First Asiatic 'iguanid' lizards in the Late Cretaceous of Mongolia

MAGDALENA BORSUK-BIAŁYNICKA and VLADIMIR R. ALIFANOV

Borsuk-Białynicka, M. & Alifanov, V. R. 1991. First Asiatic 'iguanid' lizards in the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* **36**,3, 325-342.

The first Asiatic records of iguanids are described from the Campanian of Mongolia. The Laurasian origin of the Iguania is therefore equally as likely as the Gondwanan origin, suggested by all previous data. The Asiatic, instead of African provenience of Malagasy 'iguanids', as suggested by Rage (1988), is also possible. *Igua minuta* gen. et sp. n. and *Polrussia mongoliensis* gen. et sp. n. are recognized.

Key words: Reptilia, Sauria, Iguanidae, taxonomy, Cretaceous, Gobi Desert.

Magdalena Borsuk-Białynicka, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.
Владимир Р. Алифанов, Палеонтологический Институт Академии Наук СССР, Профсоюзная ул. 123, Москва, Россия.

Introduction

America has always been, and is to day, the main area of distribution of the 'iguanids'. The extant 'iguanids' also occur on Madagascar and on the Fiji and Tonga islands. The fossil 'iguanids' have been known, up to now, from the Cretaceous and Cenozoic of America (Estes & Price 1973, Gilmore 1928, Fries *et al.* 1955, Estes 1970, Estes 1983a, Sullivan 1982) and from the Eocene of Europe (Kuhn 1944, Hoffstetter 1942, Augé 1987). The supposed Asiatic iguanid relatives, *Qianshanosaurus* (Hou 1974) from the Paleocene of China and *Arretosaurus* (Gilmore 1943) from the Eocene of Mongolia, are quite aberrant lizards of still questionable affinity (Estes 1983a). For a long time the oldest record of the 'iguanids' was the Late Cretaceous *Pristiguana* Estes & Price 1973, known only from poorly preserved material. The present disjunct distribution of the 'iguanids', along with the South American Cretaceous record, led Estes (1983b) to suggest a Gondwanan origin of the Iguania. The Asiatic material described herein provides an equally plausible hypothesis.

The paper comprises description of two new genera and species *Igua minuta* and *Polrussia mongoliensis* discovered in the Cretaceous of the Gobi Desert and assigned to the infraorder Iguania. The dentition of these lizards, continually replaced and attached to the medial side of the jaw, is critical for excluding them from the Chamaeleonidae *sensu* Frost & Etheridge (1989), the only iguanian family having the dentition at least partially permanent and more or less apically attached (said to be acrodont). They are thus located within the squamate system with the remaining eight iguanian families (formerly placed in the family Iguanidae) recognized by the same authors, which have the dentition similar to all non-iguanian lizards. This affiliation of *Igua* and *Polrussia* makes the informal name 'iguanids', traditionally used for all the non-acrodont iguanians, applicable to them. The quatation marks are used to indicate the paraphyletic status of the old 'Iguanidae'. Since we are unable to indicate precisely the affinity of the here described genera with any family of 'iguanids' (*sensu* Frost & Etheridge 1989), nor could we found a new family to include them, we just indicate their position within the Iguania.

The present paper is based on the collections of the Polish-Mongolian Paleontological Expeditions to the Gobi Desert (1964 and 1971). The specimens were collected at the locality Khulsan from the Barun Goyot Formation of the ?middle Campanian age (Gradziński *et al.* 1968, Gradziński & Jerzykiewicz 1978, Gradziński *et al.* 1977). The material is housed at the Institute of Paleobiology of the Polish Academy of Sciences (abbreviated as ZPAL) in Warsaw, Poland.

Relationships of the Mongolian 'iguanids'

The following section is intended to contrast characters of the described fossil lizards with the nested set of synapomorphies most recently proposed by Estes *et al.* (1988), Etheridge & de Queiroz (1988) and Frost & Etheridge (1989) for Sauria. The full agreement (excluding incompletness of data caused by imperfect preservation) with the infraordinal level of the Estes *et al.* (1988) scheme resulted in assignment of the fossils to the infraorder Iguania. The present study confirms the existence of difficulties in the clear understanding of the familial level within this infraorder, and allows for discussing the taxonomic value of some character states not used for this scheme.

Six cranial synapomorphies of the Iguania of the eight listed by Estes *et al.* (1988) occur in the lizards described herein, although not all of them are preserved in every case. Both *Igua* and *Polrussia* have the frontals unpaired and hourglass-shaped, *Polrussia* has the prefrontal bosses developed. In *Igua* the parietal foramen is preserved on the frontoparietal suture. The base of the finger-like angular process is preserved in both

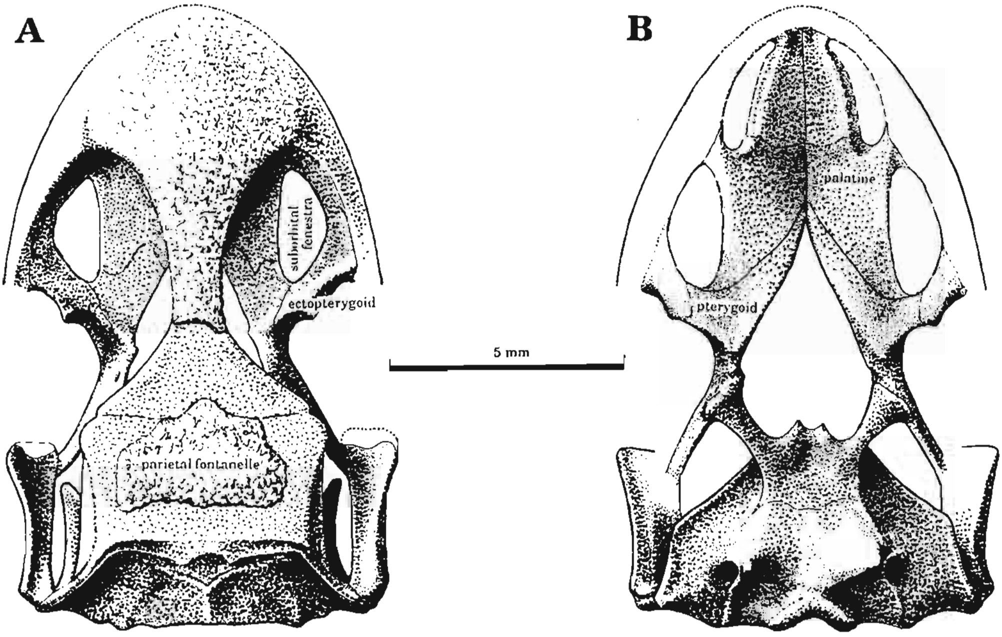

Fig. 1. Reconstruction of skull of *Igua minuta* gen. et sp. n. □A. Dorsal view. □B. Ventral view.

Igua and *Polrussia*. Three symplesiomorphies (prefrontal bordering of the orbitonasal fenestra, short vomers and small, shallow and far anterior choanal fossae) endorse the reference to the Iguania. Some other character states considered helpful for assignment of the lizard material described herein will be discussed below.

Though the presence of the parietal fontanelle (Figs 1A, 2A) is not sufficiently understood in terms of polarity as yet, it is here considered as supportive for the iguanian affiliation of *Igua minuta*. This character, reflecting the late ossification of the parietal in ontogeny, is very common in the Agamidae and in those 'iguanids' that lack strong lateral parietal crests fused into a sagittal crest - a character late to appear in ontogeny of some 'iguanids' according to Etheridge & de Queiroz (1988), and synapomorphic for the Corytophanidae according to Frost & Etheridge (1989).

The presence of large, triangular, transversally expanded postorbital is here considered as supportive for the iguanian affiliation of *Polrussia*.

The next character available for studies in the present material (in *Igua*) is a structure of the lateral braincase wall. In *Igua* this wall is concave between semicircular canals (Fig. 2A) exactly as it is in the Late Cretaceous priscagamines (Borsuk-Białynicka & Moody 1984) and in the agamids. This character state, considered synapomorphic for the Agamidae (including priscagamines) by Borsuk-Białynicka & Moody (1984), seems to be a character of a more inclusive group according to the present studies. It consists mainly in lateral bending of the anterior part of the braincase wall under an angle of about 90° at a point situated behind the anterior semicircular canal. This bending is consistent within the Iguania (in 19 of 20 genera studied) in contrast to the Scleroglossa which have the lateral braincase wall only gently concave laterally (in 19 of 24 genera studied. The character 8 of Etheridge & de Queiroz (1988) referred to as 'rising of the osseous labyrinth above the surface of the braincase' stresses the effect of the braincase bending if derived (states 1 and 2 observed in 57% of the 'iguanid' genera studied by these authors) by making the depression deeper. Still, the plesiomorphic state of this character does not make the iguanian braincase wall flat, as shown by *Uromastyx*, *Physignathus* and seven 'iguanid' genera available to us of the 26 genera scored 0 by Etheridge & de Queiroz (1988). The examples of shallowing of the concavity of the iguanian braincase wall (*Chamaeleo*, *Iguana*, *Phrynosoma*) are mainly the results of actual swelling of the wall along the prootic-supraoccipital suture, which is most probably a secondary phenomenon. On the other hand, a lateral flexion of the anterior part of the braincase wall found in some autarchoglossan genera studied (*Varanus*, *Gerrhosaurus*, macroteiids) is here tentatively regarded as a secondary transformation of the scleroglossan 'flat' type. A strong projection of both canals may sometimes produce a false concavity in the flat type of braincase wall, which may be the case of the braincase wall of the Late Cretaceous gekkonid (*Gobekko cretacicus* Borsuk-Białynicka 1990).

The lack of data about the above discussed aspect of the braincase wall in the outgroup of the Squamata prevents from determining the depression of this wall as synapomorphic or plesiomorphic for the Iguania. In any case, it is here considered as characteristic for this infraorder, in contrast to a rather flat braincase wall of the Scleroglossa, and is used as a case for the iguanian affiliation of *Igua*.

The indication of the exact systematic position of *Igua* and *Polrussia* within the infraorder Iguania is difficult in view of their state of preservation. Two iguanian groups: the Chamaeleonidae *sensu* Frost & Etheridge (1989) (equivalent of the Acrodonta of Estes *et al.* 1988) and the Corytophanidae *sensu* Frost & Etheridge (1989) (former basiliscines) diagnosed by distinct synapomorphies (permanency of at least a part of dentition in the for and a sagittal crest on the Y-shaped parietal in the latter), have been excluded from further considerations.

The typically pleurodont attachment and possible continuous replacement of teeth in the both lizards discribed (Figs 2C, E, 4A, 5B, 6E) are consistent with the 'iguanid' structure of their mandibles and mainly with a tendency to closing the Meckelian canal into a tube (in the case of *Polrussia*), and presence of the lateral coronoid process (small but distinct in *Igua*, tiny in *Polrussia*). These characters are the subject to variability at the family level and may be helpful to dismiss a membership of the described genera in at least some 'iguanind' families recognized by Frost & Etheridge (1989) other than the Corytophanidae mentioned above. On this basis the possible affinities of *Polrussia* are limited to the Opluridae,

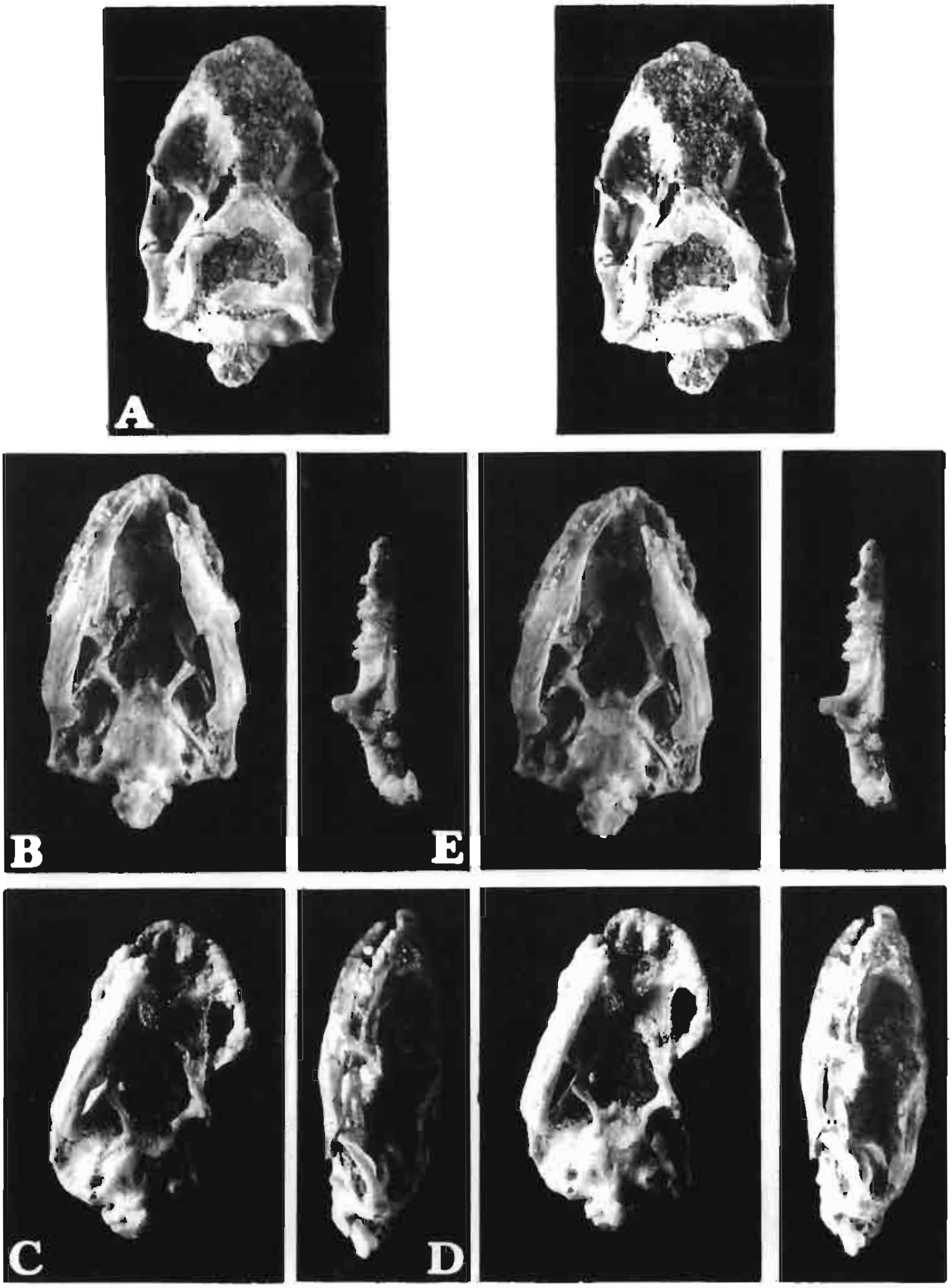

Fig. 2. *Igua minuta* gen. et sp. n. Holotype ZPAL MgR-I/60, Khulsan, Gobi Desert, ?middle Campanian. ❑A, B, D. Skull with both mandibles. ❑C. Skull with left mandible removed. Dorsal (A), ventral (B, C), and left side (D) views. ❑E. Left mandible, lingual view. All stereophotographs × 3.

non-anole Polychridae and two subfamilies of the Tropiduridae (Tropidurinae and Leiocephalinae), all of them presently Gondwanan in distribution, oplurids endemic to Malagasy region (Frost & Ehteridge 1989). *Igua* recalls the tropidurids as far as its fragmentary state of preservation allows.

The exact affiliation of the Cretaceous and Paleogene 'iguanids' known from America and Europe has also been difficult. *Pristiguana brasiliensis* from the Late Cretaceous of Brasil (Estes & Price 1973) and *Paradipsosaurus mexicanus* (Fries *et al.* 1955) from the Eocene or Oligocene of Mexico display a hoplocercid level of mandible structure (open Meckelian canal and long splenial), but according to Estes (1983a) may not be definitely assigned to the morunasaurines (to the Hoplocercidae *sensu* Frost & Etheridge 1989). *Aciprion formosum* from the Oligocene of United States and its possible relative (according to Estes *et al.* 1983a) *Geiseltaliellus longicaudus* from the Middle Eocene of Germany (Kuhn 1944, Haubold 1977) were presumed to be related to the Corytophanidae (Estes 1983a: 25). Other than those, the 'iguanid' remains from the Paleogene of America have been referred to as Iguanidae *incertae sedis* (Estes 1983a) and provide no comparative data.

Biogeographic interpretation

Two 'iguanid' lizards from the Late Cretaceous of Mongolia described herein affect our view of the Mesozoic zoogeography. Up to now, only the priscagamines (Borsuk-Białynicka & Moody 1984, Alifanov 1989), recognized as primitive acrodontans, represented the Iguania in the lizard Cretaceous fauna of Asia. Presently, this fauna has been supplemented by new genera representing another stem, or stems, of primitive iguanians. The existence of a whole spectrum of closely related genera exclusively on a certain territory, Central Asia in the present case, tends to indicate their autochtony. The early radiation of the Iguania in Asia is thus suggested. Presence of the iguanians in the Asiatic faunas more ancient than the Campanian presently studied by Russian authors (Nessov 1985, 1988, Alifanov in preparation) would endorse this hypothesis, but such remains are quite scarce (the oldest known priscagamines reported by Nesov 1988 from the Coniacian of Central Asia). The Asiatic radiation of one iguanian group does not mean the Asiatic origin of the infraorder, the more so that the 'iguanids' are also known from the South America at the equally early date (*Pristiguana* Estes & Price 1973 from the Late Cretaceous of Brasil), followed by a differentiated Late Paleocene 'iguanid' fauna (Estes 1970, 1983a). Suggested by the above evidence, the existence of two centers of iguanian radiation at the end of the Cretaceous, in Asia and in the South America, implies an earlier divergence of the Iguania from some other place of origin. The North American origin seems best founded in view of the position of this continent between two most ancient areas of distribution of this group of lizards. The directions of dispersal would be (1) from North

America to Asia by a possible Bering route, probably prior to the Late Cretaceous; (2) from North America to South America by a Central American route (across a land bridge or a series of islands) about the same time, and (3) from North America to Europe in the Paleogene by the North Atlantic route.

The Gondwanan provenience of the Malagasy fauna, the oplurids included, has usually been considered as most probable. In contrast to this view, Rage (1988b) suggested the Laurasian origin of this fauna via a terrestrial route: Eurasia, India to Madagascar at about the Cretaceous Paleocene boundary. The Cretaceous 'iguanids' of Asia provide a good fundation for the latter supposition. A possibility of the oplurid relationships of *Polrussia* (see p. 340) gives an interesting perspective to a future inquiry about this problem.

Descriptions

Order Squamata Merrem 1820
Infraorder Iguania Cuvier 1807
Family uncertain
Genus *Igua* nov.
Type species: *Igua minuta* sp. n.
Stratigraphic and geographic range: Genus is monotypic, known only from the type horizon and locality.

Diagnosis.– A small non-acrodontan iguanian lizard with a *Tropidurus*-like but more flattened skull. Palatines very large, restricting suborbital fenestra. Interpalatine contact present. Long quadrate. Superficial outlines of the osseous labyrinth distinct. Splenial extending far anterior towards the midpoint of the tooth row. Angular present.Teeth tricuspid. Number of mandibular teeth and/or tooth positions about 13.

Igua minuta gen. et sp. n.
Figs 1, 2, 3A, 4A.
Holotype: ZPAL MgR-I/60
Type horizon: Barun Goyot Formation, Late Cretaceous (?middle Campanian).
Type locality: Khulsan, Nemegt Basin of the Gobi Desert, Mongolia.

Diagnosis.– As for the genus.

Material.– The unique specimen is a damaged skull with associated mandibles of a possibly juvenile individual.

Measurements.– Total skull length about 14 mm. For remaining measurements see Table 1. According to Etheridge (personal communication) tropidurid lizards with skull length 14 mm have a snout-vent length of 55-65 mm.

Description.– The frontal is unpaired and strongly constricted between the large orbits. A thin furrow parallels each of the orbital margins of the frontal. The parietal is subrectangular, with its length being slightly more than half of the width. The supratemporal processes, almost 0.9 times the length of the parietal body, are only slightly divergent and bend posteroventrally. They are subtriangular in transverse section, two walls facing obliquely dorsolaterally and dorsomedially, while the third one is ventral. The dorsolateral wall passes into the lateral wall of the parietal table. The dorsomedial wall passes into the oblique posterior bone lamina of the parietal that bridges the occipito-parietal gap. The anterior border of what was certainly a large, circular parietal foramen is situated on the frontoparietal suture, and is confluent with the large parietal fontanelle. The parietal slightly overlaps the frontal laterally. The postfrontal, postorbital and squamosal are missing from the type specimen. The left posterolateral border of the frontal bears a slit-like articular surface for a bone constituting the postorbital bar. Both anterolateral corners of the parietal are damaged and lack traces of articulation with any bone.

Only the orbital lamina of the prefrontal is preserved, and forms the lateral boundary of the orbitonasal fenestra. Both maxillae are extensively damaged. The posterior process of the maxilla, very low and acute, extends under more than half of the orbital length.

Palate. The vomers are rather short, wide and ventrally convex as a whole. They contribute to a longitudinal concavity that results from the oblique position of the palatines and pterygoids. The palatines are large blades broadly sutured with the vomers, contacting each other in the midline and restricting the suborbital fenestra. The choanal fossa is small and shallow. The maxillary process of the palatine is rather long. The pterygoid has an extensive triangular palatine process that touches its mate in the midline anteriorly. The pterygopalatine suture is oblique. The quadrate process is thin but rather deep. It bears a rounded fossette for the epipterygoid on its dorsal side. The epipterygoid is missing from the specimen. The L-shaped ectopterygoid overlaps the ectopterygoid process of the pterygoid with its longer stem, while extending parallel to the maxilla with the shorter one. The suborbital fenestra is long and oval. The ectopterygoid-palatine contact was probably present, but only dorsally. Ventrally, the maxilla contributes to the border of the fenestra. As a whole, the palate is bent in such a way that the plane of the vomers is parallel to that of the pterygoids, but lies at a different level, whereas the main body of the palatine ascends anterodorsomedially.

Quadrate. The length of the quadrate is about equal to the total length of the parietal. The shaft is slightly arched. It is situated very oblique in what is probably a slightly protracted position of the jaws preserved in the holotype (as judged by the position of the pterygoid relative to the basipterygoid processes). The proximal head is incised for the supratemporal. The distal extremity has the lateral condyle more distally protruding. The tympanic crest is broken off.

Braincase. The braincase bones are well preserved and delimited by unfused sutures. The base of the braincase is strongly convex in a sagittal

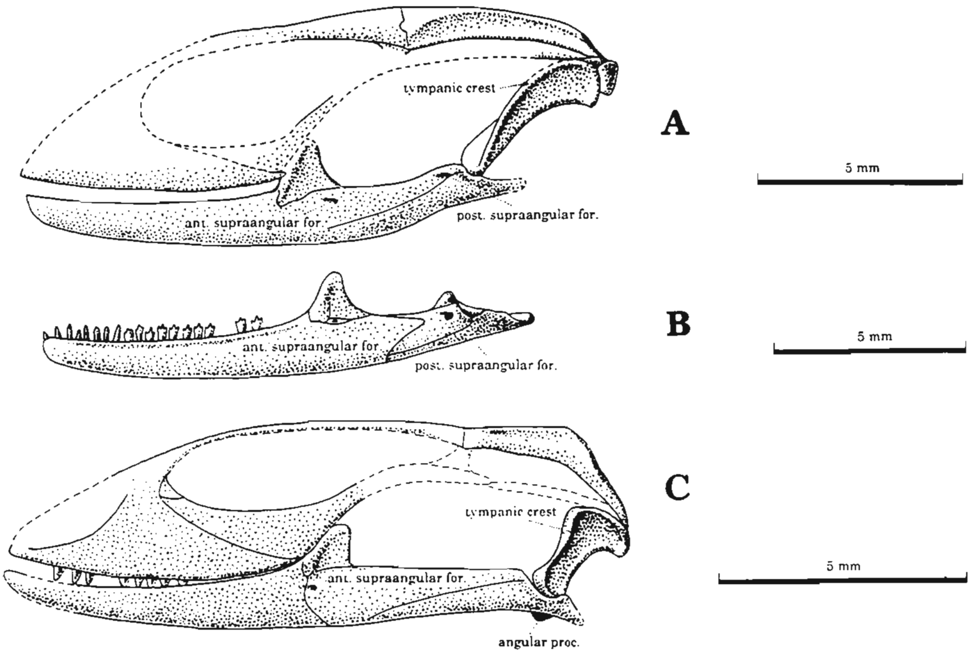

Fig. 3. Reconstructed skulls with mandibles of ❑A. *Igua minuta* gen. et sp. n. ❑C. *Polrussia mongoliensis* gen. et sp. n. in left side view. ❑B. Mandible of *Tropidurus etheridgei*, ZPAL zp.RI/46, in left side view.

section. The ventrolateral crests occur only at the very bases of the basipterygoid processes. The basipterygoid processes have long slender stalks extending anterolaterally. The sphenoccipital suture is sinuous, anteriorly concave in the midline, and the sphenoccipital tubercles are feeble. The posterior ventral surface of the basioccipital gradually turns to face more posteriorly, forming surfaces that are separated from each other by the triangular, tripartite occipital condyle.

The outlines of the posterior semicircular canal is prominent on the occipital skull surface. The external surface of the braincase is concave between the three semicircular canals. The alar process of the prootic is absent. The large jugular fossae bordered by sharp prootic crests extend subhorizontally.

Mandible. The ventral profile of the mandible is only slightly convex and the shaft is only slightly concave medially. The labial wall of the dentary is strongly damaged and particularly so at its ventral border. Preserved for about 1/3 the length of the tooth row, the natural border of the medial dentary wall indicates that the Meckelian canal was open and faced ventrally in this section of the mandible. The tooth bearing border descends extremely low ventrally.

The outline of the splenial may be reconstructed on the both strongly damaged mandibles. The bone probably reached the level of about the sixth tooth position from the posterior end of the tooth row and extended up to the posterior process of the coronoid. The course of its suture with the angular is unknown.

The angular wraps around the ventral border of the mandible to extend on its lateral surface almost up to the level of the mandibular joint. Its anterior part is not preserved.

The lateral process of the coronoid is tiny. It interdigitates with the coronoid process of the dentary. The surface for the mandibular adductor is delimited by a thick posterolateral and a thin posteromedial border of the coronoid. The adductor crest extends from the mandibular joint towards the mid-height of the shaft. Bordered by this crest the surface for the pterygomandibularis muscle faces ventrally but no furrow for this muscle is developed. The retroarticular process is broken off. Its preserved part is bent medially with respect to the mandibular ramus and suggests a presence of the angular process (Figs 2E, 4A). The anterior and posterior supraangular foramina are preserved on the supraangular. The postcoronoid ramus of the mandible is rather narrow in transverse section but situated obliquely in life position. The mandibular fossa is slit-like.

Dentition. Preserved in the mandibles, the teeth are pleurodont, tricuspid in shape, each of them with a large apical cusp and smaller anterior and posterior cusps. The teeth have more or less parallel sides, slightly converging towards the tooth bases. The teeth are rounded in transverse section except for apical parts bilaterally flattened. The number of teeth and tooth positions is 12 or 13 in the mandible and is estimated as about the same in the maxilla. There are no palatal teeth.

Cervical vertebra. Preserved are the following elements of the cervical vertebral column: the first intercentrum articulated with the occipital condyle; the right half of the first neural arch not fused with the intercentrum; the second intercentrum articulated with the first one and joined to the centrum of the epistropheus by a distinct suture.

Remarks.– A possibility that the type of *Igua minuta* is a juvenile is indicated by unfused sutures of the braincase, very large fontanelle, nearly rectangular parietal roof and the very small size of the specimen. *Igua minuta* differs from *Polrussia mongoliensis* in skull and mandible proportions, palate structure and teeth morphology. The differences are considered generic at least. The snout is more rounded in outline than in *Polrussia*. The teeth are tricuspid in *Igua minuta*, while being unicuspid and pointed in *Polrussia mongoliensis*. The palatines are much larger in *Igua*, the suborbital fenestra narrower and the anterior angle of the pyriform recess less acute than in *Polrussia*. The quadrate relatively longer than in the latter genus. The mandible is more stout with a proportionately longer precoronoid and proportionately shorter postcoronoid section in *Igua* than in *Polrussia*.

Igua minuta differs from two Paleogene North American 'iguanids', *Paradipsosaurus mexicanus* and *Parasauromalus olseni*, primarily in frontal and parietal proportions tooth structure, and from *Aciprion formosum*,

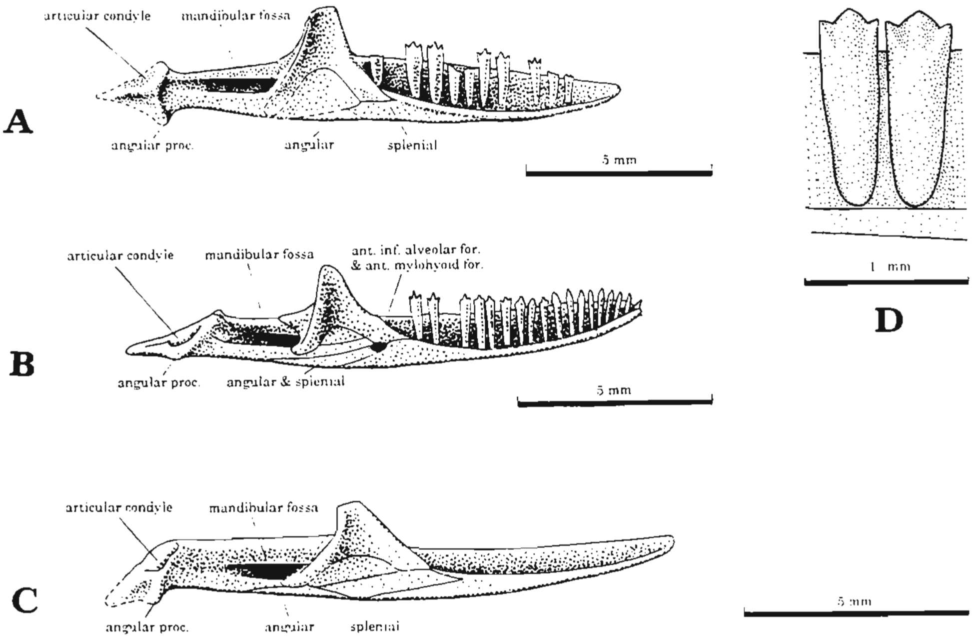

Fig. 4. Reconstructed mandibles of □A. *Igua minuta* gen. et sp. n. and □C. *Polrussia mongoliensis* gen. et sp. n. □B. Mandible of *Tropidurus etheridgei* ZPAL zp.R I/46. All in lingual view. □D. Lower teeth of *Igua minuta* gen. et sp. n.

the third adequately known Paleogene 'iguanid', in a very large plate-like parietal (which may be a juvenile character). It lacks a sagittal parietal crest of the corytophanid type and any suggestion of its development later in ontogeny. In contrast such crest has been known from the Eocene European *Geiseltaliellus*, and probably present in an unpublished specimen of *Aciprion* (Estes 1983a). *Igua minuta* is smaller than any of these four lizards.

In overall skull habitus, *Igua* recalls very much representatives of the genera *Tropidurus* and *Liolaemus*. Particular similarities occur between *Igua minuta* and *Tropidurus etheridgei* in frontal and parietal proportions, size and directions of the posttemporal processes, presence of parietal fontanelle and brain-case details such as a degree of ventral convexity, course of sphenoccipital suture, size and orientation of sphenoccipital tubera, occipital recesses and jugular fossae, prominence of superficial outlines of the osseous labyrinth. At least some of these characters may be size and/or individual age dependent and are thus not used as cases for relationships of *Igua* with the Tropiduridae. More significant may be similarities of mandible construction between *Igua* and Tropiduridae or at least some of them (*Tropidurus*, *Liolaemus*), and particularly the same, very low ventral reach of the tooth crowns on the lingual side of the mandible (Figs 4A, B). The lateral coronoid process is similar to that of the

Table 1
Character state matrix for some of the Late Cretaceous Paleogene and extant iguanids *sensu lato.*

Specimens	**Frontal** length	**Frontal** posterior width to length	**Frontal** minimum to posterior width	**Maxilla** position*	**Mandible** length**	**Mandible** length to maximum depth	**Mandible** tooth count
ZPALMgR-I/60 *Igua minuta*	6.2	0.82	0.20	0.53	**11.0**	6.40	12
ZPALMgR-I/119 *Polrussia mongoliensis*	4.8	1.00	0.19	0.35	**10.0**	9.00	18
ZPALMgR-I/32 *Priscagama gobiensis*	**10.0**	0.95	0.27	0.87	**24.0**	6.10	**16**
ZPAL zpR-I/40 *Liolaemus tenuis*	**7.6**	0.86	0.30	0.64	**14.0**	5.60	**18**
ZPAL zpR-I/45 *Liolaemus poecillochromus*	**4.3**	1.20	0.20	0.60	**12.0**	6.00	**19**
ZPAL zpR-I/46 *Tropidurus etheridgei*	**4.5**	0.90	0.25	0.40	**11.0**	9.10	**21**
Estes 1983a: Fig. 7D	E *Paradipsosaurus mexicanus*	11.0	1.00	0.42	0.50	29.5	7.90
Estes 1983a: Fig. 5D *Aciprion formosum*	10.0	0.86	0.35	0.36	23.5	8.00	23-25
Estes 1983a: Fig. 7A	B *Parasauromalus olseni*	20.0	1.20	0.38	0.30	53.0	6.70

* length of maxilla part underlying orbit to orbit length
** up to articulation
All measurements in milimeteers, estimated from badly preserved specimens or from figures, except for those notified by bold numerals.

Tropidurinae and Leiocephalinae while differing from a large process of the Liolaeminae. On the other side, the presence of a large angular (reduced angular being synapomorphic for the Tropiduridae according to Frost & Etheridghe 1989), the broad, plate-like palatines and much narrowed suborbital fenestra, the very long quadrate, more lateral direction of basipterygoid processes and very flat instead of convex parietal discriminate *Igua* from the Tropiduridae.

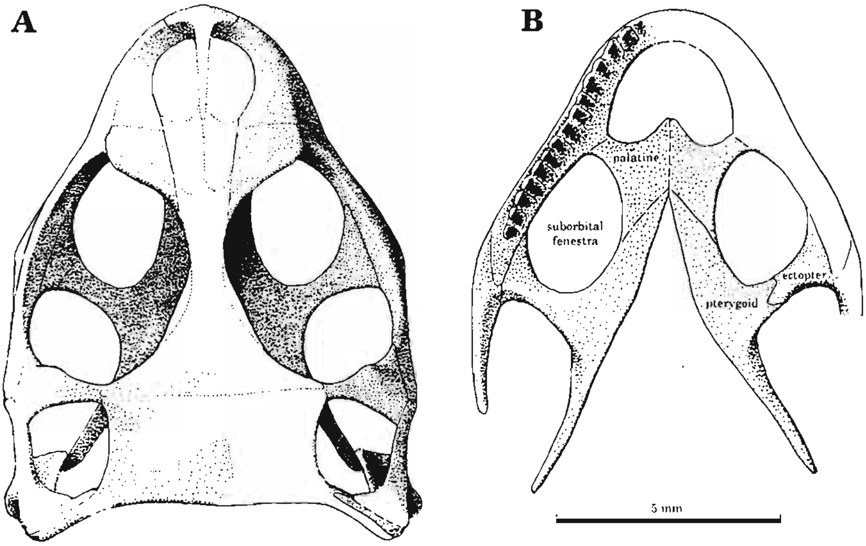

Fig. 5. Reconstruction of skull of *Polrussia mongoliensis* gen. et sp. n. ❑A. Dorsal view. ❑B. Ventral view.

Genus *Polrussia* nov.

Type species: *Polrussia mongoliensis* sp. n.

Etymology: Description of the genus results from the cooperation of Russian and Polish collegues.

Stratigraphic and geographic range: Genus is monotypic, known from the type horizon and locality.

Diagnosis.– A small non-acrodont iguanian lizard with a flat snout, very narrow frontal, parietal wider than long with almost no mid-length constriction. Postfrontal lost. Palatines and pterygoids slender. Suborbital fenestra large and oval. Lateral coronoid process rudimentary. Dentary not exceeding the level of anterior suprangular foramen. Dental tube fused. Teeth unicuspid. About 15-16 maxillary, 5 premaxillary and about 18 dentary teeth and tooth positions.

Polrussia mongoliensis gen. et sp. n.

Figs 3C, 4C, 5, 6.

Holotype: ZPAL MgR-I/119

Type horizon: Barun Goyot Formation, Late Cretaceous (?middle Campanian).

Type locality: Khulsan, Nemegt Basin of the Gobi Desert, Mongolia.

Diagnosis.– As for the genus.

Material.– The unique specimen is a damaged skull with mandibles.

Measurements.– Total skull length about 12 mm. For remaining measurements see Table 1.

Description.– The body and the preserved, ventral part of the nasal process of the premaxilla are unpaired.

The frontal is a single, hourglass-shaped bone (see Table 1), as estimated from the mould. Anteriorly, the bone extends to about 2/5 the length of the prefrontal in the midline and laterally, while being notched in between on both sides of the midline. The fragments of bone contacting the anterior 3/5 of the prefrontal probably belong to the nasal. The latter would be extremely narrow, if this strip of bone represented the maxilla-frontal bridge, which is, therefore considered absent. However, the exact outlines of bones in that region remain unknown. Judging from the natural cast the frontal had shallow subolfactory processes, that did not contribute to border of the orbitonasal fenestra.

The exact outline of the parietal is not visible. The length of this bone is slightly more than a half of the width. The region of the frontoparietal suture is missing and the position and state of the parietal foramen are unknown.

The maxilla is a low triangle supplemented by a nasal process facing dorsally and slightly anteriorly and overlapping the anterior part of the prefrontal. The long posterior process of the maxilla underlies the anterior 0.4 of the orbit length, and the tooth row only 0.1 of this length. This process is overlapped by a huge jugal and anteriorly by a lacrimal (see Fig. 3C). The posterior ramus of the jugal ascends at an angle of only about 45 to the tooth row, while changing to horizontal at the end and almost touching the squamosal. Its contact with the postorbital is long. The prefrontals protrude laterally, almost overhanging the vertical lamina of the maxilla, producing the so-called prefrontal bosses (Estes *et al.* 1988). No trace of a postfrontal occurs at the posterolateral corner of the frontal, which suggests a loss of this bone. The postorbital is a huge triangular bone, transversally expanded and provided with a postorbital boss on its anterior margin. The posterior part of the crescent-shaped squamosal is poorly preserved; the anterior part has a short contact with the postorbital and almost touches the jugal. The quadrate length is equal to about the mid-length of the parietal. The state of preservation of this bone does not permit detailed description.

Palate. Preserved on the left side, the palatine process of the pterygoid and a fragment of the palatine extend in the same plane inclined dorsomedially to produce a midline concavity. The pterygopalatine suture is strongly oblique, the pterygoid extending far anterior on the midline. Its long flat blade is separated from its mate by a triangular pyriform fenestra that probably extends up to its anteriormost tip. An interpalatine contact is probable, judging from the position of the right bone. The ectopterygoid does not completely exclude the maxilla from the border of the suborbital fenestra, but it produces a long anterior process to be seen in dorsal aspect of the skull.

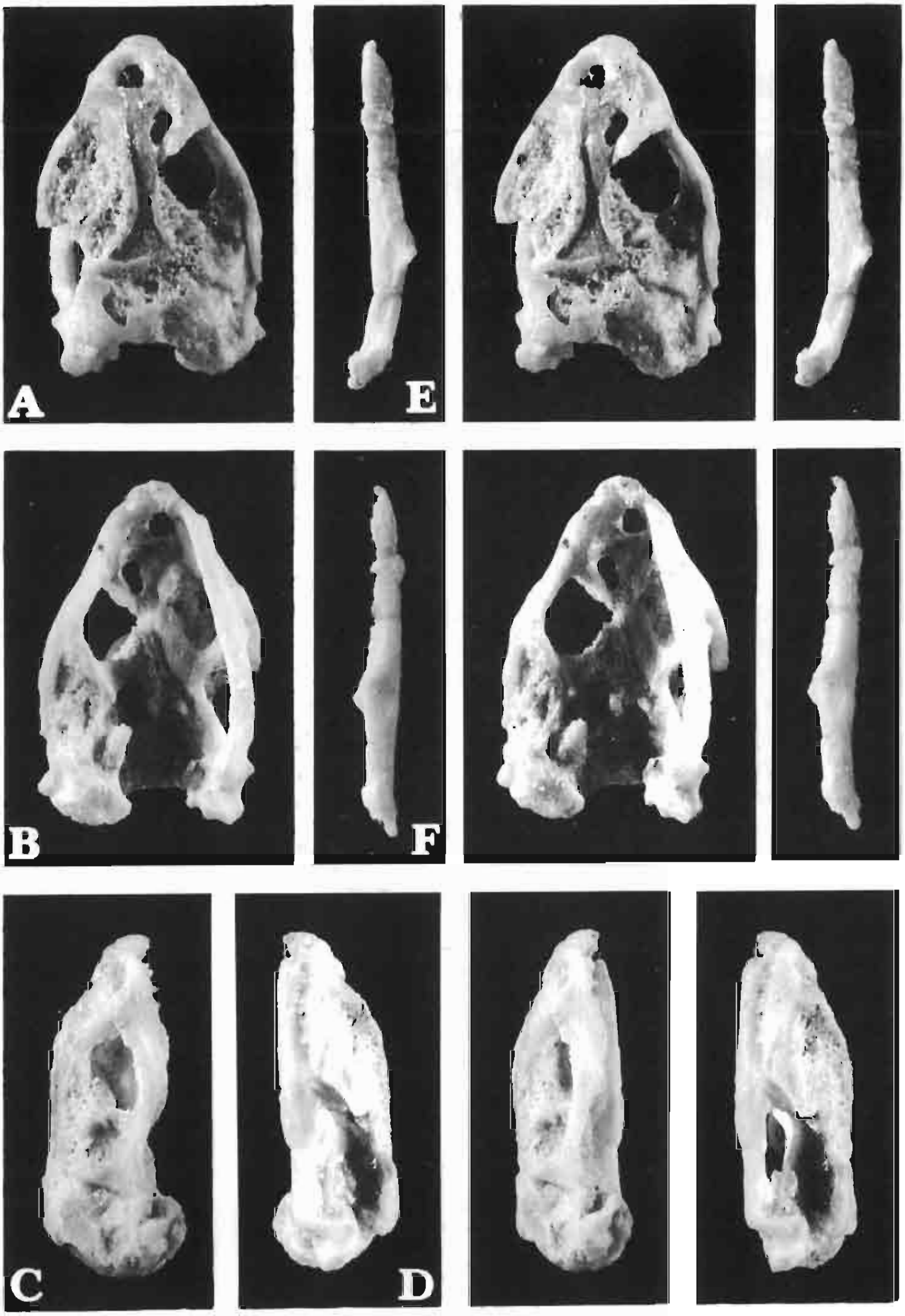

Fig. 6. *Polrussia mongoliensis* gen et sp. n. Holotype ZPAL MgR-I/119, Khulsan, Gobi Desert, ?middle Campanian. Skull with left mandible. □A. Dorsal view. □B. Ventral view. Right mandible. □E. Lingual-occlusal view. □F. Labial view skull with right mandible removed. □C. Right side view. □D. Left side view. All stereophotographs × 4.

Mandible. The ventral profile of the mandible is almost straight and the shaft is strongly madially concave. The posterior extent of the dentary does not exceed the anterior part of the coronoid and its posterior suture is vertical and only slightly posteriorly concave. The splenial is reduced. Anteriorly it reaches to approximately the level of the third or fourth tooth position from the end of the tooth row. Anterior to this point, the dentary is fused into a tube without leaving any trace of suture. Posteriorly, the splenial extends almost to the posterior ramus of the coronoid, but does not reach it. The anterior extent of the angular is up to about the level of the coronoid apex. Anteromedial of the retroarticular process there is a bone projection interpreted as a base of the angular process (Fig. 4C) The coronoid is produced high above the dorsal profile of the ramus.The postcoronoid ramus is not very much expanded laterally, but the adductor crest is distinct. The mandibular fossa is slit-like.

Dentition. The number of tooth positions is estimated as 5 in the premaxilla and about 18 in the dentary. Up to 16 teeth and tooth positions are present in the maxilla. The teeth are unicuspid, columnar in shape and pointed at the top (as shown by the undamaged left jaws in occlusion), rounded in transverse section and closely spaced. They protrude high above the parapet of the jaw. The type of implantation is pleurodont. No palatal teeth are preserved.

Remarks.– *Polrussia mongoliensis* differs considerably from *Igua minuta* with respect to characters regarded as generic. In *Polrussia* the maxilla is situated less posterior with respect to the anterior orbital border, the palatine is much narrower and the suborbital fenestra larger than in *Igua*. The mandible is more slender in *Polrussia* and it has a precoronoid section proportionately shorter and a postcoronoid section proportionately longer than in the second genus (see Table 1). The snout is more pointed, the anterior angle of the pyriform recess more acute and the quadrate relatively shorter in *Polrussia* than in *Igua*.

The unicuspid teeth of *Polrussia mongoliensis* are more columnar and pointed than the distally dilated teeth of the Paleogene North American lizard *Paradipsosaurus mexicanus*. They also differ from the tricuspid teeth occurring in *Igua minuta*, *Pristiguana brasiliensis* and in all the Paleogene 'iguanids', in which the teeth structure is known.

According to Etheridge & de Queiroz (1988), the uniformly unicuspid, non-acrodont teeth are known in only a few members of the family Phrynosomatidae within the living Iguania. But, the fusion of the Meckel's groove excludes *Polrussia* from this family as well as from the Hoplocercidae and Crotaphytidae. The membership of *Polrussia* in the Iguanidae, the anole group of Polychridae and Liolaeminae of the Tropiduridae is also excluded on the basis of the tiny size of the lateral coronoid process contrasting with a derived large process of these taxa (Frost & Etheridge 1989). On the basis of the present knowledge the Opluridae, non-anole Polychridae, Tropidurinae and Leiocephalinae may not be excluded as possible relatives of *Polrussia*.

Polrussia mongoliensis is the smallest of the known Cretaceous and Paleogene 'iguanids'. It also differs from all the 'iguanids' by its small posterior extent of the dentary.

Acknowledgments

We are greatly indebted to the late Professor Richard Estes, San Diego State University, who reviewed the first draft of this paper. His comments and those of his student David Hauser were of great use for us. Thanks are also due to Professor Richard Etheridge, San Diego State University, who reviewed a final version of the manuscript and provided us with many additonal informations concerning the living 'iguanids'. Shaded drawings have been prepared by Mrs E. Gutkowska (partly by the junior author), and photographs by Mr M. Dziewiński, both from the staff of the Institute of Paleobiologic of the Polish Academy of Sciences.

References

Alifanov, V.R. (.Алифанов, В.Р.) 1989. Новые прискагамы (Lacertilia) из верхнего мела Монголии и их положение в системе Iguania. *Палеонтологический Журнал* **4**, 73-87.

Augé, M. 1987. Confirmation de la presence d'Iguanidae (Reptilia, Lacertilia) dans l'Éocène européen. *Comptes Rendues de l'Academie de Sciences Paris Palèontologie* **305**, 633-636.

Borsuk-Białynicka, M. 1990. *Gobekko cretacicus* gen. et sp. n., a new gekkonid lizard from the Cretaceous of the Gobi Desert. *Acta Palaeontologica Polonica*, **35**, 67-76.

Borsuk-Białynicka, M. & Moody, S.M. 1984. Priscagaminae, a new subfamily of the Agamidae (Sauria) from the late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* **29**, 51-81.

Estes, R. 1970. Origin of the Recent North American lower vertebrate fauna: an inquiry into the fossil record. *Forma and Functio* **3**, 139-163.

Estes, R. 1983a. Sauria terrestria, Amphisbaenia. In: P. Wellnhofer (ed.) *Handbuch der Palaeoherpetologie* **10A**, 1-249. Gustav Fisher Verlag, Stuttgart.

Estes, R. 1983b. The fossil record and early distribution of lizards. In: A.G.J. Rhodin & K. Miyata (eds) *Advances in herpetology and evolutionary biology*, 365-398. Museum of Comparative Zoology of the Harvard University.

Estes, R., de Queiroz, K., & Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: R. Estes & G. Pregill (eds), *Phylogenetic relationships within lizard families*, 119-281. Stanford University Press, Stanford, California.

Estes, R. & Price, L. 1973. Iguanid lizard from the Upper Cretaceous of Brasil. *Science* **180**, 748-751.

Etheridge, R. & de Queiroz, K. 1988. A phylogeny of Iguanidae. In: R. Estes & G. Pregill (eds), *Phylogenetic relationships within lizard families*, 283-368. Stanford University Press, Stanford, California.

Frost, D.R. & Etheridge, R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Miscelaneous Publication of the University of Kansas Museum of Natural History* **81**, 1-62.

Fries, C., Hibbard, C., & Dunkle, D. 1955. Early Cenozoic vertebrates in the red conglomerate at Guanajuato, Mexico. *Smithsonian Miscelaneous Collection* **123**, 1-25.

Gilmore, C. W. 1928. The fossil lizards of North America. *Memoires of National Academy of Sciences* **22**, 1-197.

Gilmore, C.W. 1943. Fossil lizards of Mongolia. *Bulletin of the American Museum of Natural History* **81**, 361-384.

Gradziński, R. & Jerzykiewicz, T. 1978. Additional geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. *Palaeontologia Polonica* **27**, 17-32.

Gradziński, R., Kaźmierczak, J., & Lefeld, J. 1969. Geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. *Palaeontologia Polonica* **19**, 33-82.

Gradziński, R., Kielan-Jaworowska, Z., & Maryańska, T. 1977. Upper Cretaceous Djadochta, Barun Goyot and Nemegt Formations of Mongolia, including remarks on previous subdivisions. *Acta Geologica Polonica* **27**, 281-318.

Haubold, H. 1979. Zur Kenntnis der Sauria (Lacertilia) aus dem Eozän des Geiseltales. In: H. Matthes & B. Thaler (eds) *Eozäne Wirbeltiere des Geiseltales. Wissenschafliche Beitrage der Martin-Luther Universität Halle* **1977**/2 (P5) 107-112.

Hoffstetter, R. 1942. Sur les restes de Sauria du Nummulitique européen rapportes a la famille Iguanidae. *Bulletin du Muséum de l'Histoire Naturelle Paris* **14**, 233-240.

Hou, L. 1974. Paleocene Lizards from Anhui, China. *Vertebrata Palasiatica* **14**, 48-52.

Kuhn, O. 1944. Weitere Lacertilier, insbesondere Iguaniden aus dem Eozän des Geiseltales. *Paläontologische Zeitschrift* **23**, 360-366.

Nessov, L.A. (Нессов, Л.А.) 1985. Редкие костные рыбы, наземные ящерицы и млекопитающе зоны лиманов и приморских низменностей мела Кызылкумов. *Ежегодник Всесоюзного Палеонтологического Общества* **28**, 199-219.

Nessov, L.A. 1988. Late Mesosoic amphibians and lizards of Soviet Middle Asia. *Acta Zoologica Cracoviensia* **31**, 475-486.

Rage, J.C. 1988a. Histoire Paléobiogoégraphique des vertébres terrestres depuis la fin de Paléozoique, principeaux événements. *Comptes Rendues de la Societé Biogéographique* **64**, 3-17.

Rage, J.C. 1988b. Gondwana, Thethys and terrestrial vertebrates during the Mesozoic and Cenozoic. In: M.G. Audley Charles & A. Hallam (eds) *Gondwana and Thethys. Geological Society Special Publications* **37**, 255-273.

Sullivan, R. 1982. Fossil lizards from Swain Quarry, 'Fort Union Formation', Middle Paleocene (Torrejonian), Carbon County, Wyoming. *Journal of Paleontology* **56**, 996-1010.

Streszczenie

Na podstawie górnokredowych materiałów zebranych przez polsko-mongolskie ekspedycje na pustynię Gobi w latach 1964-1971 opisano pierwsze azjatyckie "iguanidy", *Igua minuta* gen. et sp. n. i *Polrussia mongoliensis* gen. et sp. n. Materiały pochodzą ze ?środkowokampańskiej formacji Barun Gojot ze stanowiska Chulsan. Nazwa "iguanidy" odpowiada tradycyjnie rozumianej rodzinie Iguanidae. "Iguanidy" znane są współcześnie z Ameryki, Madagaskaru i płd. Mikronezji. Na podstawie takiego rozprzestrzenienia i pochodzenia najstarszych dotąd znanych legwanów z górnej kredy Brazylii Iguania uważane były za grupę pochodzenia gondwańskiego.

Na podstawie materiałów mongolskich bardziej prawdopodobne wydaje się powstanie tej grupy jaszczurek w Ameryce Pn. i jej następne rozprzestrzenienie się na sąsiednie kontynenty: Amerykę Płd. i Azję w górnej kredzie oraz Europę w paleogenie.

Opisane jaszczurki przypominają niektóre Tropiduridae a *Polrussia* również nieanolidowe Polychridae i Opluridae, jednak do żadnej z tych grup zaliczyć ich nie można.