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NEW DATA ON THE GENUS ADAMISAURUS SULIMSKI 1972 (SAURIA) FROM THE UPPER CRETACEOUS OF MONGOLIA

(plates 12-14)

Abstract. — Osteological description and revision of the genus and species diagnoses of the Upper Cretaceous lizard Adamisaurus magnidentatus Sulimski 1972 from three localities of Mongolia: Bayn Dzak (Djadokhta Formation, ?upper Santonian and/or ?lower Campanian), Khulsan (Barun Goyot Formation, ?middle Campanian), and Khermeen Tsav II (red beds of Khermeen Tsav, ?middle Campanian) are given. More complete new material indicates that the previous assignment of Adamisaurus to the family Agamidae is not justified. On the basis of pseudoacrodont tooth implantation, presence of resorptional pits, aberrant iguanid mode of tooth replacement, structure of the temporal and palatal regions, and roofing bones, Adamisaurus is put into a new monotypic family Adamisauridae within infraorder Scincomorpha CAMP 1923.

INTRODUCTION

The first description of Adamisaurus (see SULIMSKI 1972) was based on two specimens -ZPAL MgR-II/80 (holotype) and ZPAL MgR-II/49 from the sandstones of the Djadokhta Formation at Bayn Dzak on the Gobi Desert. Preliminary studies suggested a relationship with agamid lizards, but new material indicates a different systematic position of Adamisaurus. A new collection of lizards has been assembled by members of the Polish-Mongolian Expeditions in 1970 and 1971 (see KIELAN-JAWOROWSKA and BARSBOLD 1972) from the sandstones of the Djadokhta Formation, as well as from sandstones of the younger Barun Goyot Formation and its stratigraphic equivalent called red beds of Khermeen Tsav (see GRADZIŃSKI et al. 1977) referred to by KIELAN-JAWOROWSKA 1975 a as Khermeen Tsav formation). The sediments of the Djadokhta Formation crop out at the locality of Bayn Dzak on the Gobi Desert (LEFELD 1965, 1971), those of the Barun Goyot Formation in the Nemegt Basin, and the red beds of Khermeen Tsav at the localities of Khermeen Tsav I and Khermeen Tsav II, situated some 40 km southwards from the southwestern end of the Nemegt Basin (GRADZIŃSKI and JERZYKIEWICZ 1974). The age of the Djadokhta Formation has been estimated as ?upper Santonian and/or ?lower Campanian, and the age of the Barun Goyot Formation (and red beds of Khermeen Tsav) as ?middle Campanian (GRADZIŃSKI et al. 1977).

In the collection of lizards assembled during the 1970 and 1971 expeditions there are new specimens of *Adamisaurus magnidentatus*. The new material described herein shows that the stratigraphic range of this species is greater than previously believed, as it occurs also in the

sandstones of the Barun Goyot Formation and in red beds of Khermeen Tsav. A. magnidentatus is only the second vertebrate species, among all the fossils so far described from the formations discussed herein, which is common to the Djadokhta Fm. Barun Goyot Fm, and red beds of Khermeen Tsav¹).

The new material of *Adamisaurus* is more complete and provides new information on the cranial and postcranial anatomy of the genus. It can now be demonstrated that the previous assignment of *Adamisaurus* to the family Agamidae (see SULIMSKI 1972) is not justified. A new monotypic family Adamisauridae, assigned to infraorder Scincomorpha CAMP 1923, is now erected for this species.

The specimens described in the present paper are housed in the Institute of Paleobiology of the Polish Academy of the Sciences in Warsaw (Zakład Paleobiologii).

All figures in the text are prepared by the author. Anatomical abbreviations used in the text are given in figs 1-3.

Abbreviations used for institutions:

AMNH — American Museum of Natural History, New York.

ZPAL - Institut of Paleobiology of the Polish Academy of Sciences, Warsaw.

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DESCRIPTIONS

Order Squamata OPPEL 1811 Suborder Sauria MACCARTNEY 1802 Infraorder Scincomorpha CAMP 1923 Family Adamisauridae nov.

Type genus: Adamisaurus SULIMSKI 1972.

Diagnosis. — As for the genus. **Discussion.** — See p. 50.

Genus Adamisaurus SULIMSKI, 1972

Type species: Adamisaurus magnidentatus SULIMSKI 1972.

Revised diagnosis. — Premaxilla single with long dorsal process; nasals and frontals paired; postfrontal and postorbital separated; parietal foramen always in fronto-parietal suture; maxilla in contact with frontal; lacrimal reduced; lacrimal foramen single; tendency to the reduction of the supratemporal fossa; very large ectopterygoid with strong vertical posterior process; strong, vertically directed palato-coronoid process; very long anterior process of the pterygoid; vomero-pterygoid contact present; dentition pseudoacrodont in implantation; aberrant iguanid mode of tooth replacement; isodont teeth strongly increasing in size posteriorly; presence of resorptional pits; dentary with two-lobed postero-dorsal extremity.

Discussion. — See p. 50.

¹⁾ The first vertebrate species, known to occur in both the Djadokhta and Barun Goyot formations is *Deltatheridium* pretrituberculare, represented, however, in each formation by a different subspecies (see KIELAN-JAWOROWSKA 1975 b).

Adamisaurus magnidentatus SULIMSKI 1972

(pls 12-14; figs 1-3)

1972. Adamisaurus magnidentatus gen. n., sp. n.; SULIMSKI: 34-40, figs. 1-2, pl. 4.

Diagnosis. — As for the genus.

Stratigraphic and geographic range. — Known from the Djadokhta Formation (?upper Santonian and/or ?lower Campanian) at Bayn Dzak; Barun Goyot Formation (?middle Campanian) at Khulsan and Nemegt, and red beds of Khermeen Tsav (?middle Campanian) at Khermeen Tsav II; all from the Gobi Desert, Mongolian People's Republic.

Material. — See SULIMSKI 1972: 36 and moreover: Djadokhta Formation, Bayn Dzak, Main Field: ZPAL MgR-II/50 — anterior part of the left and right jaws and right maxillary fragment with teeth. - Barun Goyot Formation, Khulsan and Nemegt, Nemegt Basin: ZPAL MgR-I/13 — dorsoventrally compressed skull with upper and lower jaws with teeth, and bones of the cranial roof, associated with anterior cervical vertebrae, fragments of pectoral girdle and fragment of right hand. ZPAL MgR-J/35 - left lower jaw with 3 last cheek teeth. ZPAL MgR-1/42 — incomplete skull with nearly complete maxillary dentition. — Red beds of Khermeen Tsav, Khermeen Tsav II: ZPAL MgR-III/I — damaged skull with well preserved medial tooth rows in upper and lower jaws. ZPAL MgR-III/2 — fragment of right maxilla and lower jaw fragments with incomplete teeth. ZPAL MgR-III/3 - right maxilla with nearly complete dentition and fragment of jugal process. ZPAL MgR-III/4 — facial part of skull with tooth rows partly preserved. ZPAL MgR-III/5 — nearly complete skull with well preserved dentition on both sides and almost complete postcranial skeleton without distal part of the tail. ZPAL MgR-III/14 --- much destroyed rostral skull fragment. ZPAL MgR-III/23 --fragment of left maxilla with four teeth. ZPAL MgR-III/25 — dorsoventrally depressed skull with nearly complete dentrition. ZPAL MgR-III/26 — left maxilla with teeth and anterior part of left frontal and nasal bones, badly damaged. ZPAL MgR-III/27 --- rostral skull fragment with four last cheek teeth on both sides preserved.

Measurements. — See tables 1—3.

Description. — Skull (pls 12-14; figs. 1-3). In all specimens the skull is not very wide, rather elongated, massive, on the dorsal side tapering anteriorly. Jugal arches somewhat widened externally. On the lateral side skull is relatively high with facial part rounded. Premaxilla is always single with long dorsal process. This bone on the skull ZPAL MgR-II/50 is divided, due to the post mortem breaking of the skull (see fig. 2 D). External nares small, nearly terminal. Nasals small, rectangular, rather wide, their suture with frontals zigzagging. Frontals narrowed between orbits and widened posteriorly, not fused. The interorbital space is 2.2 to 2.5 mm. Frontals contact on a short distance the maxilla (pl. 14: 1b; fig. 1 B). Prefrontal relatively large, subtriangular, with long dorsal process. Parietal always single, wide and rather short with long posterior processes, without sagittal crest. The nuchal ridges are visible on posterior processes. Parietal foramen is always situated in the fronto-parietal suture, 0.8 mm in diameter approximately. Surfaces of roofing bones smooth. Maxilla anteriorly reaching the medial line of outer nares, dorsally contacts the nasal, prefrontal, lacrimal and frontal. Posteriorly maxilla broadly sutured with the jugal. Lacrimal splintlike, situated on the extreme ventral margin of the orbit, isolated or sometimes fused to prefrontal, and with one foramen. Jugal rather strong with relatively wide and strong posterior process, about 4 mm in length. Posterodorsal end of jugal bone not reaching the squamosal. Postfrontal with two medial processes (long frontal and short parietal) joined to postorbital bone with straight suture. Postorbital relatively long, widened, dorsoventrally depressed, articulates with squamosal and reaches the orbit anteriorly. Postorbital arch contains the postfrontal, anterior part of postorbital and posterodorsal end of jugal. Orbits rather large, directed more upwards than laterally. A fairly long, rather wide posteriorly

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ZPAL mus. cat. numbers	MgR-II/80	MgR-II/50	MgR-I/13	MgR-1/23	MgR-III/3	MgR-III/4	MgR-III/5
Skull Length	22.0		ca 18.0	ca 20.0			26.0
Height	10.5			8.0			12.0
Width across jugals	12.0	9.5		12.0	· _ · .		16.0
Length of maxilla	10.5	8.0	ca 10.0	9.0	13.5		14.0
Height of maxilla	5.2	4.6	ca 4.5	ca 5.0	7.0		7.0
Length of tooth row	8.2	6.0	7.0	ca 7.5	9.0	ca 7.0	7.0
Length of jugal process	3.8			4.0	4.0	· · · _	4.2
Lower jaw					i.		
Length	19.0	ca 16.0		ca 17.5	23.0	-	24.0
Length of	h.			a he was the s			
tooth row	8.5	6.2		8.2	8.5	7.8	8.0
Height of coronoid							8
process	6.5	5.0	7.0	ca 5.5	6.5	— ,	6.0

Table 1

Measurements of skull in Adamisaurus magnidentatus (in mm)

Table 2

Measurements of dentition in Adamisaurus magnidentatus (in mm)

ZPAL mus. cat. numbers		Length of tooth row	Height of M 1	Diameter of M 1	Height of M 8	Diameter of M 8	"Occlusal angle"
MgR-11/50	mx	6.0	0.5	0.4	1.3	1.2	8°
	d	6.2	0.4	0.3	1.3	1.3	9°
MgR-11/80	mx	8.2	0.7	0.5	1.6	1.5	7 °
	d	8.5	0.6	0.4	1.6	1.8	8°
MgR-I/13	mx	7.0	0.5	0.4	1.6	1.5	9°
	d			<u> </u>	_		· · · ·
MgR-I/42	mx	7.5	0.6	0.5	1.6	1.8	9 °
·	d	8.2	0.6	0.5	1.5	1.8	8°
MgR-III/3	mx	9.0	0.6	0.5	2.5	2.4	14°
	d	8.5	0.7	0.6	2.6	2.5	15°
MgR-III/4	mx	7.0	0.6	0.5	1.8	1.8	13°
	d	7.5	0.5	0.4	1.7	1.8	12°
MgR-III/5	mx	7.0	0.5	0.4	1.8	1.9	12°
	d	8.0	0.5	0.4	2.0	1.9	13°

mx — maxilla d — dentary

directed squamosal contacts the postorbital laterally and does not reach the jugal. Widened posterior end of the squamosal lies in a small notch of the cephalic condyle of the quadrate. Supratemporal bone very small, situated between squamosal and posterior process of the parietal. A small, anteroposteriorly elongated supratemporal fossa is transversely reduced, but is not

ZPAL mus. cat. numbers		MgR-I/15		MgR-II/50		MgR-II/80		MgR-III/3		MgR-III/4		MgR-III/5	
		h	d	h	d	h	ď	h	d	h	d	h	d
	8 1)	1.5	1.8	1.3	1.2	1.6	1.7	2.5	2.4	1.8	1.8	2.0	2.0
	7	1.2	1.1	1.1	1.0	1.5	1.4	2.0	2.0	1.4	1.2	1.6	1.4
	6	0.9	1.0	0.9	0.7	1.1	1.1	1.5	1.5	1.1	0.9	1.2	1.0
	5	0.8	0.7	0.7	0.6	0.9	0.8	1.2	1.1	0.9	0.7	1.0	0.9
	4	0.7	0.6	0.7	0.5	0.9	0.8	0.7	0.9		0.7	0.7	0.6
	3.	0.6	0.5	0.6	0.5	0.7	0.6	0.9	1.1	_	—	0.9	0.4
	2	0.7	0.5	0.8	0.4	0.8	0.5		0.8			0.6	0.4
- 7	1	0.5	0.5	0.5	0.4	0.7	0.5					0.5	0.4
1	8.	1.5	1.8	1.3	1.3	1.6	1.8	2.6	2.5	1.7	1.8	2.0	1.8
ŕ	7	1.2	1.5	1.1	1.2	1.5	1.6	2.3	2.0	1.5	1.5	1.5	1.6
	. 6 .	0.9	1.4	1.0	1.0	1.2	1.3	1.6	1.5	1.2	1.0	1.1	1.3

1 4 0 1 0 0	T	à	bl	le	3
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dantist

1) Tooth number in series

5

4

3

2

1

0.8

0.7

0.6

0.7

0.6

0.9

0.6

0.5

0.5

0.5

0.8

0.6

0.5

0.6

0.4

0.7

0.5

0.4

0.4

0.3

1.1

0.9

0.7

0.8

0.6

1.0

0.8

0.6

0.5

0.4

1.2

0.9

0.7

1.0

0.7

1.0

0.8

0.6

0.8

0.6

1.1

0.6

0.5

0.6

0.5

0.9

0.5

0.4

0.4

0.3

0.5

0.4

h --- height

Maxilla

Mandible

d - diameter of tooth base

covered by osteoderms. Quadrate streptostylic, situated obliquely (the cephalic condyle directed backwards) to the longer axis of the skull, with large external conch. The tympanic crest well developed. Posttemporal fossa small and short. Supraoccipital bone large with weak sagittal crest. Sutures between exoccipitals and paroccipitals fused.

Vomers short, paired, sutured to premaxilla, maxillae and pterygoids. Vomero-nasal foramina or notches not visible. Palatine small, contacting the anterior process of pterygoid and vomer, ectopterygoid lateroposteriorly, and prefrontal and maxilla dorsally. Internal choanal canals (pl. 14: 1a, 2; figs. 1 C, 2 A-B) are separated by sagittal ridge containing medial part of palatines, anterior pterygoid processes and posterior processes of vomers. Pterygoid with very long anterior process and laterally bent posterior one. Anterior process contacts the vomer (figs. 1 C, 2 A). Epipterygoid thin and rodlike. Palate toothless. Suborbital fenestrae not reduced, rimmed by pterygoids, ectopterygoids and palatines. Interpterygoid vacuity small, anteriorly closed by pterygoids. Basioccipital and basisphenoid fused or sutured. Basipterygoid processes short, wide and strong. Basioccipital condyle with well developed auditory recess. Parasphenoid process short and wide, partly preserved. Ceratobranchial bones, perhaps I, thin and long (fig. 3 A₂). Well developed palato-coronoid process (pl. 12: 3a-b; pl. 14: 1c; fig. 2A, D-C, H, I-J) points almost vertically down, its lateral surface fits into the perilingual depression of the coronoid process.

Lower jaw (pl. 12: 1-2, 4-5; fig. 1 D-G) relatively short and strong posteriorly. Precoronoid section somewhat longer and slender, narrows rapidly anteriorly. Postcoronoid section high and strong, slightly shorter than the anterior one. Anterior submental foramen lies in an elongated groove. Posterodorsal extremity of the dentary is two-lobed and reaches the base of coronoid. The latter is well developed, wide at base, stout, projects upwards but without external process or crest. Lingual feet of the coronoid strongly developed. Anterior foot penetrates between dentary and splenial bones, the posterior one strongly arches backwards and joins the



В



Adamisaurus magnidentatus SULIMSKI 1972. A. Reconstruction of the skull and lower jaw in lateral view, B — in dorsal view, C — ventral view of the skull. Lower jaw: D — outer view, E — inner view (small individual), F — outer view, G — inner view (large individual). Abbreviations: an — angular, apo — postorbital arch, apt — posttemporal arch, ar — articular, ast — supratemporal arch, bo — basioccipital, bs — basisphenoid, c — coronoid, cad — adductor crest, cex — external quadrate conch, co — occipital condyle, d — dentary, ec — ectopterygoid, ep — epipterygoid, f — frontal, fad — adductor fossa, faa — anterior alveolar foramen, fd — dental foramen, fipt — interpterygoid vacuity, fl — lacrimal foramen, fma — anterior mylohyoid foramen, fM — Meckelian foramen, fmc — fronto-maxillary contact, fne — external narial foramen, fpln — palato-narial vacuity, fp — parietal foramen, frp — resorptional pits, fso — suborbital fenestra, fst — supratemporal fossa, fvn — vomero-nasal foramen, j — jugal, l — lacrimal, m — maxilla, n — nasal, o — orbit, p — parietal, pbpt — basipterygoid process, pd — dorsal premaxillary process, pf — postfrontal, pj — jugal process, pl — palatine, pm — premaxilla, po — postorbital, pot — prooticum, ppc — posterior coronoid process, ppc — paraccipital process, ps — parasphenoid, pt — perceptional process, ps — parasphenoid, pt — perceptional process, ps — parasphenoid, pt — perceptional process, ps — parasphenoid, pt — posterior pterygoid process, prf — prooticum, ppc — posterior coronoid process, ps — parasphenoid, pt — perceptional, sq — supratemporal, sq — supratemporal, tc — tympanic crest, v — vomer.

articular bone. Surangular is visible in a lingual depression of the coronoid. Coronoid is not deflected either outwards or towards the posterior part of the jaw. Surangular short, occupies small area between dentary and articular and has two small foramina. Angular bandlike, visible laterally, long. Adductor fossa rather small, deep. Articular well developed, wide and slightly inwards directed. Retroarticular process strong, wide and short, points backwards. Articular and prearticular fused. Splenial is well developed but does not completely cover Meckel's groove anteriorly, leaving the latter open more or less for half (in large specimens) or one third (in smaller ones) of the length of dentary. Two foramina are visible on the splenial, located midway and are probably homologues of the anterior alveolar and anterior mylohyoid foramina (MESZOELY 1970: 98, fig. 4). The height of lower jaw under the coronoid is about 4 mm and in anterior teeth 0.7 to 0.8 mm.

Dentition (pl. 12:1a, b, 2a-c, 4a, b, 5; figs 1A, C-G, 2E, F). Upper and lower teeth are of the pseudoacrodont type, differentiated in size, fused with the jaw-bones at their wide bases. They are closely spaced but not fused together. The size of teeth increases considerably posteriorly and ratio of the length of the anterior teeth to the posteriormost one in the jaw is 1:3 or more. Teeth are isodont, conical, with broad bases (homodont). The serial differentiation of the teeth refers to their non-uniform size and function. Anterior teeth are small, conical and somewhat slightly recurved. The second tooth in the lower jaw and usually the third in the upper jaw are slightly larger but also conical. The posterior four teeth in the series of both jaws increase in size so that the last ones are almost four times larger than the first ones. In all specimens the enamel is smooth without additional sculpture. It reaches almost to the crown bases and the teeth are closely spaced. Resorptional pits show traces of enamel of the teeth of the new generation. Replacement of teeth is similar to the iguanid type (see EDMUND 1960, 1969) through resorption of the crown bases of the functional teeth and replacement by the new ones. The replacement was probably continuous, and based on rhythmic waves that proceeded probably towards the front (OSBORN 1973). On the specimen ZPAL MgR-I/13 (pl. 13; 1 b; fig. 2 G) an erupting tooth is visible in the left lower jaw.

Large specimens have high and large posterior teeth narrowed at the bases. Teeth are conical with more slender crowns. Small specimens also have conical teeth with wide bases but without distinct constrictions and swellings. The wearing surface of lower and upper teeth is on the distolingual side. Occlusal angle of small individuals is 7-9°, of larger ones 12-15° (fig. 2 K-L).

Postcranial skeleton (pls 13: 1 c-d, 14: 1 d; fig. 3). Vertebral column. In ZPAL MgR-I/13 five badly damaged but articulating vertebrae of the cervical section are preserved. The cervicals are comparatively short and broad and on the two last ones diapophyses are visible to which possibly the first cervical ribs were attached. Atlas and axis not preserved, but near the occipital condyle there is a small bone fragment that may belong to axis. Anterior thoracic section preserved in ZPAL MgR-III/5 contains six vertebrae, four cervical and two thoracic. The four anterior ones have slightly elongated centra with distinct articular processes and rather well developed diapophyses and parapophyses. Condyles are as wide as the posterior width of centrae. Articular sockets are well developed and the articulation of vertebrae is procelous. The two posterior vertebrae are elongated with distinct synapophyses. Zygosphenal articulation cannot be observed. None of the vertebrae have the neural processes preserved, but they were probably well developed. Between the cervical-thoracic section until the last presacral vertebra there are bone fragments that may belong to the remaining presacral vertebrae. The lumbar-sacral-caudal section is best preserved (pl. 14: 1 d; fig. 3 B, C). It includes one lumbar vertebra (the last presacral one), two sacral ones with well developed transverse processes and six or seven caudal vertebrae. The whole section is articulated. The last presacral vertebra is relatively large and broad and has no ribs. The sacrals have large and broad transverse processes, that are joined at an angle one to another and the processes of the first vertebra are slightly raised at their anterior edges. Processes of the second vertebra are horizontally arranged. Slightly broadened lateral terminations of these processes join the internal wall of the ilium. Rather high neural processes are preserved on both sacral vertebrae. The first caudal vertebrae (1-3) possess long perpendicular processes distinctly pointing backwards. There are no traces of planes of fracture on these vertebrae. The fourth vertebra has shorter transversal processes that point slightly backwards. The last two or three vertebrae have these processes broken and their bases show that they were also long and pointing perpendicularly to the vertebral column.

Pectoral girdle and forelimb (fig. $3 A_1$). Scapula is slender probably with one emargination. Coracoid shows one anterior emargination, an additional intermediate one occurs between scapula and coracoid. Interclavicula is preserved in fragments, the arrangement of which suggests that it was cruciform or T-shaped. Clavicle shows gradual ventral broadening with a trace of perforation. Forelimb is well developed (humerus, ulna and radius in fragments) with elongated digits, the IV-th digit was probably the longest. Clawed phalanges short. Pectoral ribs are preserved only in fragments.

Pelvic girdle and hindlimb (pl. 14: 1 d; fig. 3 B, E-G). Only the left half of the ilium is preserved completely (ZPAL MgR-III/5). Ilium is thickened at its base and pointed posteriorly. In front there is a prominent anterior process. Pubis is massive, bent inwards, without a tubercle. About 4 mm from the anterior process of ilium there is a distinct obturate foramen. Ischium is well developed with characteristic bending of the anterior margin and distal broadening. Pubo-ischiadic opening is vast, not closed by the pubis and ischium ventrally. Almost complete left posterior limb is preserved. Femur has a prominent head that fits into a deep acetabulum. Shaft of the bone is long with a curve pointing slightly backwards. Trochanter major is well developed. Its shape together with elongated zeugopodium shows that *A. magnidentatus* was adapted probably for running. Epiphyses of femur are bent at an angle of almost 60°. Tibia and fibula, although preserved in fragments, are well developed and probably of the same length as the femur. Proximal broadening of the tibia and fibula is distinct. The phalanges are slightly broadened and rather long. The limb was pentadactyl as the anterior one.

Discussion. — The family Adamisauridae nov. with one genus and species *A. magnidentatus* is placed within the infraorder Scincomorpha CAMP 1923 on the basis of the following characters: presence of lingual resorptional pits at the tooth bases; tendency to the reduction of the supratemporal fossa; concave postorbito-squamosal arch; fronto-maxillary contact; reduced lacrimal, sometimes fused to prefrontal; structure of the choanal canals (see figs. 1 C, 2 A-B); maxilla not rimming the suborbital fenestra; large ectopterygoid, and reduced, splintlike supratemporal.

The family Adamisauridae differs from all the present-day scincomorphs in: existence of vomero-pterygoid contact; posterior increase of cheek teeth; pseudoacrodont tooth implantation; very small interpterygoid vacuity; Meckelian groove open anteriorly; anterior process of the pterygoid very long reaching the vomer; small number of teeth; more medially situated suborbital fenestra, and well developed jugal with strong and short posterior process.

The Upper Cretaceous Macrocephalosauridae and Polyglyphanodontidae are the closest relatives of the Adamisauridae. The resemblances of the Adamisauridae to both families concern single premaxilla with long dorsal process; paired nasals and frontals; separated postfrontals

Fig. 2

Adamisaurus magnidentatus SULIMSKI 1972. Reconstruction of the palate, dentition and skull elements. A-E — skull of small individual with dentition (ZPAL MgR-II/50); A — palatal view, ca ×5; B — cross section of choanal canals, ca ×5; C — palate from dorsal side (partly restored), ×5; D — the same skull from the front, ×5; E — lower M6-M8, lingual view, ×10; F — lower M6-M8 of large individual, ×10 (ZPAL MgR-III/3); G — posterior two lower teeth in lingual view (the last one erupting), ca ×12.5 (ZPAL MgR-I/13); H-J — reconstructions of skull elements based on various individuals, not to scale; H — palato-quadrate region in lateral view; I — ectopterygoid, ventral view; J — palato-coronoid process, posterior view; K — occlusal angle in small individual, ×10; L — occlusal angle in large individual, ×10. Abbreviations: apec — anterior ectopterygoid process, cch — choanal canal, frp — resorptional pits, ic — coronoidal noth, fah — horizontal articular facet, papt — anterior palatal pterygoid process, pot — palato-co-ronoid process, vptc — vomero-pterygoid contact. Other abbreviations see fig. 1.





Fig. 3

Adamisaurus magnidentatus SULIMSKI 1972. A — skull (ZPAL MgR-I/13); A_1 — dorsal view, A_2 — posterior part of the same skull, ventral view. B-G — posterianial skeleton (ZPAL MgR-III/5); B — skeleton in matrix, general view; C — lumbar-sacral-caudal section: C_1 — dorsal view, C_2 — lateral view; D — cervical-thoracic section, dorsal view; E — left half of the pelvis, inner view; F — left femur: F_1 — lateral side, F_2 — distal part of the same bone, posterior side, ca $\times 4$; G — tibia and fibula: G_1 — proximal parts of left bones, medio-posterior side, G_2 — the same parts of right bones, posterior side, ca $\times 4$. Abbreviations: Cd — caudals, Cv — cervicals, cf — fibular condyle, cF — femoral head, cl — clavicle, cor — coracoid, ct — tibial condyle, cT — tibial head, ctb I — ceratobranchial I, F — femur, Fi — fibula, fo — obturate foramen, H — humerus, il — ilium, is — ischium, pb — pubis, pil — anterior process of the ilium, PS — presacrals, ptr — transversal process, S — sacrals, sc — scapula, sil — ilium spine, sis — ischium symphysis, T — tibia, trm — trochanter major. Other abbreviations see fig. 1.

and postorbitals; parietal foramen in fronto-parietal suture; reduced lacrimal; postorbito-squamosal arch flattened dorsoventrally in cross-section; small, splintlike supratemporal; frontomaxillary contact; existence of vomero-pterygoid contact; maxilla not rimming suborbital fenestra; small, reduced interpterygoid vacuity; well developed jugal with short posterior process; quadrate with wide external conch and well marked tympanic crest; large ectopterygoid; strong, well developed dentary; coronoid without external process or crest; splenial with two foramina, and small surangular.

The similarity of the Adamisauridae to Agamidae suggested earlier (SULIMSKI 1972: 35) was based only on acrodont like type of tooth implantation. The adamisaurid type of dentition which is morphologically similar to the acrodont type, differs from it by the existence of iguanid-like tooth replacement. Functional teeth are fused with jaw bones until the resorption of their bases, but not laterally, as it is common in pleurodont lizards. In the Agamidae cheek teeth are fused permanently with jaw bones. They remain through the entire life-span and are gradually worn down. Replacement of teeth in the Agamidae is of complex "iguanid-agamid" type, whereas in the Adamisauridae it is of aberrant "iguanid" type (terminology of EDMUND 1960, 1969 and COOPER *et al.* 1970). It proceeds as in scincomorphs and in most other lizards through resorption of bases of functional teeth and replacement by the new ones. Such replacement must have been rhythmic and oscillatory in character also in the adamisaurids, following the trend described by OSBORN (1973). Heterodontism of the Adamisauridae is reflected in strong posterior increase of the size of the teeth, whereas in the Agamidae the teeth are morphologically differentiated.

Some affinities to the Agamidae may be suggested by the existence of a well developed palatocoronoid process (pl. 12: 3 b; fig. 2 A-C, H-J), high internal choanal canals, two-lobed posterodorsal extremity of the dentary and short surangular. Similar characters are observed also in some cordylids and lacertids. These characters, however, may be a result of convergence to analogous modes of life between *Adamisaurus* and the primitive agamids (e. g. *Uromastix aegyptius* MER-REM; pl. 12: 6).

In the collection of Adamisaurus magnidentatus there are large individuals of stout skull construction and with larger occlusal angle $(12-15^{\circ})$ and smaller ones more delicate in structure with smaller occlusal angle $(7-9^{\circ})$. There are some differences in tooth morphology as well (particularly of the last 4-5 check teeth) which are expressed by more or less marked constrictions and swellings of the crown bases. It is of interest that large specimens have been found only at the Khermeen Tsav II, whereas the smaller ones at Bayn Dzak, Khulsan and Nemegt. A small collection from all three localities (16 skulls only) may suggest that the differences between the particular individuals may be accidental and are due to rather large intraspecific variability, which could be connected with different ecological conditions at Khermeen Tsav II and at the other sites.

The differences in teeth (the variable "occlusal angle" in particular) may also suggest that we are dealing with populations of two subspecies or even two separated species. This supposition is based on the fact that the present-day saurian faunas contain different species of the same genus, which do not differ in skull structure, **b**ut significantly differ in body sizes. For example the species of *Phrynocephalus* KAUP of Central Asia: *P. reticulatus* EICHW., *P. helioscopus* (PALL.), *P. versicolor* STR., *P. guttatus* (GMEL.), and twice as large *P. mystaceus* (PALL.) have similar skull morphology but differ in other characters. The similar observations have been made by LUNDELIUS (1957) for the iguanid genus *Sceloporus*.

From the comparison of characters of the Adamisauridae it appears that the resemblance of the Adamisauridae to Scincomorpha seems to be closer than to other saurian infraorders, the presence of vomero-pterygoid contact in *Adamisaurus magnidentatus* and in other primitive scincomorph lizards of Mongolia (see Sulimski 1975) is undoubtedly phylogenetically ancestral character (it does not exist in Recent and Tertiary lizards — see CAMP 1923, WILLIS-TON 1925, ZITTEL 1932, HOFFSTETTER 1955, Huene 1956, ROMER 1956, and GUIBE 1970). The vomero-pterygoid contact qualifies the Adamisauridae, the Macrocephalosauridae and Polyglyphanodontidae as more primitive than the other known families of the Scincomorpha; similarities of the Adamisauridae to the Recent Scincidae are smaller than to the Macrocephalosauridae and Polyglyphanodontidae. The presence of vomero-pterygoid contact, paired nasals and frontals, separated postfrontals and postorbitals, position of parietal foramen in the fronto-parietal suture, and dorsoventrally flattened supratemporal arch are regarded as primitive characters of *Adamisaurus magnidentatus*. Strong palato-coronoid process in *A. magnidentatus* is most probably corelated with the development of big cheek teeth, and strong pterygoid muscles.

ADDENDUM

When this paper was submitted to publication the specimen AMNH 6648, from the Djadokhta Formation at Bayn Dzak, described by Gilmore (1943: 383) as Sauria indeterminata, has been borrowed from the American Museum of Natural History (courtesy of Dr. Eugene Gaffney). After additional preparatory work done in the Institute of Paleobiology, Warsaw, it became obvious that it belongs to *Adamisaurus magnidentatus* Sulimski, 1972.

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EXPLANATIONS OF THE PLATES

PLATE 12

Adamisaurus magnidentatus SULIMSKI 1972

Upper Cretaceous, ?upper Santonian and/or ?lower Campanian, Djadokhta Formation, Bayn Dzak, Mongolia

- 1. Left lower jaw: I a inner view, Ib outer view, Ic coronoidal part with two-lobed posterior extremity of the dentary; ZPAL MgR-11/50, a-b × 5, c × 10.
- 2. The same specimen, right lower jaw: 2a outer view, 2b inner view, 2c last four teeth, lateral view. $a-b \times 5$, $c \times 10$.
- 3. The same specimen, facial skull part: 3a posterodorsal view, 3b right lateral view, $\times 5$.

Adamisaurus magnidentatus SULIMSKI 1972

Upper Cretaceous, ?middle Campanian, Red beds of Khermeen Tsav, Khermeen Tsav II, Mongolia

- 4. Right lower jaw: 4a -- inner view, 4b -- outer view; ZPAL MgR-III/3, ×5.
- 5. The same specimen, left lower jaw, last three teeth, lateral view, $\times 10$.

Uromastix aegyptius MERREM 1820

Recent

6. Skull, left lateral view; ZPAL Rw/1, \times 5.

ANDRZEJ SULIMSKI

PLATE 13

Adamisaurus magnidentatus SULIMSKI 1972

Upper Cretaceous, ?middle Campanian, Barun Goyot Formation, Khulsan, Mongolia

- 1. Skull: 1a anterior part, dorsal view, 1b ventral view, 1c posterior part, dorsal view, 1d ventral view; ZPAL MgR-I/13, ×5.
- 2. Skull, palatal view; ZPAL MgR-I/42, \times 5.

Adamisaurus magnidentatus SULIMSKI 1972

Upper Cretaceous, ?upper Santonian and/or ?lower Campanian, Djadokhta Formation, Bayn Dzak, Mongolia

3. Facial part of holotype skull, posterodorsal view; ZPAL MgR-II/80, ca $\times 4$.

PLATE 14

Adamisaurus magnidentatus SULIMSKI 1972

Upper Cretaceous, ?middle Campanian, red beds Khermeen Tsav, Khermeen Tsav II, Mongolia

- 1. Skull: 1a palatal view, 1b dorsal view, 1c left lateral view, 1d postcranial skeleton; ZPAL MgR-III/5, a-c × 5, d × 2.5.
- 2. Skull, palatal view; ZPAL MgR-III/1, $\times 5$.



A. SULIMSKI: Adamisaurus SULIMSKI 1972 (SAURIA) FROM THE UPPER CRETACEOUS



