	MAE 83/93-89	1993	<i>Mimeosaurus crassus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/75	MAE 63/93-153	1993	<i>Mimeosaurus crassus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/76	MAE 96-105	1996	<i>Mimeosaurus crassus</i>	skull with mandibles	Zos Wash
IGM 3/77	MAE 62/93-153	1993	<i>Priscagama gobiensis</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/78	MAE 120/93-93	1993	<i>Priscagama gobiensis</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/79	MAE 130		<i>Priscagama gobiensis</i>	skull with mandibles	Khulsan
IGM 3/80	MAE 307/93-162	1993	? <i>Priscagama gobiensis</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/81	MAE 258/92-63	1992	<i>Phrynosomimus asper</i>	skull with mandibles	Khulsan
IGM 3/82	MAE 96-31	1996	<i>Phrynosomimus asper</i>	skull with mandibles	Ukhaa Tolgod (First Strike)
IGM 3/83	MAE 152/93-40	1993	<i>Phrynosomimus asper</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/84	MAE 96-113	1996	<i>Isodontosaurus gracilis</i>	skull with mandibles	Ukhaa Tolgod (Xanadu)
IGM 3/85	MAE 27/93-192	1993	<i>Isodontosaurus gracilis</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/86	MAE 42/93	1993	<i>Isodontosaurus gracilis</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/87	MAE 49/93-163	1993	<i>Isodontosaurus gracilis</i>	skull with mandibles	Ukhaa Tolgod (Zofie's Hill)
IGM 3/88	MAE 161/93-40	1993	<i>Isodontosaurus gracilis</i>	upper and lower jaws	Ukhaa Tolgod
IGM 3/89	MAE 94-16-1	1994	<i>Isodontosaurus gracilis</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/90	MAE 94-54	1994	<i>Isodontosaurus gracilis</i>	skull with mandibles	Zos
IGM 3/91	MAE 261/92-123	1992	<i>Isodontosaurus gracilis</i>	cranial + postcranial skeleton	Tugrugeen Shireh
IGM 3/92	MAE 23/93-28	1993	<i>Isodontosaurus gracilis</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/93	MAE 221/93-8	1993	<i>Isodontosaurus gracilis</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/94	MAE 88/93-19	1993	<i>Isodontosaurus gracilis</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/95 [6]	MAE 271/93-65	1993	<i>Myrmecodaptia microphagosa</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/96	MAE 95-78	1995	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/97	MAE 31/93-164	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/98	MAE 95-45	1995	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/99	MAE 94-10	1994	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/100	MAE 45/93-163	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/101	MAE 48/93-163	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/102	MAE 32/93-91	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/103	MAE 38/93-90	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/104	MAE 117/93-93	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/105	MAE 118/93-93	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/106	MAE 122/93-93	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/107	MAE 449/93-124	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/108	MAE 94-36	1994	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/109	MAE 95-62	1995	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/110	MAE 138/93-140	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/111	MAE 64/93-45	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/112	MAE 56/93-110	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/113	MAE 119/93-93	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/114	MAE 107/93-86	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/115	MAE 23		<i>Adamisaurus magnidentatus</i>	skull with mandibles	Ukhaa Tolgod

APPENDIX 1  
Continued

IGM number <sup>a</sup>	MAE field number	Year collected	Taxon	Material	Locality
IGM 3/116	MAE (no field number)		<i>Adamisaurus magnidentatus</i>	cranial + postcranial skeleton	Tugrugeen Shireh
IGM 3/117	MAE 252/92-14	1992	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/118	MAE 18/93-2	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/119	MAE 167/93-5	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/120	MAE 168/93-5	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/121	MAE 226/93-3	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/122	MAE 227/93-27	1993	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Tugrugeen Shireh
IGM 3/123	MAE 196/92-25	1992	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Khermeen Tsav
IGM 3/124	MAE 209/92-39	1992	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Khermeen Tsav
IGM 3/125	MAE 211/92-39	1992	<i>Adamisaurus magnidentatus</i>	skull with mandibles	Khermeen Tsav
IGM 3/126	MAE 61-91	1991	<i>Gobinatus arenosus</i>	skull with mandibles	Khulsan
IGM 3/127	MAE 212/92-67	1992	<i>Gobinatus arenosus</i>	skull with mandibles	Khulsan
IGM 3/128	MAE 268/93-65	1993	<i>Gobinatus arenosus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/129 [7]	MAE 95-92	1995	<i>Tchingisaurus multivagus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/130	MAE 91-30	1991	<i>Pyramicephalosaurus cherminicus</i>	skull with mandibles	Khulsan
IGM 3/131	MAE 70-244		<i>Pyramicephalosaurus cherminicus</i>	maxilla with teeth	Khulsan
IGM 3/132	MAE (no field number)		<i>Macrocephalosaurus</i> sp.	partial cranial + postcranial	Ukhaa Tolgod
IGM 3/133	MAE 51/93-25	1993	<i>Macrocephalosaurus</i> sp.	disarticulated vertebrae	Ukhaa Tolgod
IGM 3/134	MAE 215/92-47	1992	<i>Macrocephalosaurus chulsanensis</i>	skull with mandibles	Khulsan
IGM 3/135	MAE 129/92-31	1992	<i>Erdenetesaurus robinsonae</i>	skull with mandibles	Khermeen Tsav
IGM 3/136	MAE 256/92-23	1992	<i>Cherminisaurus kozlowskii</i>	skull with mandibles	Khermeen Tsav
IGM 3/137	MAE 267/92-35	1992	<i>Cherminisaurus kozlowskii</i>	skull with mandibles	Khermeen Tsav
IGM 3/138 [8]	MAE 95-30	1995	<i>Parmeosaurus scutatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/139	MAE 475/93-152	1993	<i>Parmeosaurus scutatus</i>	skull with mandibles	Ukhaa Tolgod (Amy's Pocket)
IGM 3/140	MAE 96-27	1996	<i>Parmeosaurus scutatus</i>	skull with mandibles	Ukhaa Tolgod (Xanadu)
IGM 3/141	MAE 95-70	1995	<i>Parmeosaurus scutatus</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/142	MAE 94-16	1994	<i>Parmeosaurus scutatus</i>	skull with mandibles	Ukhaa Tolgod (Xanadu)
IGM 3/143	MAE 93-53	1993	<i>Parmeosaurus scutatus</i>	partial cranial + postcranial	Ukhaa Tolgod
IGM 3/144	MAE 94-51	1994	<i>Parmeosaurus scutatus</i>	partial skeleton	Ukhaa Tolgod (Xanadu)
IGM 3/145	MAE 96-1	1996	<i>Slavoia darevskii</i>	cranial + postcranial skeleton	Ukhaa Tolgod
IGM 3/146	MAE (no field number)		<i>Slavoia darevskii</i>	cranial + postcranial skeleton	Ukhaa Tolgod
IGM 3/147	MAE 178/92-21	1992	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/148	MAE 160/93-40	1993	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/149	MAE 95-7	1995	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/150	MAE 94-66-1	1994	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/151	MAE 94-66-2	1994	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/152	MAE 94-66-3	1994	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/153	MAE 94-66-4	1994	<i>Slavoia darevskii</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/154	MAE 63	1992	<i>Slavoia darevskii</i>	cranial + postcranial skeleton	Kulsan
IGM 3/155	MAE 175/92-21	1992	<i>Slavoia darevskii</i>	skull with mandibles	Khermeen Tsav
IGM 3/156	MAE 176/92-21	1992	<i>Slavoia darevskii</i>	skull with mandibles	Khermeen Tsav
IGM 3/157	MAE 181/92-21	1992	<i>Slavoia darevskii</i>	skull with mandibles	Khermeen Tsav



APPENDIX 1  
Continued

IGM number <sup>a</sup>	MAE field number	Year collected	Taxon	Material	Locality
IGM 3/158	MAE 185/92-21	1992	<i>Slavoia darevskii</i>	skull with mandibles	Khermeen Tsav
IGM 3/159	MAE 198/92-25	1992	<i>Slavoia darevskii</i>	skull with mandibles	Khermeen Tsav
IGM 3/160	MAE 95-89	1995	<i>Globaura venusta</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/161	MAE 21/93-176	1993	<i>Globaura venusta</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/162	MAE 95-24	1995	<i>Globaura venusta</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/163	MAE 95-40	1995	<i>Globaura venusta</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/164	MAE 217/92-61	1992	<i>Globaura venusta</i>	skull with mandibles	Khulsan
IGM 3/165	MAE 173/92-21	1992	<i>Globaura venusta</i>	skull with mandibles	Khermeen Tsav
IGM 3/166	MAE 172/92-21	1992	<i>Globaura venusta</i>	skull with mandibles	Khermeen Tsav
IGM 3/167	MAE 183/92-21	1992	<i>Globaura venusta</i>	skull with mandibles	Khermeen Tsav
IGM 3/168	MAE 95-90	1995	<i>Eoxanta lacertifrons</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/169	MAE 17/93-184	1993	<i>Estesia mongoliensis</i>	mandibles with teeth	Ukhaa Tolgod
IGM 3/170	MAE 24/93-26	1993	<i>Cherminotus longifrons</i>	cranial and vertebrae	Tugrugeen Shireh
IGM 3/171 [9]	MAE 283/93-108	1993	<i>Aiolosaurus oriens</i>	skull with mandibles	Ukhaa Tolgod
IGM 3/172	MAE 105/93-42	1993	"Varanoidea, gen. et sp. undet."	maxilla and vertebrae	Ukhaa Tolgod

<sup>a</sup> Numbers in brackets refer to comments listed below.

1. Holotype and only known specimen.
2. Holotype; with clear impressions of the left mandible and teeth.
3. Skull articulated with first nine vertebrae and a scapula.
4. Holotype; illustrated in this paper.
5. Holotype; illustrated in this paper.
6. Holotype and only known specimen.
7. The only skull material known for this species so far.
8. Holotype; incomplete skeleton with osteodermal armor.
9. Holotype and only known specimen.