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The fossil record of Cretaceous lizards from Mongolia

VLADIMIR R. ALIFANOV

Introduction

Lizards, represented by several thousand extant species, are one of the most successful groups of modern reptiles. The first lizards of modern type are known from the Middle Jurassic (Evans, 1993) and the first representatives of modern families appear in the Late Cretaceous (Alifanov, 1989a). By the Late Cretaceous the diversity, at the family level, of Asian lizards had reached its apogee, with both Mesozoic and modern families found together following the beginning of the Asian–American faunal interchange.

In this chapter, extraordinarily rich and diverse lizard complexes from the Lower and Upper Cretaceous deposits of the Gobi Desert in the People's Republic of Mongolia, known mainly from palaeontological discoveries in the South Gobi, are briefly outlined. Lizard remains from the Upper Cretaceous of this region include thousands of specimens, many of them well preserved, often with articulated skulls and sometimes with postcranial skeletons. This concentration of fossil material is unusual for lizards because of their small size and kinetic skulls, which renders them particularly susceptible to rapid disarticulation after death.

The most important aspect of the Cretaceous lizards of Mongolia is their surprisingly high taxonomic diversity. Almost twenty families, representing all infraorders of lizards, have so far been described, and some of these families contain large numbers of genera and species. The origin of this abundance is enigmatic and requires explanation. A brief comparative analysis of Early and Late Cretaceous lizard faunas helps to clarify some of the main stages in the evolution of lizards on the territory of Central Asia.

The first fossil Mongolian lizards were described by Gilmore (1943) on the basis of several rather poorly preserved specimens collected from Upper Cretaceous and Palaeogene localities of the Gobi Desert by expeditions of the American Museum of Natural History in the years 1923 to 1930. Sulimski (1972, 1975, 1978, 1984) and later Borsuk-Białynicka (1984, 1985, 1987, 1988, 1990), Borsuk-Białynicka and Moody (1984) and Borsuk-Białynicka and Alifanov (1991) described numerous new Upper Cretaceous taxa from the Gobi Desert of Mongolia, based on specimens collected by the Polish–Mongolian Expeditions (1965–1972). Recently, Alifanov (1988, 1989a, b, 1991, 1993a, 1996) described further new Cretaceous taxa found by the Soviet (Russian)–Mongolian expeditions which began in 1969. These papers also included information on fossil remains from the Lower Cretaceous and the Palaeogene (Alifanov, 1993b, c). More recently, a brief review of fossil lizards from the Upper Cretaceous Djadokhta and Baruungoyot Svitas of Mongolia was conducted by Borsuk-Białynicka (1991) and further remains were collected by the Joint expedition of Mongolian Academy of Sciences and American Museum of Natural History (Dashzeveg *et al.*, 1995).

The fossil material referred to in the systematic section of this paper was collected from several highly productive localities in the Mongolian Cretaceous, also famous for their fossil mammals and dinosaurs (see Chapters 12–13, 22–26, 29). The Upper Cretaceous lizard material comes from three consecutive svitas (Gradziński *et al.*, 1977; Jerzykiewicz and

Russell, 1991): the Djadokhta (localities of Bayan Zag, Tögrögiin Shiree, Zamyn Khond), the Baruungoyot (localities of Nemegt, Hermiin Tsav and Khulsan) and the Nemegt (localities of Bügiin Tsav, Guriliin Tsav and Tsagaan Khushuu), the terminal Cretaceous sequence and in which lizard remains are rare. The oldest fossil material discussed in this work comes from the locality of Höövör. Deposits at this site are thought to belong to the Hühteeg Svita, originally dated as Aptian–Albian (Shuvalov, 1974). Fossil material from this locality is disarticulated and was collected by screen washing.

Repository abbreviations

AMNH, American Museum of National History, New York; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow; ZPAL, Palaeobiological Institute, Polish Academy of Sciences, Warsaw.

Systematic palaeontology

IGUANIA Cope, 1864

The families Iguanidae, Agamidae and Chamaeleonidae are traditionally included within this infraorder. Moody (1980), Estes *et al.* (1988), Etheridge and Queiroz (1988) and Frost and Etheridge (1989) have noted the possibility that the first two families may be paraphyletic and propose that they be divided into several separate family groups for the Agamidae (*sensu lato*) (Moody, 1980) and Iguanidae (*sensu lato*) (Frost and Etheridge, 1989).

'IGUANIA' indet.

Remarks. Numerous unpaired and rugose iguanian-like frontals with a clear incision on their parietal border for the parietal opening have been found in late Lower Cretaceous deposits at Höövör. The exact systematic position of these remains is still unclear, but they appear to represent the earliest iguanian lizards yet known.

PHRYNOSOMATIDAE Fitzinger, 1843

Record. This family is represented by two genera from Khulsan: *Polrussia mongoliensis* Borsuk-Białynicka and Alifanov, 1991 (holotype: ZPAL MgR-I/119), is represented by a partly broken skull with mandible (Figure 18.1A–D) and *Igua minuta* Borsuk-Białynicka and Alifanov, 1991 (holotype: ZPAL MgR-I/60) is based on a skull with a damaged preorbital region and mandible.

Polrussia is distinguished by its wide and flat skull with short snout, large orbits, largely unreduced splenial and conical teeth. *Igua* has wide and non-rugose parietals, fusion of tbe dentary tube anterior to the splenial, which reaches the mid-level of the dentary, clearly tricuspid teeth and very long quadrates.

Remarks. The two Mongolian genera were described by Borsuk-Białynicka and Alifanov (1991) as members of the Iguanidae *sensu lato*, without clear definition of their relationships to extant lizards. In my opinion, both genera belong most likely to the family Phrynosomatidae because of similarities between the construction of the posterior processes of the dentary with the same element in the extant forms *Phrynosoma* and *Sceloporus*. In these taxa the dentary has a distinct surangular process which does not cross the level of the anterior angular opening, and an elongate angular process. Occasionally, there is an extensive incision between these processes.

Among Asiatic lizards the genera *Anchaurosaurus* and *Xihaina*, described by Gao and Hou (1995) from the Upper Cretaceous of Inner Mongolia (China), can also be preliminarily assigned to rhis group. A sceloporine lizard has also been reported from the Upper Cretaceous of North America (Denton and O'Neill, 1993).

PRISCAGAMIDAE Borsuk-Białynicka and Moody, 1984 (=AGAMIDAE, PRISCAGAMINAE Borsuk-Białynicka and Moody, 1984)

Record. Six genera belonging to the subfamily Priscagamidae have been described from the Upper Cretaceous of Mongolia. *Priscagama gobiensis* Borsuk-Białynicka and Moody, 1984, is based on a holotype (ZPAL MgR/III-32) consisting of a damaged skull with mandible (Figure 18.2A–C) from the locality of Hermiin Tsav, and other specimens have been found

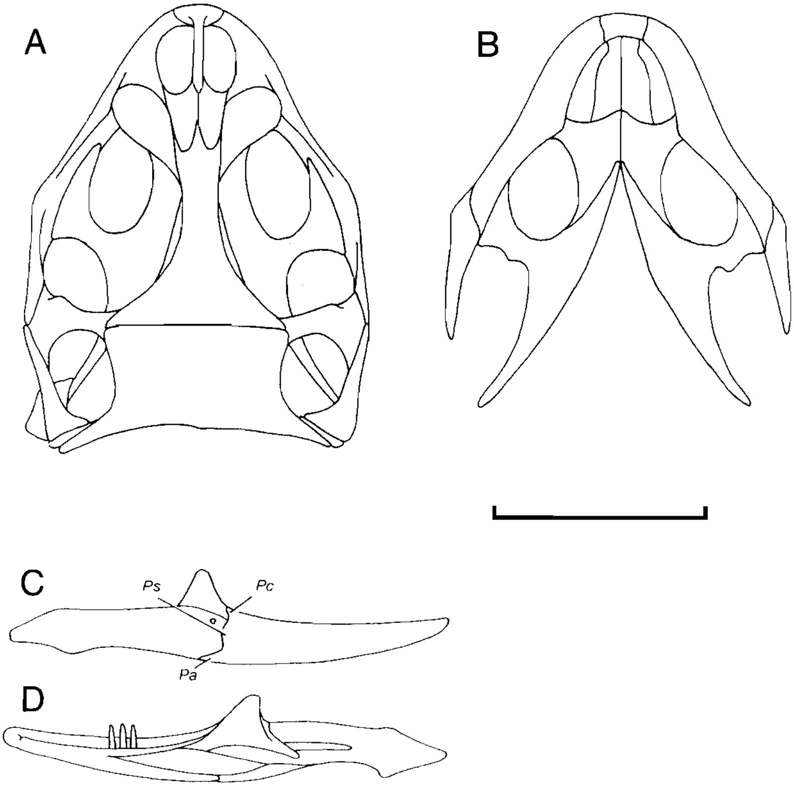

Figure 18.1. *Polrussia mongoliensis* Borsuk-Białynicka and Alifanov, 1991: reconstruction of the skull in (A) dorsal and (B) ventral view, and the right mandible in (C) lateral and (D) medial view. Abbreviations: Pa, angular process; Pc, coronoid process; Ps, surangular process. Scale bar = 5 mm.

at Bayan Zag. *Chamaeleognathus iordanskyi* Alifanov, 1996, is known from a very well preserved skull with mandible (holotype: PIN 3142/345) and one other specimen collected from Hermiin Tsav. The only known specimen of *Cretagama bialynickae* Alifanov, 1996 also consists of a well preserved skull and mandible (holotype: ZPAL MgR/III-32). *Flaviagama dzerzhinskii* Alifanov, 1989b (holotype: PIN 3143/101) is based on a well preserved skull with mandible from Tögrögiin Shiree and *Morunasius modestus* Alifanov, 1996 (holotype: PIN N 3142/317) on a well preserved skull and mandible from Hermiin Tsav. *Phrynosomimus asper* Alifanov, 1996 (holotype: PIN 3142/318), is represented by a skull, lacking palatal bones, and a fragmentary mandible, also from Hermiin Tsav.

In addition to these records, Nesov (1988) reported the discovery of representatives of Priscagamidae in the Upper Cretaceous of Middle Asia and *Priscagama* has also been found in Inner Mongolia, China (Gao and Hou, 1995).

Remarks. The Priscagamidae is a group of Upper Cretaceous Asiatic acrodontan iguanians, that are distinguished by an unusual combination of derived and plesiomorphic characters: the bones of the skull roof are sculptured; the maxillae contact behind the premaxilla; the postfrontal is completely reduced; the labial process of the coronoid covers the posterior part of the dentary; the splenial is large; and the dentition is agamid-like: canine-like teeth are present in hatchlings and the post canine-like teeth are sub-triangular

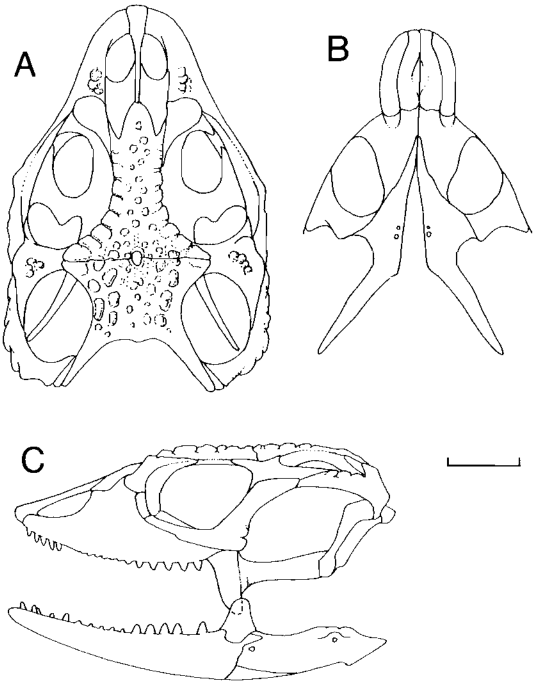

Figure 18.2. *Priscagama gobiensis* Borsuk-Białynicka and Moody, 1984: reconstruction of the skull in (A) dorsal, (B) ventral and, with the left mandible in (C) left lateral view. Scale bar = 5 mm.

in form (conical with an expanded base) and do not undergo replacement.

Initially, this group was established as a separate subfamily, the Priscagaminae, in the family 'Agamidae' by Borsuk-Białynicka and Moody (1984). Alifanov (1989b) noted the possible non-agamid nature of priscagamids and proposed that they be recognized as a separate family, and subsequently argued (Alifanov, 1996) that their closest relationships lay with the extant Hoplocercidae (*sensu* Frost and Etheridge, 1989). The Priscagamidae–Hoplocercidae group has some characters also found in the Chamaeleonidae including: sculptured bones of the skull roof, posterior expansion of the surangular process of the dentary above the anterior surangular foramen, and absence of the coronoid process of the dentary. Thus, the agamid-like condition of the priscagamid dentition may be homoplastic.

The family Priscagamidae was divided by Alifanov (1996) into two subfamilies: Priscagaminae Borsuk-Białynicka and Moody, 1984, including *Priscagama*, *Chamaeleognathus*, and *Cretagama*, and Flaviagaminae Alifanov, 1996, comprising *Flaviagama*, *Morunasius* and *Phrynosomimus*. The Priscagaminae are distinguished by caudally lengthened and dorsally oriented nares, lack of contact between pterygoids and vomers, the wide and short labial process of the coronoid, isolation of the nasals following contact between the ascending process of the premaxilla and the frontal, and the presence of four or more canine-like teeth. Flaviagamines are distinguished by their larger parietal foramen, the narrow and elongate labial process of the coronoid and the presence of, at most, three canine-like teeth.

HOPLOCERCIDAE Frost and Etheridge, 1989

Record. Four species of this family are known from Mongolia. *Pleurodontagama aenigmatodes* Borsuk-Białynicka and Moody, 1984, is based on a single specimen from Hermiin Tsav (holotype: ZPAL MgR-III/35), consisting of a fairly complete skull with mandible. *Gladidenagama semiplena* Alifanov, 1996, from the same locality, is based on a single specimen (PIN 3142/319), consisting of a fairly complete skull with mandible. The holotype of *Mimeosaurus crassus* Gilmore, 1943, consists of a left maxilla and associated incomplete jugal and ectopterygoid (AMNH 6655) from Bayan Zag, which has yielded further remains of this lizard including isolated maxillae and dentaries (Borsuk-Białynicka and Moody, 1984). *Mimeosaurus tugrikinensis* Alifanov, 1989 was established upon a single specimen, consisting of a disarticulated skull and fragmentary mandible (PIN 3143/102, Figure 18.3A, B) from Tögrögiin Shiree.

Pleurodontagama aenigmatodes and *Mimeosaurus* cf. *tugrikinensis* have also been reported from Djadokhta sediments of Inner Mongolia, China (Gao and Hou, 1995), and further *Mimeosaurus* material from China was referred by Gao and Hou (1995) to *M. crassus*. However, judging from their illustrations (Gao and Hou 1995, fig. 8c), this material is more similar to *M. tugrikinensis* in that the first two teeth are enlarged and 'canine-like' and there are clear diastemas between

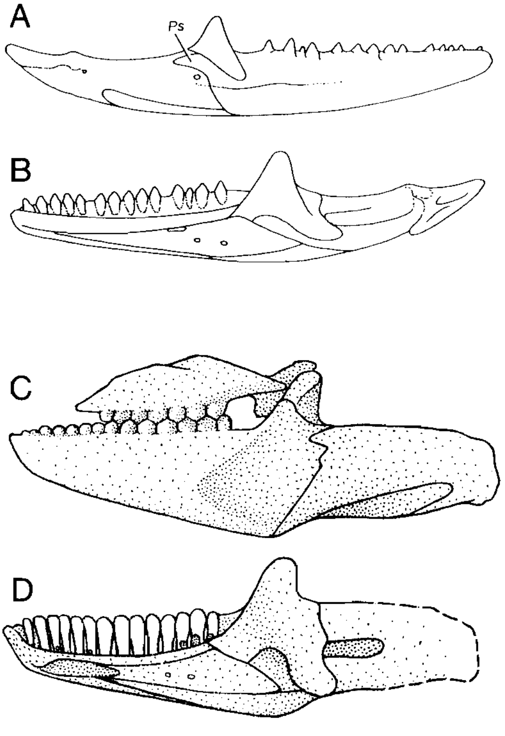

Figure 18.3. *Mimeosaurus tugrikinensis* Alifanov, 1989b: reconstruction of the right mandible in (A) lateral and (B) medial view. *Isodontosaurus gracilis* Gilmore, 1943 (ZPAL MgR-II/39): reconstruction of the left mandible in (C) lateral view and the right mandible in (D) medial view. Abbreviations: Ps, surangular process. Scale bar = 5 mm.

adjacent teeth. Resolution of this problem may be possible after further preparation of the Chinese specimens and re-evaluation of all *Mimeosaurus* material.

A series of as yet undescribed remains belonging to this subfamily has also been collected from the Upper Cretaceous of Middle Asia (Nesov, 1988).

Remarks. The Hoplocercidae, erected by Frost and Etheridge (1989), is a relatively small family of modern lizards now restricted to South America. They resemble the Priscagamidae, but are distinguished from them by their pleurodont non-agamid-like dentition, with tooth crowns that have narrow bases and are non-conical.

The four Mongolian taxa listed above were assigned to a separate subfamily, the Pleurodontagaminae by Alifanov (1996). This taxon is characterized by contact between the maxillae behind the premaxilla, contact between the frontal and the dorsal process of the maxilla, large and wide vomers, a long anterior process of the pterygoids that sometimes reaches the vomers, labio-lingual compression of the upper parts of the tooth crowns, and the enlargement of one or two maxillary teeth which become caniniform.

The first hoplocercid to be recovered from the Late Cretaceous of Asia, *Mimeosaurus crassus*, was assigned by Gilmore (1943) to the Chamaeleonidae. Later, this lizard was redescribed by Borsuk-Białynicka and Moody (1984) and placed in their Priscagaminae together with the poorly known *Pleurodontagama*. The latter has some general similarity to *Priscagama*, though not in the dentition which is pleurodont and undergoes replacement.

Mimeosaurus tugrikinensis Alifanov, 1989 was declared by Gao and Hou (1995) with reference to the International Code of Zoological Nomenclature (ICZN; Ride *et al.*, 1985) as an invalid taxon for which 'Alifanov (1989) provided no diagnosis' (Gao and Hou, 1995, p. 73). However, according to Article 13a of the ICZN, establishment of a taxon requires a 'description or diagnosis'. Alifanov's erection of *Mimeosaurus tugrikinensis* conforms to this requirement, since a description was given under the special heading 'description', both in the original Russian version of the paper and in the English translation.

ISODONTOSAURIDAE Alifanov, 1993a stat. nov. (=AGAMIDAE, ISODONTOSAURINAE Alifanov, 1993 b)

Record. In the Upper Cretaceous of Mongolia this family is represented by a single form, *Isodontosaurus gracilis* Gilmore, 1943, based on a fragmentary right ramus of a mandible from Bayan Zag (AMNH N 6647). A partially damaged and compressed skull with mandibles (ZPAL MgR-II/39, Figure 18.3C, D) also appears to belong to this species. Remains of *Isodontosaurus* have also been found in Djadokhta sediments of the Gobi Desert in China (Gao and Hou, 1995) and further remains of isodontosaurids, with various forms of teeth, are also known from the Upper Palaeocene and Middle Eocene of Mongolia. The latter are similar to Chinese finds, including *Qianshanosaurus* from the Palaeogene (Hou, 1974) and *Creberidentat* from the Middle Eocene (Li, 1991), both of which probably belong to the Isodontosauridae.

Remarks. Previously, the systematic status of *Isodontosaurus* and *Qianshanosaurus* was uncertain, and Estes (1983) listed them as 'Incertae sedis'. Alifanov (1993a) showed that the Isodontosauridae are Late Cretaceous Asiatic iguanians with an agamid-like skull and mandibles. The bones of the skull roof are smooth, the coronoid has no labial process, the surangular process of the dentary extends above the anterior surangular foramen, the coronoid process of the dentary expands on to the labial surface of the coronoid and the anterior end of the angular is situated below the lower border of the splenial. The dentition is pleurodont, or hyperpleurodont, and shovel-like (teeth have narrow bases and labio-lingually flattened apices), but there are no fang-like teeth and there is no tooth replacement. The absence of maxillary fangs and presence of narrow-based teeth shows some similarities to the dentition of the extant lizard *Uromastyx*.

Isodontosauridae was first described by Alifanov (1993b) as a subfamily within the Agamidae *sensu lato*. However, the hyperpleurodont dentition with unusual shovel-like teeth (similar to those of pleurodontagamine hoplocercids) does not permit unification of *Isodontosaurus* with known agamoid taxa and thus it is placed within its own family.

SCINCOMORPHA Camp, 1923

Scincomorpha is a rather heterogeneous and controversial lizard group originally proposed by Camp (1923) for uniting Amphisbaenia and Cope's Leptoglossa. At present there is no satisfactory phylogenetic concept for the numerous fossil and living families assigned to this most problematic taxon and cranial characteristics valid for all members of this group seem impossible to find. Rieppel (1988), Estes (1983), Estes *et al.*, (1988) and Presch (1988) give further, more extended accounts of this problem.

TEIIDAE Gray, 1827

Records. A maxilla and dentary, identified as cf. *Leptochamos*, was collected at the locality of Tsagaan Khushuu.

Remarks. The Teiidae is distinguished by a complex of cranial characters including: a dorsal process on the squamosal, fused frontals, lateral contact between the ectopterygoids and palatines medial to the supradental ridge of the maxilla, expansion of the medial process of the postfrontal behind the postorbital to reach the parietal, a deep incision between the surangular and angular processes of the dentary, which is short, and a series of bicuspid teeth.

The extant subfamily Teiinae is known mainly from South America and was present there from at least the Late Cretaceous (Valencia *et al.*, 1990). North American Upper Cretaceous representatives of this family were placed by Denton and O'Neill (1995) in a new subfamily, Chamopinae, separating them from the extant Teiinae and Tupinambinae.

MACROCEPHALOSAURIDAE Sulimski, 1975

Record. The type genus *Macrocephalosaurus* is represented by three Mongolian species: *M. ferrugenosus* Gilmore, 1943 (holotype: AMNH 6520, based on a single incomplete skull with part of the right ramus of the mandible from Bayan Zag; *M. gilmorei* Sulimski, 1975 (holotype: ZPAL MgR-III/18, a complete skull with lower jaw from Hermiin Tsav); and *M. chulsanensis* Sulimski, 1975 (holotype: ZPAL MgR-I/14, a complete skull and postcranial skeleton from Khulsan). The latter species is also represented by many other remains.

The following macrocephalosaurids have also been described from Hermiin Tsav, Mongolia: *Darchansaurus estesi* Sulimski, 1975 (holotype: ZPAL MgR-III/6, based on a complete skull with lower jaw) (Figure 18.4A–D); *Erdenetosaurus robinsonae* Sulimski, 1975 (holotype: ZPAL MgR-III/19, based on a single skull with lower jaw); and *Cherminsaurus kozlowskii* Sulimski, 1975 (holotype: ZPAL MgR-III/24 based on a skull with lower jaw).

Remarks. Macrocephalosaurids are unusual Upper Cretaceous Asiatic lizards with a massive skull,

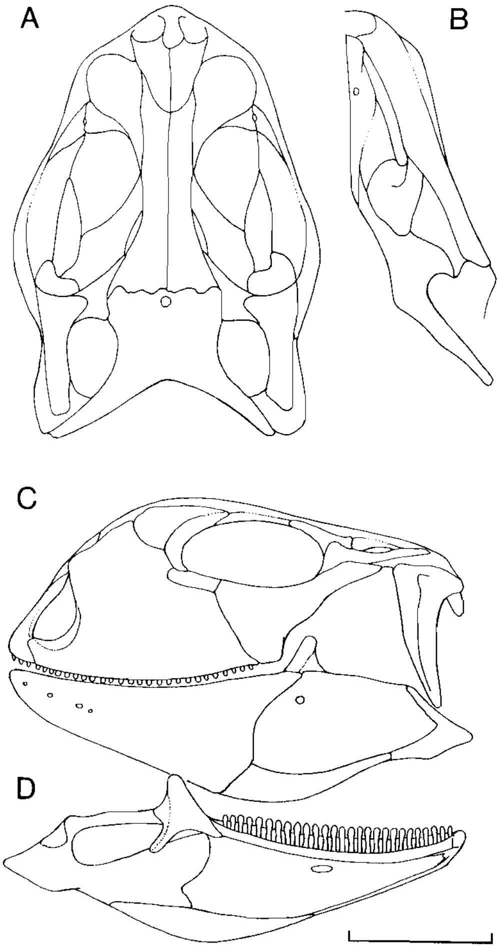

Figure 18.4. *Darchansaurus estesi* Sulimski, 1975 (ZPAL MgR-III/6): reconstruction of the skull in (A) dorsal, (B) ventral and, with the left mandible, in (C) left lateral view, and the left mandible in (D) medial view. Scale bar = 20 mm.

Iguana-like teeth with 4–6 small cusps, and trunk vertebrae with clear zygosphenes and zygantra. They exhibit a complex of primitive and derived cranial characters including: a wide upper temporal fenestra; a parietal fenestra on the fronto-parietal suture; a V- or U-shaped posterior edge of the nasals; contact between the prefrontal and nasal; lateral expansion of the postorbital which develops bifurcated articular surfaces forming a mutual cruciform contact with the postfrontal; transversely situated articular processes of the postorbital; paired frontals; a massive medial (dorsal) process on the squamosal which partly or completely fuses with the supratemporal; contact between the ectopterygoids and palatines medial to the supradental ridge of the maxillae; contact between the pterygoids and vomers; reduction or complete loss of the infraorbital fenestrae; a well-developed surangular process on the dentary which extends posteriorly above the anterior surangular foramen; a large splenial; and subpleurodont dentition.

Sulimski (1975) identified the Macrocephalosauridae as a family within the Scincomorpha, but Estes (1983) united it with the modern Teiidae. Alifanov (1993a) re-established this family and erected a new subfamily, the Mongolochamopinae, though this has now been recognized as a separate family (see below). Wu *et al.* (1996) proposed a relationship between Macrocephalosauridae and Amphisbaenia within the Scincomorpha, but this has been questioned by Gao and Hou (1996).

MONGOLOCHAMOPIDAE Alifanov, 1993a stat. nov. (MACROCEPHALOSAURIDAE, MONGOLOCHAMOPINAE Alifanov, 1993a)

Record. More than ten genera belonging to this family are known from the Cretaceous of Mongolia. Seven of these genera have been recovered from Hermiin Tsav: *Mongolochamops reshetovi* Alifanov, 1988 (holotype: PIN 3142/304, based on a fragmentary skull and mandible); *Altanteius facilis* (Alifanov, 1988) (holotype PIN 3142/306, based on a skull, lacking the parietal, and the associated left ramus of the mandible); *Gobinatus arenosus* Alifanov, 1993a (holotype: PIN 3142/308, known from a complete skull with mandible); *Parameiva oculea* Alifanov, 1993a (holotype: PIN 3142/310, a skull without brain case, but with a mandible; *Prodenteia ministra* Alifanov, 1993a (holotype: PIN 3142/324, based on articulated bones of the skull roof and a mandible); *Piramicephalosaurus cherminicus* Alifanov, 1988 (holotype: PIN 3142/310, represented by articulated bones of the anterior part of skull, a

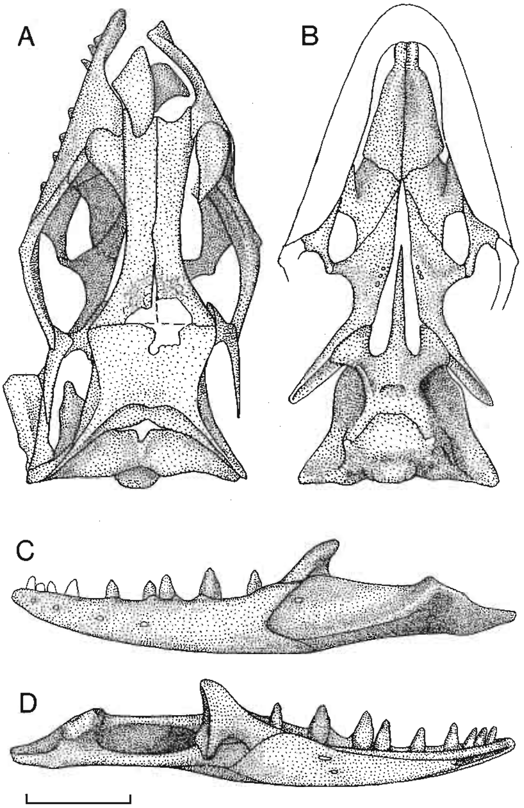

Figure 18.5. *Barungoia vasta* Alifanov, 1993a (PIN 4487/2): skull in (A) dorsal and (B) ventral view and left mandible in (C) lateral and (D) medial view. Scale bar = 5 mm.

mandible and isolated vertebrae); and *Tchingisaurus multivagus* Alifanov, 1993a (holotype: PIN 3142/309, based on a mandible).

Khulsan has produced just two taxa: *Barungoia vasta* Alifanov, 1993a (holotype: PIN 4487/2, a complete skull with mandible) (Figure 18.5A–D) and *Gurvansaurus canaliculatus* Alifanov, 1993a (holotype: PIN 4487/3, based on a right dentary with dentition). Tögrögiin Shiree has also produced two genera: *Dzhadochtosaurus giganteus* Alifanov, 1993a (holotype: PIN N3142/103, based on a complete skull with mandible) and *Gurvansaurus potissimus* Alifanov, 1993a (holotype: PIN 3143/104, a skull without roof, but with mandible). Finally, one taxon is known from Bayan Zag: *Conicodontosaurus djadochtaensis* Gilmore, 1943 (holotype: AMNH 6519 represented by a fragmentary skull and mandible). Mongolochamopids from Mongolia are distinguished from one another by their size, the proportions of separate skull bones and parts of the skull, and the numbers and morphology of the teeth.

Mongolochamopid lizards have also been reported from the Nemegt Formation (Alifanov, 1993a) and Höövör (Alifanov, 1993b, c).

Remarks. The Mongolochamopidae are Cretaceous Asian–American lizards that, like the Macrocephalosauridae, have double processes on the postfrontal and postorbital which form a mutual cruciform: a feature that is unique among lizards. The Mongolochamopidae are distinguished from the Macrocephalosauridae by their small size, a contact between the frontals and maxillae, a large infraobital fenestra, loss of the pterygoid–vomer contact, a well-developed angular process on the dentary, and teeth with two symmetrical lateral shoulders or additional denticles. This family also shows secondary similarities to macroteid genera, in particular the tricuspid subpleurodont teeth. However, mongolochamopids are distinguished by the presence of additional symmetrical cusps and the absence of bicuspid teeth.

Initially, these lizards were described by Alifanov (1993a) as a subfamily within the Macrocephalosauridae. They are raised to family rank here on the basis of their distinctive morphological characteristics and their more ancient and diverse distribution.

The Upper Cretaceous Chinese lizard *Chilingosaurus*, described by Dong (1965) and placed by Estes (1983) within 'Incertae sedis', is clearly a mongolochamopid lizard, as is *Buckantaus*, described by Nesov (1985) from the Late Cretaceous of Middle Asia (Alifanov, 1993a). The North American genera *Gerontoseps*, *Socognathus* and *Sphenosiagon*, described by Gao and Fox (1991) and originally assigned to the Teiidae, also belong in the Mongolochamopidae (Alifanov, 1993a). Another North American form *Prototeius*, described by Denton and O'Neill (1993), probably also belongs in this family.

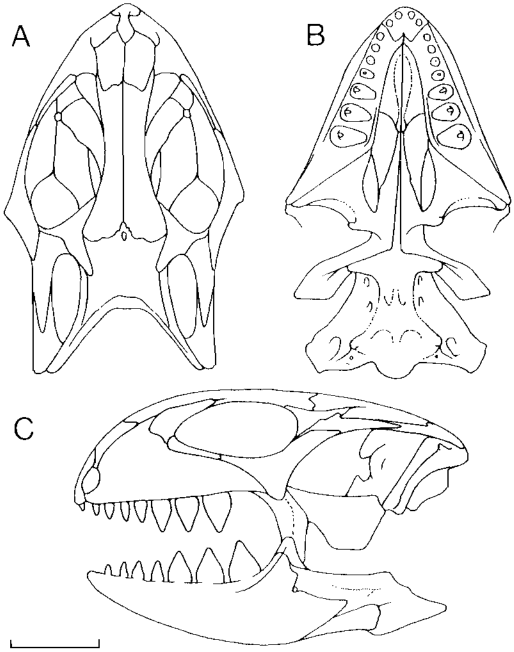

Figure 18.6. *Adamisaurus magnidentatus* Sulimski, 1972: reconstruction of the skull in (A) dorsal, (B) ventral and, with the left mandible, in (C) left lateral view. Scale bar = 5 mm.

ADAMISAURIDAE Sulimski, 1978

Record. At present this family is represented in the Mesozoic of Mongolia by a single genus and species, *Adamisaurus magnidentatus* Sulimski, 1972. The holotype (ZPAL MgR-II/80), recovered from Bayan Zag, consists of a skull with both mandibles (Figure 18.6A–C) and numerous other remains including skulls, sometimes associated with skeletons, are known from Djadokhta and Baruun Goyot localities. Moreover, remains of *Adamisaurus magnidentatus* have also been found from Djadokhta sediments in the Gobi Desert of China (Gao and Hou, 1995).

Remarks. The Adamisauridae is a distinctive Late Cretaceous family, described by Sulimski (1978) on the basis of a single genus that possesses paired frontals, a subtriangular postfrontal, a very large coronoid process on the dentary that is expanded on the labial surface of the coronoid, absence of the labial process of the coronoid, a surangular process on the dentary that is developed above the anterior surangular foramen, a large angular process on the dentary, subacrodont teeth that are slightly expanded transversely and have swollen bases, and teeth that are sharp and increase in size caudally. In addition, the dentition includes not more than eight teeth.

Like the Macrocephalosauridae this family was placed in synonymy with the Polyglyphanodontinae (Teiidae) by Estes (1983). Actually, there is some similarity between the Polyglyphanodontidae and the Adamisauridae, described from the Upper Cretaceous of North America by Gilmore (1940, 1942). They both have agamoid-like subacrodont teeth with transversely expanded tooth bases and an agamid-like dentary with posterior processes. However, there are many differences between the Adamisauridae and the Polyglyphanodontidae and they cannot be united within a single family.

The North American lizard *Peneteius*, described by Estes (1969a), has a small series of subacrodont teeth that increase in size posteriorly and have bulbous bases as in *Adamisaurus*. Thus, the inclusion of *Peneteius* in Adamisauridae seems reasonable. However, *Peneteius* is distinguished by its transversely expanded teeth that have a notch in their dorsal border, resulting in double apices. This unusual structure of the teeth is convergent with the dentition of the extant forms *Teius* and *Dicrodon*. Like *Callopistes* and some species of *Cnemidophorus* the anterior teeth of *Teius* and *Dicrodon* have additional cusps, though these are displaced lingually on the posterior teeth in the latter genus.

?EICHSTAETTISAURIDAE Kuhn, 1958

Record. The only Mongolian record is *Globaura venusta* Borsuk-Białynicka, 1988 (holotype: ZPAL MgR-III/40), based on a complete skull with mandible (Figure 18.7A–C) from Hermiin Tsav. Numerous remains of *Globaura* have also been found at the type locality, Bayan Zag and Khulsan. This lizard is characterized by its large brain case, a maxilla–frontal contact, paired premaxillae, reduced lacrimals, a wide upper temporal fenestra, fused and narrow frontals and a scincid-like dentary.

Remarks. The Family Eichstaettisauridae was des-

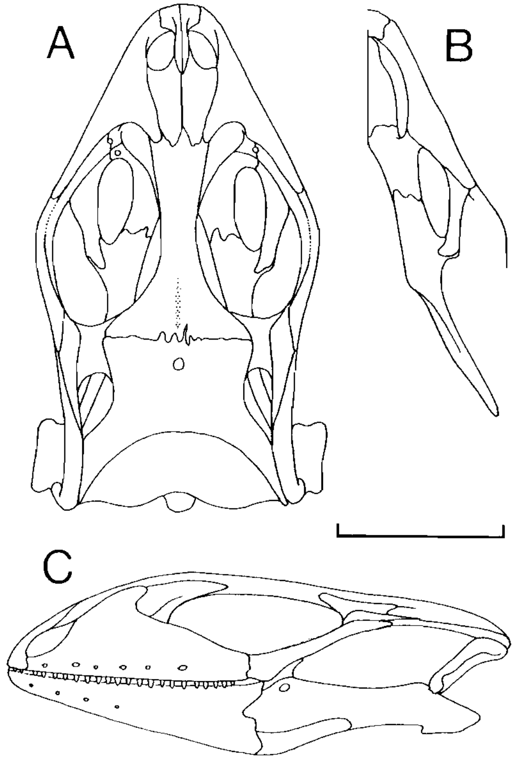

Figure 18.7. *Globaura venusta* Borsuk-Białynicka, 1988: reconstruction of the skull in (A) dorsal, (B) ventral and, wth left mandible, in (C) left lateral view. Scale bar = 5 mm.

cribed by Kuhn (1958) on the basis of a single specimen of *Eichstaettisaurus* from the Upper Jurassic of Germany. It was later synonymized with Ardeosauridae and recognized as gekkotan by Hoffstetter (1964, 1966). The history of these problematic families was well described by Estes (1983). All species of Ardeosauridae *sensu* Hoffstetter are represented by materials of different preservation and seen in dorsal aspect only, which obscures some skull characters. In my opinion, there are no formal arguments supporting the hypothesis of gekkotan relationships for both *Ardeosaurus* and *Eichstaettisaurus*. On the contrary, both genera demonstrate several non-gekkotan features, including the position of the ectopterygoid and the lateral process of the palatine dorsal to the supradental ridge of the maxilla, the complete temporal bar, a large jugal and the presence of a parietal foramen.

The reconstruction of the skull roof of *Eichstaettisaurus* by Estes (1983) exhibits many similarities to *Globaura*: a short snout, large orbits, small, separate postorbitals and postfrontals, small nasals, and an ectopterygoid–palatine contact above the supradental ridge of the maxillae. *Globaura* itself is a true scincomorphan, as Borsuk-Białynicka (1988) has shown, and this is confirmed by further scincid characters including: a labial process of the coronoid overlapped anteriorly by the coronoid process of the dentary so that the lateral exposure of this process is limited to a narrow wedge between the dentary and surangular; a postfrontal with two, short, lateral processes; the frequently poor development of the medial process of the postorbital, situated between the lateral processes of the postfrontal; and the massive angular process of the dentary. The stability of skull features in Jurassic and Cretaceous forms and the unique complex of primitive and derived characters of Eichstaettisauridae Kuhn, 1958, permit inclusion, tentatively of *Globaura* in this family.

CARUSIIDAE Borsuk-Białynicka, 1987
(= CAROLINIDAE Borsuk-Białynicka, 1985)

Record. Two forms belonging to this subfamily are known from Mongolia. *Carusia intermedia* Borsuk-Białynicka, 1985 (holotype: ZPAL MgR-III/34) is based on a skull without the upper temporal bars, but with both mandibles (Figure 18.8A, B) from Hermiin Tsav, and *Shinisauroides latipalatum* Borsuk-Białynicka, 1985 (holotype: ZPAL MgR-I/58) is based on a skull without the parietal region, but with a mandible, from the Nemegt.

Shinisauroides differs from *Carusia* in that it has a wider snout and palatines, more massive ectopterygoids, fused vomers, an unusually strongly expressed osteodermal sculpture on the skull roofing bones and more numerous teeth. These taxa are also represented by a small series of further remains from Mongolia.

Remarks. Carusiidae is an Upper Cretaceous scincomorphan family distinguished by osteodermal sculpture on the bones of the skull roof, a short and vaulted snout, paired premaxillae, reduced lacrimals, a large upper temporal fenestra, partly or completely fused

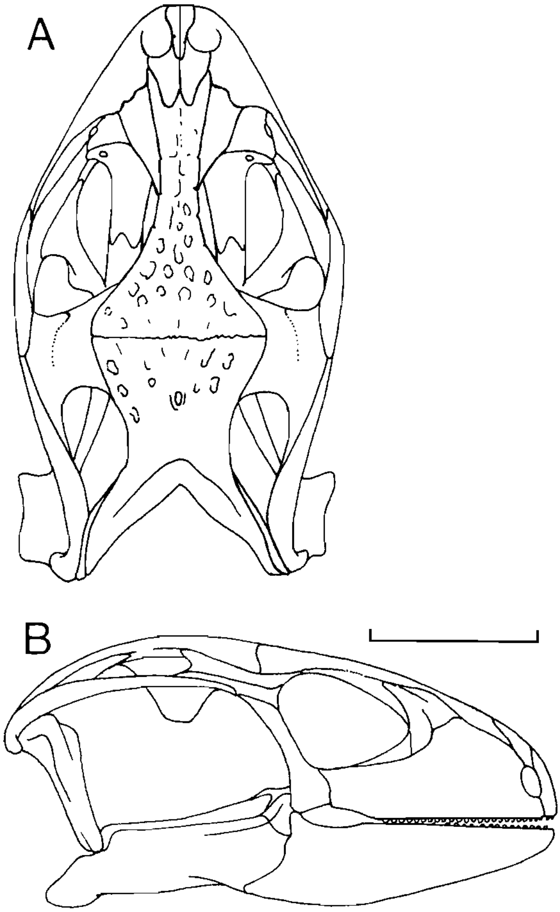

Figure 18.8. *Carusia intermedia* Borsuk-Białynicka, 1985: reconstruction of the skull in (A) dorsal and, with the right mandible, in (B) right lateral view. Scale bar = 10 mm.

postorbitals and postfrontals, the position of the medial contact of the processes of the ectopterygoid and palatine dorsal to the supradental ridge of the maxilla, unpaired and narrow frontals with closed olfactory canal, a large parietal with descending finger-like processes, a wide labial process on the coronoid that is overlapped by the coronoid process of the dentary, the exceptionally large angular and surangular processes of the dentary, and the exceptionally large, and skull-like hyperpleurodont teeth.

The relationships of Carusiidae to other scincomorphans is unclear, but there are some similarities between this family and the Late Jurassic European lizard *Ardeosaurus*, known from the dorsal aspect only. The latter was described on the basis of some incomplete fossil finds and recognized as a gekkotan by Camp (1923), Hoffstetter (1964, 1966), Mateer (1982) and Estes (1983). The best preserved specimen of *Ardeosaurus*, described by Mateer (1982), exhibits rugose skull roofing bones, an elongate parietal, paired premaxillae and frontals, expansion of the medial process of the postorbital anterior to the postfrontal, massive upper temporal bars, location of the parietal foramen in the centre of the parietal, and large adductor fossae. Most of these features are also characteristic for carusiid genera, with only the paired frontals distinguishing *Ardeosaurus* from other carusiids.

Poorly preserved remains of *Carusia* and possibly also of *Shinisauroides* have been found in Inner Mongolia, China (Gao and Hou, 1996). Gao and Hou (1996) proposed on the basis of their material that morphological differences between *Carusia* and *Shinisauroides* reflect sexual dimorphism. However, their formal conclusion does not take into consideration the absence of distinctive sexual dimorphism in the cranial features of the majority of modern lizard species and they do not state which genus should be regarded as male and which as female.

The scincomorphan *Contogenys* was described by Estes (1969b) from the Upper Cretaceous of North America on the basis of a fragmentary dentary which has teeth similar to those of *Carusia* and may thus belong to the Carusiidae.

PARAMACELLODIDAE Estes, 1983a

Record. Undescribed remains, represented by disarticulated bones, including numerous maxillae and dentaries bearing teeth, from the Early Cretaceous of Höövör are tentatively referred to this family. So far, however, paramacellodid-like lizards have not been reported from the Upper Cretaceous deposits of Mongolia.

Other Asian paramacellodids include *Sharovisaurus* from the Upper Jurassic of Kazakhstan (Hecht and Hecht, 1984) and *Mimobecklesiosaurus* from the Upper Jurassic of China (Li, 1985). *Changetisaurus*, a distinctive paramacellodid-like genus represented by an articulated skull and compound rectangular body osteoscutes from the Callovian of Fergana, Kirgizstan, was described by Nesov (Fedorov and Nesov, 1992) as a dorsetisaurid.

Remarks. Paramacellodids are Jurassic-Cretaceous cordyloid-like scincomorphans distinguished by compound rectangular body osteoscutes. Unfortunately, the skull is only poorly known. Paramacellodidae was proposed by Estes (1983) to distinguish some problematic forms that 'on present material cannot be referred to the Holocene family' (Estes, 1983, p. 115).

SLAVOIIDAE Alifanov, 1993c

Record. Two genera have been described from the Upper Cretaceous of Mongolia: *Slavoia darevskyi* Sulimski, 1984 (holotype: ZPAL MgR-I/8, based on a skull and complete postcranial skeleton from Khulsan) (Figure 18.9A–C) and *Eoxanta lacertifrons* Borsuk-Białynicka, 1988 (holotype: ZPAL MgR-III/37, represented by a complete skull with both mandibles from Hermiin Tsav). *Slavoia* is the commonest lizard from Bayan Zag, Khulsan and Hermiin Tsav and remains of *Slavoia*-like and *Eoxanta*-like genera are also known from the Early Cretaceous of Mongolia (Alifanov, 1993b, c).

Remarks. The *Acontias*-like features of the skull in *Slavoia* (wide snout, large upper temporal fenestrae, nasals and frontals, contact between the prefrontal and postfrontal above the orbits, small postfrontals, the reduced size of the orbit and teeth which lack additional anterior denticles) clearly distinguish it from *Eoxanta.* A distinctive feature of *Eoxanta* is its large and long postfrontal the enlargement of which obliterates the upper temporal fenestra.

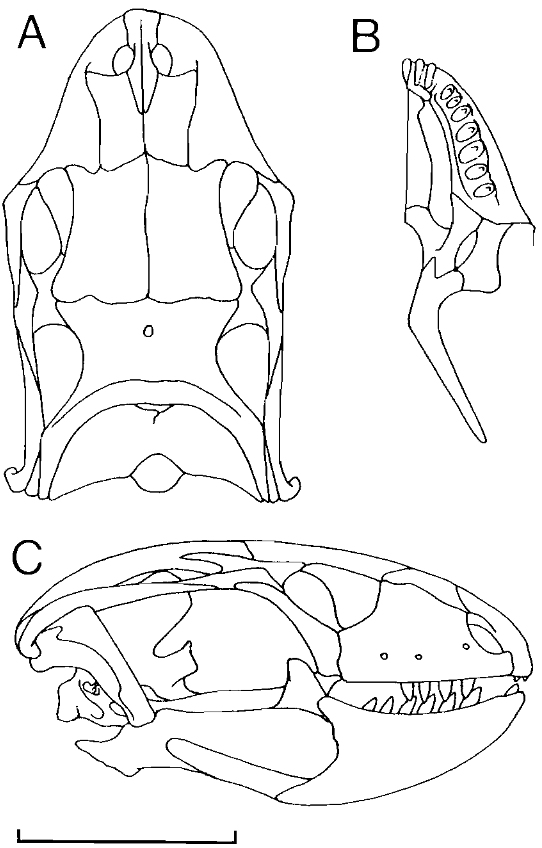

Figure 18.9. *Slavoia darevskyi* Sulimski, 1984: reconstruction of the skull in (A) dorsal, (B) ventral and, with the right mandible in (C) right lateral view. Scale bar = 5 mm.

The Slavoiidae, unique to the Cretaceous of Asia, was erected by Alifanov (1993c) and distinguished by an unusual complex of primitive and derived characters including: paired premaxillae and frontals, wide nasals and frontals, the position of the short medial process of the postorbital between the lateral processes of the postfrontal, the development of subolfactory processes of the frontals, reduced lacrimals, small orbits, contact between the lateral process of the palatine and the massive ectopterygoid medial to the supradental ridge of the maxilla, the massive angular process of the dentary, overlapping of the labial process of the coronoid by the coronoid process of the dentary, opening of the Meckelian canal in front of the partially reduced splenial and the presence of no more than fifteen conical teeth.

The structure of the posterior border of the dentary shows that the Slavoiidae are undoubtedly scincomorphans. The absence of osteodermal sculpture on the skull roofing bones and the location of the contact between the lateral process of the palatine and the ectopterygoid, medial to the supradental ridge of the maxilla, is similar to that in extant Xantusiidae, though the postorbital–postfrontal contact is comparable to the situation in some modern genera of the Scincidae. Sulimski proposed that *Slavoia* was related to the Gymnophthalmidae, while Borsuk-Białynicka (1988) described *Eoxanta* as a non-teiid lacertoid and correctly noted, for the first time, the similarity between *Slavoia* and *Eoxanta.*

GEKKOTA Cuvier, 1817

This infraorder includes lizards that are usually of small size and with a homeomorphan skull structure. Gekkota *sensu* Kluge (1987) includes Gekkonidae, Diplodactilidae and Eublepharidae, while Estes *et al.* (1988) divided the Gekkota into Pygopodidae and Gekkonidae, noting the possible paraphyly of the latter.

'GEKKONIDAE' Gray, 1825

Record. Hoburogekko sukhanovi Alifanov, 1989a (the specific epithet is emended from the original '*suchanovi*' a lapsus calami) from the Lower Cretaceous of Mongolia, has been described on the basis of a fragmentary skull (holotype: PIN 3334/ 500) and separate dentaries with an unfused Meckelian canal. *Gobekko cretacicus* Borsuk-Białynicka, 1990 (holotype: ZPAL MgR-II/4), from the Upper Cretaceous of Mongolia, is based on one of three fragmentary skulls, witb mandibles, from Bayan Zag. *Gobekko* is characterized by paired bones of the skull roof (except for the premaxillae), the paired, M-shaped posterior edge of the wide parietal and unpaired vomers.

ANGUIMORPHA Fürbringer, 1900

This taxon was proposed by Fürbringer (1900) in synonymy with Diploglossa of Cope (1900). Later, Camp (1923) united Cope's Diploglossa with Fürbringer's Platynota (Varano–Dolichosauria) and Mosasauria in his Anguimorpha. Tbe modern conception of this taxon includes Varanoidea and Anguoidea (McDowell and Bogert, 1954; Gauthier, 1982; Pregill *et al.*, 1986; Estes *et al.*, 1988).

VARANIDAE Hardwike and Gray, 1824
(= MEGALANIDAE Fejervary, 1935)

Record. The following taxa bave been described from the Upper Cretaceous of Mongolia: *Telmasaurus grangeri* Gilmore, 1943 (holotype: AMNH 6645), based on the parietal region of a skull from Bayan Zag; *Saniwides mongoliensis* Borsuk-Białynicka, 1984 (holotype: ZPAL MgRI/72), based on a complete skull with mandible from Khulsan; and *Estesia mongoliensis* Norell *et al.*, 1992 (holotype: M 3/14), based on a skull and left ramus of the lower jaw, also from Khulsan. *Cherminotus longifrons* Borsuk-Białynicka, 1984 (bolotype: ZPAL MgR-III/59) was established on a complete skull, lacking the upper temporal bars, but associated with the mandibles (Figure 18.10C–E) from Hermiin Tsav, which has also yielded vertebrae of *Saniwa* sp. *Varanus*-like vertebrae have been found in the Nemegt Formation (Alifanov, 1993b) and varanids have also been reported from the Palaeogene of Mongolia (Alifanov, 1993b, c).

Remarks. In *Saniwides,* and possibly in *Telmasaurus*, the frontals are excluded from the posterior border of tbe bony nares by nasal–maxilla contacts. In both cases, tbe palatines and pterygoids bear many teeth and the fused postorbitals and postfrontal, including the frontals, take part in forming the upper border of the orbits. The largest form, *Estesia*, described recently by Norell *et al.* (1992), and the smallest, *Cherminotus*, exhibit the alternative condition for the features mentioned above, and have distinct similarities in cranial morphology. *Cherminotus* was originally assigned to Lanthanotidae by Borsuk-Białynicka (1984), but new remains do not confirm this conclusion.

Derived osteological character states of Varanidae include: the absence of regular body osteoscutes or rugosity on the skull roof bones, posterior retraction of the bony nares, the posterior position of the nasal processes of the maxilla, well-developed subolfactory processes, intramandibular mobility (streptognathy), anterior expansion of the labial process of the coronoid and fusion of the upper borders of the labial and antero-medial processes of the coronoid, and in the vertebrae precondylar constriction leads to the formation of flanges on the condyle.

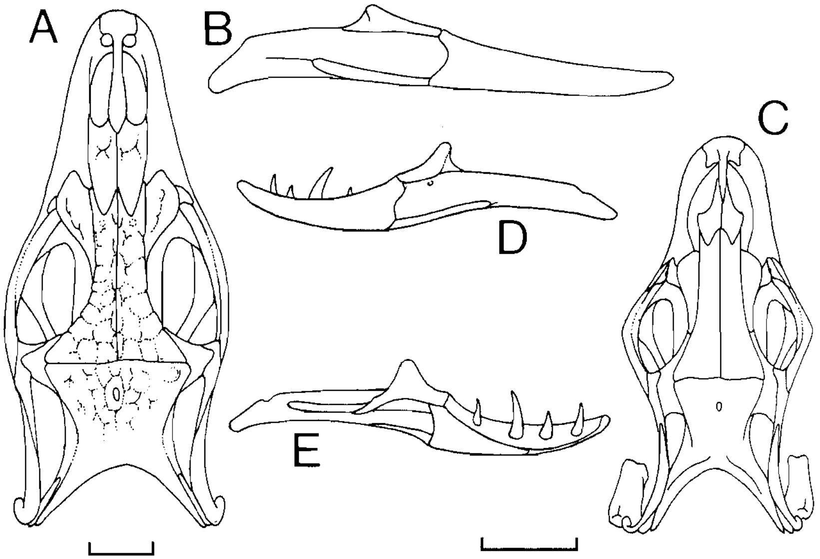

Figure 18.10. *Proplatynotia longirostrata* Borsuk-Białynicka, 1984: reconstruction of the skull in (A) dorsal view and the right mandible in (B) lateral view. *Cherminotbus longifrons* Borsuk-Białynicka, 1984: reconstruction of the skull in (C) dorsal view and the left mandible in (D) lateral and (E) medial view. Scale bar = 5 mm.

The Varanidae currently occur in the Old World and Australia, but they had a broader distribution in the Palaeogene and were also found in North America, Europe and Central Asia. The oldest reliable evidence of this family comes from the Late Cretaceous of Central Asia, but at this time varanids seem to have been absent from North America. *Paleosaniwa*, known on the basis of fragmentary remains from North America, has sometimes been identified as a varanid (Estes, 1983), but it lacks precondylar constriction of the trunk vertebrae, a characteristic of true varanids and is more likely to be a 'necrosaurid'.

'NECROSAURIDAE' Hoffstetter, 1943 (=PARASANIWIDAE Estes, 1964)

Record. The following forms have been described from the Upper Cretaceous of Khulsan, Mongolia: *Proplatynotia longirostrata* Borsuk-Białynicka, 1984 (holotype: ZPAL MgR-I/68), based on a complete skull with mandible (Figure 18.10A, B); *Gobiderma pulchra* Borsuk-Białynicka, 1984 (holotype: ZPAL MgR-III/64), represented by a complete skull with mandible; and *Parviderma inexacta* Borsuk-Białynicka, 1984 (holotype: ZPAL MgR-I/43), based on a damaged skull and mandible. Necrosaurid lizards, as yet undescribed, have also been found in the Nemegt Formation and the Upper Palaeocene of Mongolia (Alifanov, 1993b, c).

The necrosaurids from Khulsan are distinguished from one another by skull dimensions and the proportions of individual bones. *Parviderma* is distinguished by its fused and narrow frontals, while *Gobiderma* has non-imbricate rounded or polygonal osteoscutes and parietals with flattened lateral borders. The structure of the dentary and teeth of *Proplatynotia* shows clear similarity to that of *Colpodontosaurus* from the Upper Cretaceous of North America.

Remarks. The Necrosauridae are predatory anguimorphans from the Cretaceous of Asia–America. They exhibit a combination of primitive and derived characters including the unusual form of the body osteoscutes, osteodermal sculpture on the skull roof bones, distinct upper temporal arches, absence of intramandibular mobility, unretracted nares and *Anguis*-like or *Varanus*-like teeth. In addition, all Asiatic 'necrosaurids' have pterygoids and palatines that bear numerous teeth.

Estes (1983) synonymized his Parasaniwidae with Necrosauridae, erected earlier by Hoffstetter (1943), who also believed in the unity of these groups, and proposed (Estes, 1983) that helodermatids may have been derived from necrosaurid stock. More recently, Necrosauridae *sensu lato* has been interpreted by Borsuk-Białynicka (1984) as a paraphyletic group within the Varanoidea.

ANGUIDAE Gray, 1825 (=BAINGUIDAE Borsuk-Białynicka, 1984)

Record. Bainguis parvus Borsuk-Białynicka, 1984 (holotype: ZPAL MgR-II/46) from Bayan Zag, and represented by a damaged skull with both mandibles is the only record of this family in Mongolia.

Remarks. Bainguis was initially established in a separate family, Bainguidae, by Borsuk-Białynicka (1984), but later, on the basis of similarities in the configuration of the osteodermal sheets on the bones of the skull roof, it was assigned, apparently correctly, to the Anguidae (Borsuk-Białynicka, 1991).

DORSETISAURIDAE Hoffstetter, 1967

Record. Dorsetisaurus, represented by numerous isolated maxillae and dentaries is known only from Höövör.

Remarks. The Dorsetidauridae are poorly known anguimorphans from the Late Jurassic of North America and Europe and the Early Cretaceous of Europe and Asia. They are distinguished by frontal scutellation, a low and elongate braincase, wide upper temporal fenestrae, and lancet-like teeth (see Estes, 1983 for further details). So far, no *Dorsetisaurus*-like lizards have been found in the Upper Cretaceous deposits of South Gobi, Mongolia.

HODZHAKULIIDAE Alifanov, 1993c

Record. Numerous isolated maxillae, premaxillae and dentaries of a single taxon, *Hodzhakulia* sp. have been collected from Höövör. So far, hodzhakuliid lizards have not been found in the Upper Cretaceous deposits of South Gobi, Mongolia.

Remarks. Hodzhakulia, the type genus of the family Hodzhakuliidae (Alifanov, 1993c), was first described by Nesov (1985) on the basis of isolated dentaries from the Aptian–Albian of Middle Asia, but was not assigned to any particular taxon within Lacertilia. Recently, Nesov and Gao (1993) have suggested that *Hodzhakulia* may be related to amphisbaenians. However, additional material of *Hodzhakulia* from the Lower Cretaceous of Mongolia shows the following features: unpaired premaxillae; a thin and long posterior process of the maxillae; varanid-like structure of dentary; tall teeth with cylindrical or antero-posteriorly compressed bases and multiple resorbtion pits; and teeth apices that have short shoulders. Many of these features are not characteristic of Amphisbaenia. Alternatively, the tall teeth of *Hodzhakulia* show some similarities to those of *Litakis*, a problematic form assigned by Estes to Anguimorpha *incertae sedis* (1964) or Eolacertilia (1983).

?XENOSAURIDAE Cope, 1886 (=SHINISAURIDAE Ahl, 1929)

Record. Deposits at Höövör have yielded several anguoid-like dentaries with conical teeth, that have been assigned, on a preliminary basis, to Xenosauridae. By contrast, xenosaurids have not been reported from the Upper Cretaceous of South Gobi, Mongolia.

Remarks. Fragmentary remains of *Oxia karakalpakiensis* Nesov, 1985 from the Lower Cretaceous of Uzbekistan were referred to the Xenosauridae by Nesov and Gao (1993). Apart from this record and the Höövör material, the earliest xenosaurids, a small group of extant Asian–American anguimorphans, are known also from the Upper Cretaceous and Palaeogene of North America.

PARAVARANIDAE Borsuk-Białynicka, 1984

Record. A single genus and species, *Paravaranus angustifrons* Borsuk-Białynicka, 1984 (holotype: MgR-I/67, a partly damaged skull and mandible), known only from Khulsan. Additional remains of *Paravaranus* are held in the collections of PIN.

Remarks. The Paravaranidae is a somewhat doubtful monotypic family characterized by the following features: absence of a subolfactory process; squamosal with an Iguania-like dorsal process; parietals bearing concavities limited by ridges; Y-shaped vomers; strongly toothed pterygoids; slender and low mandibles; and pointed and recurved pleurodont teeth. Borsuk-Białynicka (1984) proposed that *Paravaranus* belonged within Anguimorpha, but, in my opinion, there is some evidence to suggest a possible relationship with mosasaurs. This is supported by a complex of common cranial characters: restricted bony nares; unpaired premaxillae, frontals, parietals and nasals; a deep division between the vomers; toothed palatines; and the presence of dorsal processes of the squamosal.

Discussion

Patterns of diversity

Representatives of almost 20 families of lizards, the total number of families known from Cretaceous deposits, are listed in the survey above. Some details concerning the origin of this diverse assemblage can be obtained by comparing lizard assemblages collected from localities in the southern part of the Gobi Desert in the Mongolian People's Republic and representing the following intervals: the Early and Late Cretaceous, the pre-Maastrichtian and the Maastrichtian, and the Cretaceous and the Palaeogene (see Tables 18.1–18.3).

Table 18.1 compares the diversity of lizards, at the family level, known from the Djadokhta and Baruungoyot Formations (pre-Maastrichtian) with that known from the younger Nemegt Formation (Maastrichtian). Only four families are found in the Nemegt, compared with 15 in older deposits, indicating a decline in lizard diversity in the Maastrichtian of Mongolia.

Although the history of many of the families discussed above is disputable, there is clear evidence of significant levels of extinction of lizards in Asia before the beginning of the Cenozoic. The vast majority (11 out of 16) of families of Late Cretaceous lizards became extinct at this time and only three families (Varanidae, Isodontosauridae, 'Necrosauridae') crossed the Cretaceous–Tertiary boundary in Asia, though these families (Varanidae), or their descendants (Gekkonidae, Anguidae) are still found in Asia today. The results of preliminary studies of lizards from the Mongolian Palaeogene (Tables 18.2 and 18.3) confirm this pattern. The Palaeogene yields eight families, half of them (Arretosauridae, Uromasticidae, Agamidae and Lacertidae) appearing for the first time in Asia. In the case of the Agamidae and the Uromasticidae, and possibly also the Arretosauridae, this may reflect a local radiation in Asia during the latest Cretaceous–earliest Palaeocene. The Anguidae, well known from the Late Cretaceous and Palaeogene of North America, were widely distributed during this interval, while the Lacertidae may have arrived from an ancient centre of diversity apparently located in Europe.

Table 18.1. *Comparison of the fossil record of lizards from Upper Cretaceous deposits of the Gobi Desert, Mongolia.*

Pre-Maastrichtian (Djadokhta and Baruungoyot formations)	Maastrichtian (Nemegt Formation)
†Adamisauridae	—
Anguidae	—
†Carusiidae	—
†?Eichstaettisauridae	—
'Gekkonidae'	—
Hoplocercidae	—
†Isodontosauridae	—
†Macrocephalosauridae	—
†Mongolochamopidae	†Mongolochamopidae
†'Necrosauridae'	†Necrosauridae
†Paravaranidae	—
Phrynosomatidae	—
†Priscagamidae	—
†Slavoiidae	—
Varanidae	Varanidae
—	Teiidae

Notes:
† = extinct taxon.

Comparisons between lizard assemblages from the

Table 18.2. *Comparison of the fossil record of lizards from Cretaceous and Palaeogene deposits of the Gobi Desert, Mongolia*

Lower Cretaceous	Upper Cretaceous	Palaeogene
—	†Adamisauridae	—
—	—	Agamidae
—	Anguidae	Anguidae
—	—	Arretosauridae
—	†Carusiidae	—
†Dorsetisauridae	—	—
†?Eichstaettisauridae	†?Eichstaettisauridae	—
'Gekkonidae'	'Gekkonidae'	—
—	Hoplocercidae	—
†Hodzhakuliidae	—	—
'Iguanidae' indet.	—	—
—	†Isodontosauridae	†Isodontosauridae
—	—	Lacertidae
—	†Macrocephalosauridae	—
?†Mongolochamopidae	†Mongolochamopidae	—
—	†'Necrosauridae'	†'Necrosauridae'
—	†Paravaranidae	—
?†Paramacellodidae	—	—
—	Phrynosomatidae	—
—	†Priscagamidae	—
†Slavoiidae	†Slavoiidae	—
—	Teiidae	—
—	—	Uromasticidae
—	Varanidae	Varanidae
?Xenosauridae	—	—

Notes:
† = extinct taxon.

Table 18.3. *Comparison of the fossil record of lizards in the Palaeogene of the Gobi Desert, Mongolia*

Late Palaeocene (Tsagaan Khushuu)	Early Eocene (Tsagaan Khushuu)	Middle Eocene (Khaichin Uul II)	Early Oligocene (Ergiliin Zoo, Khoyor Zaan)
Agamidae	Agamidae	Agamidae	—
—	—	?†Arretosauridae	?†Arretosauridae
—	Anguidae	—	Anguidae
†Isodontosauridae	—	†Isodontosauridae	—
—	—	—	Lacertidae
†'Necrosauridae'	—	—	—
—	Varanidae	Varanidae	Varanidae
—	Uromasticidae	Uromasticidae	Uromasticidae

Notes:
† = extinct taxon.

Early Cretaceous (Höövör) and the Late Cretaceous (Table 18.2) suggest a modest level of extinction at the family level. Only the Paramacellodidae, the Hodzhakuliidae and the problematic Dorsetisauridae disappeared completely, while the single extant family, the Xenosauridae, is not known from post-Early Cretaceous deposits in Asia.

Palaeobiogeography

Three families found in the Early Cretaceous of Mongolia (?Eichstaettisauridae, Paramacellodidae and Dorsetisauridae) are also known from the Late Jurassic or Early Cretaceous of Europe. This suggests a connection between and the possible development of Cretaceous lizards of Asia from Jurassic lizards of Panlaurasia. These families together with the extant and cosmopolitan 'Gekkonidae', also known from the Early Cretaceous of Asia, can be named Laurasian relics.

Most Early Cretaceous lizard families from Asia appear to be endemic to this region at this time. This is consistent with the supposed isolation of Asia during this interval, which, according to Russell (1993), began in the Middle Jurassic. If this is correct, then the Mongolochamopidae, Slavoiidae, Xenosauridae and Hodzhakuliidae presumably had an Asiatic origin during the Late Jurassic–Early Cretaceous, and may be named Late Jurassic–Early Cretaceous derivatives of Asia. At least some 'iguanoid' groups may also have originated in Asia during this interval.

Table 18.2 shows that 12 lizard families (which can be linked in three groups: the Hoplocercidae–Teiidae–Anguidae, the Isodontosauridae–Priscagamidae–Macrocephalosauridae–Varanidae–Paravaranidae and the Phrynosomatidae–Adamisauridae–Carusiidae–'Necrosauridae'), first appear in the Late Cretaceous. Members of the first group are usually referred to as American lizards and are currently found in North and South America. The Teiidae have been reported from the Late Cretaceous of North and South America, but the Anguidae and Hoplocercidae are known only from the Late Cretaceous of North and South America respectively. By contrast, several families from the second group (Isodontosauridae, Priscagamidae, Macrocephalosauridae, Paravaranidae and Varanidae) are found only in the Late Cretaceous of Asia. The third group includes families (Phrynosomatidae, Adamisauridae, Carusiidae and 'Necrosauridae') that occur in both Asia and America.

The appearance of American and Asian–American families in Asia indicates the establishment of an Asian–American connection toward the end of the Late Cretaceous (Russell, 1993). However, the evidence from lizards, and other taxa, of endemism in Asia in the Late Cretaceous shows that this connection was subsequently lost, leading to temporary isolation of Asia (Alifanov, 1993c), prior to the Palaeogene consolidation of all northern continents.

Faunal interchange between North America and Asia in the Cretaceous led to the introduction of the Asian lizard families Mongolochamopidae and Xenosauridae into North America. These families do not appear to have reached South America, suggesting that this continent was isolated from North America by the beginning of the Late Cretaceous Asian–American interchange. However, the Americas must have been connected prior to this, since only this configuration explains the distribution of Teiidae, Hoplocercidae and Anguidae in Asia and the Americas, and the Asiatic occurrences of Mongolochamopidae and Xenosauridae, which are otherwise only found in North America. This suggests that the Early Cretaceous lizards from Höövör existed before the beginning of the Cretaceous Asian–American connection, while Late Cretaceous lizards from the Djadokhta, Baruungoyot and Nemegt formations existed after this event. This palaeozoogeographic hypothesis is also supported by studies of other tetrapod groups (Kalandadze and Rautian, 1992) and can be used to establish the palaeozoogeographic origins of Late Cretaceous lizard groups. For example, the Asian Cretaceous endemics Isodontosauridae, Priscagamidae, Macrocephalosauridae and Varanidae are derived from the Late Cretaceous of Asia. By contrast, Teiidae and Hoplocercidae, which are so far unknown in the Early Cretaceous of Asia are possibly derived from the Neocomian of America or, perhaps more precisely, North America, since the nearest relations of all the American lizard families that appear in the Late Cretaceous of Asia originally had a Panlaurasian distribution.

The origin of the Asian–American Phrynosomatidae, Carusiidae, Adamisauridae and 'Necrosauridae', which are unknown in South America or from the rich assemblage found at Höövör, possibly happened in North America after the Neocomian, following the loss of the first inter-American connection and just before the beginning of interchanges between Asia and America.

Conclusion

The material described above fills an important gap in our knowledge of lacertilian evolution during the Mesozoic. The establishment of rich Cretaceous lizard assemblages on the territory of Central Asia is connected with the protracted and relatively stable existence of a local fauna beginning in the Middle Jurassic, when lizard families first appeared. By the Maastrichtian, the diversity of Asiatic lizards had declined and was never restored to this level, hence the Late Cretaceous lizards of the Gobi Desert would appear to represent the apogee of lacertilian diversity in this region.

The origin of some endemic Asiatic groups took place after the Jurassic disjunction of Panlaurasia which led to the isolation of Central Asia. An Asian–American contact in the late Early Cretaceous temporarily suspended this isolation and led to interchange between the two contrasting assemblages of Asia and Northern America, as a result of which some American forms appeared in Asia. By contrast to the Asiatic groups, which only appear in North America during the Late Cretaceous, the American migrants reached South America too. This indicates the possibility of direct inter-American faunal interchange before the establishment of a connection between Central Asia and North America in the Cretaceous. During the Late Cretaceous renewed isolation of Asia led to the appearance of new Asiatic families both before and after the Maastrichtian crisis.

Thus, Cretaceous lizards from the Gobi Desert of Mongolia can be characterized palaeozoogeographically as follows: Laurasian relics (?Eichstaettisauridae, Paramacellodidae, Dorsetisauridae and 'Gekkonidae'); Late Jurassic–Early Cretaceous Asian forms (Slavoiidae, Mongolochamopidae, Xenosauridae and Hodzhakuliidae); Late Cretaceous Asian forms (Varanidae, Isodontosauridae, Priscagamidae, Macrocephalosauridae and Paravaranidae); American migrants (Teiidae, Hoplocercidae and Anguidae); and Asian-American Forms (Phrynosomatidae, Carusiidae, Adamisauridae and 'Necrosauridae').

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