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PRISCAGAMINAE, A NEW SUBFAMILY OF THE AGAMIDAE (SAURIA) FROM THE LATE CRETACEOUS OF THE GOBI DESERT

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Several new and well preserved lizard skulls from the Late Cretaceous of the Gobi Desert of Mongolia, referred to as *Mimeosaurus crassus* Gilmore, 1943 in the literature, are assigned to two new genera and species, *Priscagama gobiensis* and *Pleurodontagama aenigmatodes*. They, together with *Mimeosaurus crassus*, comprise a newly described subfamily Priscagaminae of the family Agamidae. Assignement of *Mimeosaurus* to this subfamily is tentative since the new specimens of *M. crassus* are fragmentary. Comparative analysis of skull characters in different iguanian families and those of the lizards here described suggests existence of a monophyletic taxon including agamids, *Uromastix-Leiolepis* group and Priscagama group but not chamaelonids. Familial status and the name Agamidae are retained for this taxon. Agamids, uromasticids and priscagamids are consequently given subfamilial status until new evidence comes.

K e y   w o r d s : Reptilia, Sauria, Agamidae, Cretaceous, Mongolia.

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INTRODUCTION

This paper concerns several nearly complete skulls and mandibles and fragments of skulls and mandibles which were collected by the Polish-Mongolian Palaeontological Expeditions to the Gobi Desert of Mongolia between 1963 and 1971. This new material has already been referred to as *Mimeosaurus crassus* Gilmore 1943 in the literature (Moody, 1980; Estes, 1983) but the present study demonstrates that only two tooth-bearing fragments can be assigned to *Mimeosaurus*. The remaining specimens represent two new genera and species *(Priscagama gobiensis* and *Pleurodontagama aenigmatodes)* and subfamily Priscagaminae of the lizard family Agamidae. *Mimeosaurus crassus* is tentatively assigned to this new subfamily. The three fragments (including the holotype) of the maxilla

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and dentary do not have adequate character information for definite assignment. *Mimeosaurus* certainly does not, however, belong to the Chamaeleonidae to which Gilmore (1943) assigned it. The characters on which Gilmore based the assignment, acrodont dentition and tuberculate sculpturing of the jugal surface, are not unique to the Chamaeleonidae. The former character is also characteristic of the Agamidae and the latter characteristic of most genera of the Iguanidae and a few genera of the Agamidae.

Priscagama, Pleurodontagama, and *Mimeosaurus* represent the first definite Mesozoic and earliest records of the lizard infraorder Iguania. The arguments for assigning *Pristiguana brasiliensis* from the Upper Cretaceous of Brazil in the Iguanidae (Estes and Price, 1973) are not convincing, and the specimen could be assigned to the Teiidae with equally convincing counter arguments. Earlier published reports concerning the occurence of agamids in the late Cretaceous in the same geographical region were in error. *Macrocephalosaurus* and *Conicodontosaurus* (Gilmore, 1943) and *Adamisaurus* (Sulimski 1972) are not agamids as originally reported, but instead are scincomorphans as demonstrated by Sulimski (1975). Estes (1983) has placed all of these taxa in the extinct Polyglyphanodontinae, a subfamily of the Teiidae.

The new specimens described here were collected from two localities belonging to two formations of the late Cretaceous. The Bayn Dzak locality (referred to as Shabarakh Usu by Gilmore, 1943 and in other American publications) belongs to the Djadokhta Formation of ?early Santonian or ?late Coniacian age. The Khermeen Tsav locality belongs to the red beds of Khermeen Tsav which is the biostratigraphic equivalent of the Barun Goyot Formation of ?late Santonian age. The above estimates of age are based on palaeobotanical evidence from Karczewska and Ziembińska-Tworzydlo (1983). These formations had been considered younger in earlier publications (Gradziński *et al.*, 1969, Gradziński and Jerzykiewicz, 1972 and Gradziński *et al.*, 1977). The holotype of *Mimeosaurus crassus* redescribed here was collected by the palaeontological expeditions of the American Museum of Natural History to the Gobi Desert in 1923 and 1930, and was collected from the locality Bayn Dzak of the Djadochta Formation.

Numerous lizard specimens belonging to other infraorders have already been described from these localities. Several new genera and species of the Scincomorpha have been described by Sulimski (1972, 1975, 1978, and 1984) and of the Anguimorpha by Borsuk-Białynicka (1984).

ABBREVIATIONS

a alv for = anterior alveolar foramen; *a inf alv for* = anterior inferior alveolar foramen; *add c* = adductor crest; *ang* = angulare; *bpt proc* = basipterygoid process; *cor* = coronoid; *d* = dentary; *d proc* = dentiferous process; *etc* = ectopterygoid; *ep* = = epipterygoid; *f* = frontal; *for ov* = foramen ovale; *inforb for* = infraorbital foramen; *j* = jugal; *j r* = jugular recess; *l* = lacrimal; *m for* = mental foramina; *md fos* = mandibular fossa; *mart proc* = medioarticular process; *myl for* = mylohyoid foramina; *n proc mx* = nasal process of maxilla; *oc r* = occipital recess; *p* = parietal; *p proc* = paroccipital process; *p sang for* = posterior supraangular foramen; *pl* = = palatine; *pm* = portion of maxilla suturing with palatine; *po* = postorbital; *pr* = = prootic; *prf* = prefrontal; *pt* = pterygoid; *pt t* = pterygoid teeth; *ptm c* = pterygomandibular crest; *sang* = supraangular; *sp* = splenial; *sphoc s* = sphenoccipital suture; *sphoc t* = sphenoccipital tubercle; *squ* = squamosal; *sub f* = subtemporal fenestra; *sub proc* infratemporal process; *sub lab for* = superior labial foramen; *sur c* = semicircular canal; *st* = supratemporal; *v h for* = vagal and hypoglossal foramina.

The anatomical terminology for the above list of abbreviations and for the following descriptions primarily follows Oelrich (1956).

INSTITUTIONAL ACRONYMS

AMNH = The American Museum of Natural History, New York City, USA.
ZPAL = Polish Academy of Science, Institute of Paleobiology, Warsaw Poland.

SYSTEMATIC PART

Infraorder **Iguania**
Family **Agamidae**, Gray 1827

Emended diagnosis. — Following character states are regarded as uniquely shared by all agamids: (1) Brain case wall excavated between semicircular canals with proootic broadly exposed in the horizontal wall ventral to the excavation. Epiotic foramen usually pierces the center of the excavation. Prootic slopes ventrally and is poorly exposed dorsally in other lizards and there is no epiotic foramen; (2) Acrodont and heterodont dentition displays a great amount of variability in the number of pleurodont teeth contributing to the main cheek series; (3) Maxilla underlies the orbit and extends to the frontoparietal suture or almost as far; (4) Premaxillary proceses of the maxillae fuse in the midline to separate the premaxillae from the vomers.

Note: The acrodont dentition, position of the maxilla relative to the orbit and the union of the maxillae anterior to the vomers are agamid characters shared by the Chamaeleonidae, but it is difficult to say if they are synapomorphic or homoplastic or any of them is. Confirmation of the former supposition would imply a foundation of a suprafamilial taxon Agamoidea characterized by three autapomorphies.

Subfamily **Priscagaminae** nov.

Type genus: *Priscagama* nov.

Diagnosis. — Differs from other agamids in the following complex of character states: Splenial very long and posses the posterior mylohyoid foramen; highly variable tooth implantation ranging from semi-pleurodont to typical acrodont; pterygoid dentition present; maxilla does not reach to the level of frontoparietal suture; coronoid overlaps dentary with labial process; ventromedial edge of mandibular fossa lacks sharp vertical lamina. Differs from most agamids in the lack of epiotic foramen.

Assigned genera: *Priscagama* nov., *Pleurodontagama* nov., and *Mimeosaurus* Gilmore, 1943.

Stratigraphic and geographic range. — Late Cretaceous Djadochta Formation (?early Santonian and/or ?late Coniacian) Red Beds of the Khermeen Tsav Formation (?late Santonian) Gobi Desert, Mongolia.

Note: *Priscagama* was chosen as the type genus because it is represented by excellently preserved skulls and mandibles. Although *Mimeosaurus* Gilmore 1943 is an older available name, this taxon is only represented by three fragments of the maxilla and dentary and could provide only a limited description.

Genus *Priscagama* nov.

Type species: *Priscagama gobiensis* nov.

Etymology: Latin, *prisca*, earliest; *agama*, reference to the Agamidae.

Stratigraphic and geographic range. — Djadochta Formation (?early Santonian or ?late Coniacian) and Red Beds of Khermeen Tsav (?late Santonian), Gobi Desert, Mongolia.

Diagnosis. — Differs from other priscagamid genera primarily in dentition: number and shape of teeth and type of tooth implantation. Maxilla has 18—20 teeth, premaxilla 4 and dentary 18 teeth. Central but not always posterior parts of maxilla and dentary have a series of typical acrodont teeth, triangular and fused at bases. Posterior semi-pleurodont teeth number from 3 to 6. Differs also from *Mimeosaurus* by longer and flatter snout and more delicate skull bones.

Remarks. — The genus *Priscagama* differs from *Mimeosaurus*, with which it was previously lumped, in skull proportions particularly of the snout region. A long and triangular nasal process of maxilla implies a low and elongated snout in *Priscagama* instead of a steep and short snout and corresponding narrow nasal process of maxilla in *Mimeosaurus*. Other differences regarded as indicative of generic rank are: jugal extends straight posterodorsally rather than curving posterodorsomedially as in *Mimeosaurus*; the longer tooth row exhibits a lower degree of acrodonty in *Priscagama*; the ectopterygoid is situated more anterior relative to the maxilla in *Priscagama*; the degree of labial overlap of the coronoid on the dentary

is extensive in *Priscagama* but either absent or slight in *Mimeosaurus*. The differences regarding the shape of the jugal, which is enlarged and concave in the lacrimal region of *Priscagama* instead of being flat and tapered as in *Mimeosaurus*, may be of specific rank but the range of variability of this character is not known. *Priscagama* differs from *Pleurodontagama* in its acrodont and heterodont dentition, in a shorter tooth row, and in a slightly shorter and relatively higher mandible.

Priscagama gobiensis sp. nov.
(pls. 14; 15: 1; 16; 17: 6; 18: 3; 19: 1, 2; figs. 1; 2; 3A; 4A-C; 5A)

Holotype: ZPAL MgR/III-32. Damaged skull with both mandibles. pl. 14: 1; pl. 19: 1, 2.
Type horizon: Red Beds of Khermeen Tsav (?Late Santonian).
Type locality: Khermeen Tsav, Gobi Desert, Mongolian.
Etymology: gobiensis, referring to the geographic distribution in the Gobi Desert of Mongolia.

Diagnosis. — *Priscagama gobiensis* differs from the other representative of the genus, *Priscagama* sp., by the more slender mandibular ramus, the relatively lower coronoid with a less accentuated muscular crest and closely spaced teeth.
Material. — Specimens from the type locality of Khermeen Tsav are the following:
ZPAL MgR/III-32 Holotype. Damaged skull lacking anterior part of snout, most of brain case, and both supratemporal arches. Both mandibles preserved but right lacks coronoid and postcoronoid ramus.
ZPAL MgR/III-31. Damaged skull lacks anterior part of snout and most of skull roof. Preserved parts include brain case, damaged right mandible and right epipterygoid with missing dorsal process.
ZPAL MgR/III-72. Damaged skull of a small specimen with both mandibles and several cervical vertebrae. Teeth preserved but not accessible for study.
ZPAL MgR/III-33. Juvenile skull with left mandible intact and several cervical vertebrae. Both temporal regions crushed.
ZPAL MgR/III-83. Fragment of mandible lacking both the anterior portion of precoronoid ramus and posterior portion of postcoronoid ramus.
The following two specimens come from the Bayn Dzak locality.
ZPAL MgR/II-77. Fragmentary skull lacking brain case and large portion of the left side. Nasals and premaxilla lacking. Fragments of both mandibles preserved.
ZPAL MgR/II-101. Fragmentary skull, lacking mandibles.
The last two specimens above from Bayn Dzak are probably conspecific with *Priscagama gobiensis* but this can not be determined with certainty because of the fragmentary nature of the specimens. If they are conspecific, then this would be the second vertebrate species (the first is the mammal *Deltatheridium pretrituberculare*) common to both the Djadochta Formation and the Red Beds of Khermeen Tsav (see Gradziński *et al.*, 1977).
Measurements: See Table 1 and 2.
Description. — Skull as a whole: Subpentagonal in outline and relatively flat with its largest transverse dimension across the posterior half of the orbits. The fenestra exonarina is posteriorly extended and faces upward. The orbits and supratemporal fenestra are large. The adductor muscles attach ventrally and laterally rather than dorsolaterally on the parietals. Nodule-like sculpturing, highly variable between specimens, is present on the frontals, parietals, nasals, postorbitals, jugals and maxillae.

Dermocranial roofing elements: the semicircular body of the premaxilla is laterally overlapped by the maxilla. The nasal process of the premaxilla is long and dorsoventrally flattened and has a trace of a medial suture distally. It contacts the frontals by a short transverse suture in the juvenile specimen ZPAL MgR-III/33. The nasals overlap this region, have midline contact and separate the premaxilla from the frontal. The ventral blade of the premaxilla is very short. The nasal is a lozenge shaped bone wedged between two anterior processes of the frontal. It is sutured laterally to the prefrontal and maxilla. A robust tuberose sculpture is located just in front of the line of the anterior reach of the prefrontals and frontals. It tends to appear on other parts of the bone with increasing size of the specimens which is probably ontogenetic.

The frontals are completely fused with a median suture visible only between their anteromedial processes. Deep, acute incisions, articular facets for the nasals, separate these processes from the anterolateral ones giving the frontals a fork-like appearance. The anterolateral processes probably reach as far anteriorly as the anteromedial ones but the maxillofrontal contact does not exist. The strongest constriction of the frontals is about the midlength of the orbit. Anteriorly, the frontals are only slightly broader. However, the posterior width (at frontoparietal suture) is about three times larger then the minimal width. The ratio of the posterior frontal width to the total frontal length is approximately 1:1. The descending processes of
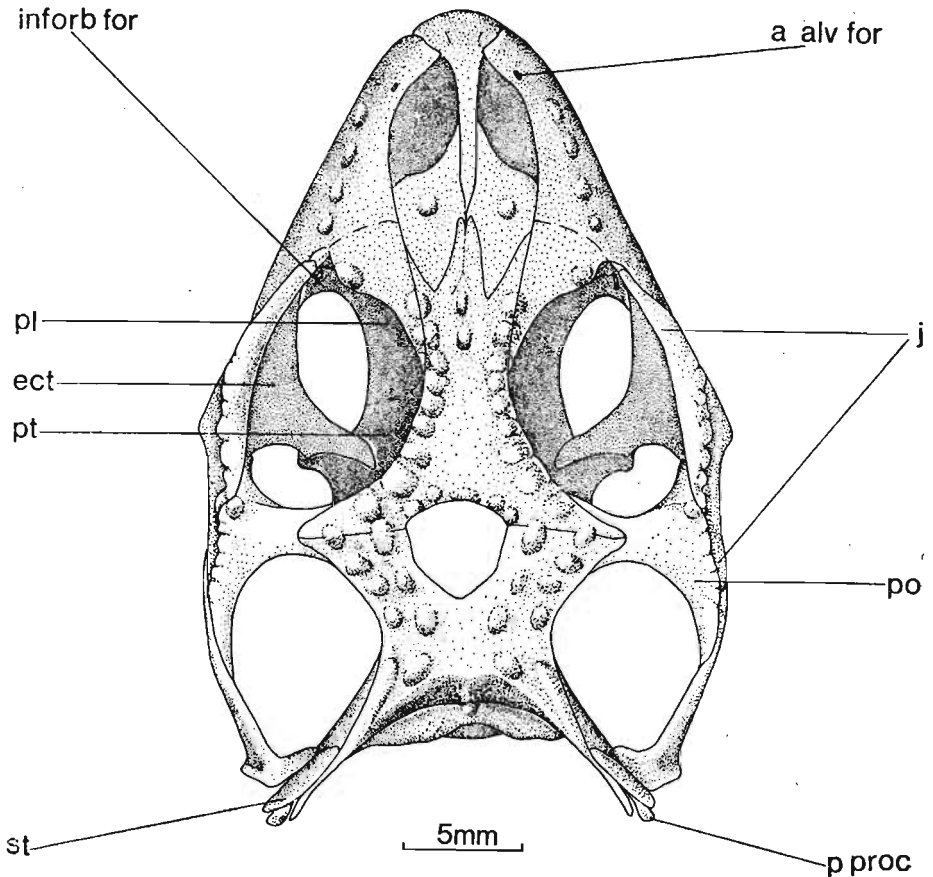

Fig. 1. *Priscagama gobiensis* gen. et sp. n. Reconstructed skull; dorsal view.

the frontals do not project ventrally but only add to its thickness. Anteriorly they contact with the prefrontals extending slightly ventral to their posterior processes, but do not contact the maxillae. A large circular parietal foramen (25% the size of the posterior frontal width) emarginates both the parietal and frontal. The dorsal surface of the frontals is slightly concave in transverse section with the supraorbital borders projecting dorsally, especially exaggerated when sculptured. When fully developed, the sculpture of the frontals (pl. 14: 1) consists of a paired row of nodule-like tubercles extending along the supraorbital margins. At the narrowest region of the frontals, the sculptured orbital borders almost contact. Anterior and posterior to this frontal constriction, the bone surface is covered with tubercular thickenings.

The width of the parietal at the frontoparietal suture is slightly less than the corresponding width of the frontal. The length of the main parietal body is about the same. The parietal is constricted about the midlength of its main body. Anterior to this region the temporal musculature attaches to the ventral border of the parietal as well as to the descending processes. Posterior to the constriction, the muscles attach to the lateral surface of the posterolateral extension of the parietal and supratemporal. The posterolateral processes define an angle of 70 degrees. At the base of this angle and oriented dorsally is a smooth surface which is the site of the spinalis capitis muscle insertion. The surface of the parietal is slightly concave and deeply incised anteriorly by the parietal foramen. The sculpture, when developed, consists of two series of tubercles bordering the parietals and two additional series lying medial to the marginal series.

The maxilla is outlined like a low isosceles triangle in lateral view (pl. 16: 1). Its surface is moderately convex just above the teeth but becomes flattened anterodorsally. The premaxillary processes probably meet each other in the midline to separate the premaxilla and vomers (fig. 2). The nasal process slopes posterodorsally and is angled medially. The dorsal surface is separated by an acute ridge which becomes tuberculately sculptured in older individuals. The maxilloprefrontal contact was not preserved but the maxilla probably strongly overlapped the prefrontal. The maxilloprefrontal suture can be restored given the maxillolacrimal and premaxillofrontal contacts. The line linking these contacts divides the nasal into anterior and posterior parts, but prokinesis cannot be directly proved by this apparent situation. The posterior process of the maxilla extends posteriorly beneath the orbit to join the infratemporal process produced primarily by the jugal. This process lies just anterior to the frontoparietal suture. The triangular palatal process of the maxilla is produced below the lacrimal, prefrontal and anterior part of the orbit. It gradually turns into the premaxillary process of the maxilla. The oblique maxillopalatine suture is very loose (syndesmotic). A very narrow triangular ectopterygoid process of the maxilla is present at the level of the posteriormost tooth position but anterior to the infratemporal process.

The frontal border of the prefrontal has sculpturing which contributes to the tubercles found on the marginal row on the frontal. Along the lateral border of the prefrontal and overlapping the lacrimal are several other tubercles. The concave palatine process of the prefrontal forms a subhorizontal suture and the lateral border defines the medial border of the lacrimal foramen.

The lacrimal contributes only a small part to the anteroventral rim of the orbit. The external surface is concave. The orbital surface is oriented dorsally and is posteriorly overlapped by the jugal. It contributes to the lateral margin of the small lacrimal foramen.

The jugal overlies the maxilla along the orbital border but is overlapped in turn by the maxilla on the ventrolateral side. It becomes deeper at the lacrimal-jugal contact and its surface becomes concave in this region. At the midpoint of the

orbit, the jugal:maxilla ratio in vertical transect is 1:2. Just posterior to the maxilla, the jugal produces the infratemporal process and then turns abruptly dorsoposteriorly to meet the postorbital and squamosal. The horizontal ramus of the jugal broadly articulates with the ectopterygoid. The orbital border of the jugal, primarily the ascending ramus, has tuberculate sculpturing, increasing from front to back in size. The posteroventral angle of the horizontal ramus is also sculptured.

The postorbital is a large triradiate bone. It lies in a subhorizontal plane and is supported by the ascending ramus of the jugal and the ectopterygoid. The medial process of the postorbital has a shelf-like incision to accomodate equally the frontal and parietal, giving it a forked appearance dorsally. The small frontal process may represent a fused postfrontal. The posterior process extends along the anterior half of the supratemporal fossa and tapers posteriorly. The amount of its contact with the squamosal is equal to that of the jugal-postorbital contact. Postorbital has tuberal sculpturing along both lateral and medial margins.

The dorsal process of the squamosal extends for a short distance along the lateral margin of the supratemporal which gives the squamosal a U-shaped outline in dorsal view. A ventral projection of the posterolateral corner fits into a notch in the lateral border of the dorsal head of the quadrate. It was probably quite strong as demonstrated by ZPAL MgR-III/31. The anterior process is sutured, for a fairly long distance, with the postorbital and its apex fits into an articulating facet situated on the posteroventral surface of the posterior corner of the jugal.

The supratemporal is a small bone closely adherent to the lateral surface of the posterolateral extension of the parietal. Distally it articulates with the quadrate head and the paroccipital process (figs. 1 and 3A), while being separated by the latter from the posterolateral process of the parietal.

The main body of the quadrate is arched so that the proximal extremity faces posterodorsally and the distal ventrally. The tympanic crest is separated from the proximal condyle with a deep notch in which the squamosal peg fits. Its posterior surface is concave, particularly in the proximal part. Anterodorsal of the proximal part of the tympanic crest, a thick tubercle is found and probably is the origin of the levator anguli oris. A small medial conch extends anteromedial and bears a flattened facet for articulation with the pterygoid. The resting position of the quadrate is subperpendicular to the skull roof with only a slight anteroventral angling of the quadrate shaft.

The epipterygoid is long and slender. It ascends obliquely posterodorsally up to the part of the brain case directly superior to the anterior semicircular canal, and probably contacted the parietal.

Palatal complex: vomers are nearly flat plates, rounded in outline, and articulate together on the midline. The surface of the vomers is angled obtusely with the anterior part of the palatines and produces a longitudinal concavity in the anterior palate. As demonstrated by ZPAL MgR/III-33, the vomers are separated from the premaxilla by the palatal extensions of the maxilla. The sutural contact with the palatines is very broad, transverse, and slightly interdigitated.

Ventrally the palatine has an extensive flat surface. The pterygoid process has a distinct medial shelf tapering anteriorly (hemipterygoid?, Lakjer, 1927) and is overlapped by the pterygoid from the ventral surface. It is bent mediodorsally relative to the lateral portion of the palatine and is laterally overhung by a crest extending along the medial border of the lateral part (fig. 2). The maxillary process is separated from the vomerine process by a very short and deeply concave palatine sulcus. The palatomaxillary suture is very loose, the maxilla overlaps the palatine ventrally. The vomerine processes do not fuse in the midline. The pterygopalatine contact and ectopterygopterygoid contact lie in a single obliquely directed line. The

triangular anterior part of the pterygoid is nearly flat except for the thickened medial border which bears several palatal teeth. This part of the pterygoid extends posteriorly into a relatively narrow subrectangular shaft. This shaft is situated in one line with the medial border of the pterygoid while transforming into the quadrate process laterally. The posteromedial corner underlies the basipterygoid articulation. It is excavated dorsomedially to accomodate the basipterygoid process. The collumellar fossa is present dorsally. The quadrate process of the pterygoid is a long thin and deep blade which forms an angle of circa 130 degrees with the medial border of the anterior part of the pterygoid.

The ectopterygoid has a long process extending along the maxilla but it does not exclude the maxilla from contributing to the border of the suborbital fenestra. The pterygoid process overlaps the pterygoid from the anteroventral surface and contributes an important part to the strongly protruding process for the pterygomandibularis muscle.

Brain case: the parabasisphenoid and basioccipital contribute equally to the ventral aspect of the brain case. Their suture is angled with the apex anterior. The posterolateral processes of the parasphenoid extend only a short distance along the bases of the sphenoccipital processes. They are laterally delimitted by sharp ventrolateral crests extending to the basipterygoid processes. Basipterygoid proces-
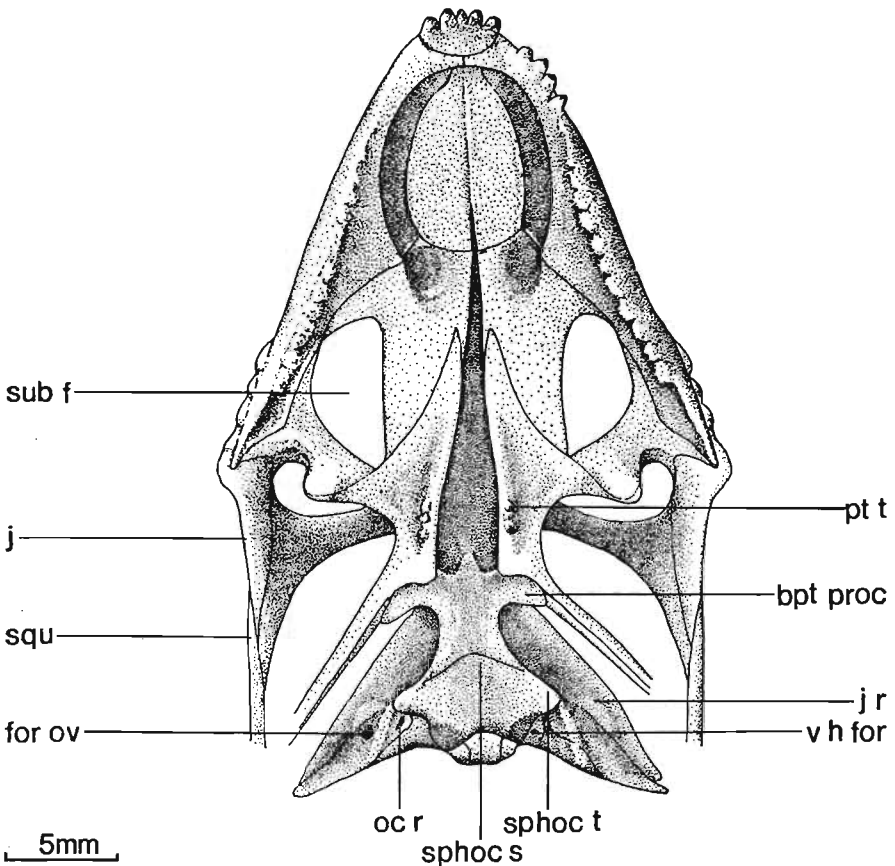

Fig. 2. *Priscagama gobiensis* gen et sp. n. Reconstructed skull; ventral view.

ses, which are very large, project ventrolaterally with an angle of circa 80 degrees to each other. Their articular surfaces face more laterally than anterolaterally. The sphenoccipital processes project ventrolaterally at about the same angle as do the basipterygoid processes but their distal ends are not laterally bent, but instead are oriented ventrally. The presence of epiphyses at their tips can not be ascertained from the fossil material. Each sphenoccipital process is laterally excavated for the occipital recess which is bounded posteriorly by a tuberal crest and anteriorly by the interfenesteral crest. They fuse together to form the posteroventral margin of the paroccipital process. The jugular recess is a broad, triangular furrow facing ventrally rather than laterally. It is bordered by a sharp prootic crest directed to the ventral corner of the paroccipital process.

A suture between the prootic and exoccipital extends parallel to the prootic crest. The occipital recess is pierced by the foramen rotundum in its dorsal portion. Directly anterior to it, the brain case wall is swollen to include the ventral part of the labyrinth. The foramen ovale is situated just posterior to this swelling and lateral to the foramen rotundum. The occipital condyle is semilunar and projects strongly posteriorly. Its tripartite structure may be recognized only on some specimens. Anterior to it, two concave areas for the insertion of the rectus capitis anterior muscle reach the tops of the sphenoccipital processes and meet in the midline. The foramen magnum is large. The paroccipital processes project slightly above the horizontal plane. Longitudinal swellings of the posterior semicircular canals cross the paroccipital processes directly lateral and parallel to the margin of the foramen magnum.

The anterior semicircular canals are very distinct and produce the anterior borders of the brain case. Together with a tiny alar process which is situated close to the processus ascendens and protruding directly upwards, the anterior semicircular canal produces a flat vertical sheet of bone. Posterior to it the brain case wall extends horizontally, corresponding to the plane of the horizontal semicircular canal. The brain case wall is, therefore, strongly acutely concave between the semicircular canal protuberances, but an epiotic foramen is absent.

Mandible (Pl. 19: 1, 2; fig. 4A, B, C): relative to the straight dentary portion, the supraangular and prearticular curve medially resulting in a circa 30 degree angle between the postcoronoid ramus and the primary long axis of the mandible. This curvature is accentuated by the strong adductor crest extending on the lateral side of the supraangular from about the middepth of the precoronoid ramus to the lateral corner of the articular surface. Posterior to this crest the labial surface of the mandible faces ventrally. The trochlea for the pterygomandibularis muscle is poorly developed. The crest delimitting it from the anterolateral side (fig. 4A) is widely separated from the adductor crest as are the muscle insertions. Because of the shape of this surface, the angular is hardly visible along the ventral margin of the mandible in lateral view. The mandibular fossa is deep and its ventral border does not produce a sharp medial vertical wall.

Labial surface of the dentary is convex but becomes acutely convex near the suture with the supraangular. This suture extends vertically directly below the coronoid process. A variable number of mental foramina (3—5) are present anteriorly on the lateral side. The meckelian groove is posteriorly wide but strongly tapering anteriorly. It is ventrally bordered by the dentary but turns to the ventral surface of the mandible at the symphysis. The dental gutter is deep and broad, particularly along the main cheek tooth series.

The splenial is very long, extending from the level of the coronoid apex through about 4/5 of the horizontal ramus. It covers the meckelian groove, including most of its narrow portion. Three foramina are present on the surface of the splenial: anteriorly, a very large elliptical foramen for the lingual branch of the inferior

alveolar nerve, and posteriorly, two small foramina oriented longitudinally cor-
responding to the anterior and posterior mylohyoid nerves. The angular is lacking
a foramen for the latter nerve.

The postcoronoid part of the mandible is comprised mainly of the supraangular.
It is not fused with the articular and prearticular. The supraangular foramen is
located at the posterior extremity of the adductor crest.

The coronoid is broadly triangular and has a long broad anteromedial ramus
and a ridged posteromedial ramus which does not reach the ventral edge of the
mandible. Labially a broad process overlaps the dentary and supraangular. The flat,
long and oval angular lies on the ventral edge of the mandible, but wraps around
to the labial surface posteriorly. It overlaps the suture between the prearticular and
supraangular. The medioarticular process is a small process protruding anteromedial-
ly and connected by a short ridge with the retroarticular process. The length of
the retroarticular process is not known but its preserved proximal portion suggests
that it was ventrally flattened which corresponds with the flattened ventral face of
the adjacent part of the mandible. The articular facet is bilobed, saddle-shaped, and
has a distinct tubercle in the anteromedial part to which the supraangular con-
tributes.

Dentition (pls. 17: 6; 18: 3; figs. 4B, C; 5A): the dentition is heterodont, differently
sized teeth of both pleurodont and acrodont modes of implantation. The anterior
parts of the maxillae and dentaries and the premaxilla have pleurodont teeth. The
main cheek series is acrodont but followed by some pleurodont teeth tending to fuse
with the cheek series in the ontogeny. The number of acrodont teeth is increased
by addition of new teeth posteriorly. Lack of interdental spaces and replacement pits
and presence of occlusal wear indicate that the acrodont teeth are permanent. The
teeth of the main cheek series are closely spaced and fused basally with each other,
which produces a uniform dentiferous process extending along the jaw and per-
pendicular with the palatal shelf (fig. 4B, C). The process is only slightly dorsal to
the parapet of the jaw. The conical parts of the teeth may be considered as the whole
tooth crowns conical and widely spaced. That the dentiferous process is homo-
logous with the fused basal portions of the tooth crowns is evident by the posterior
teeth of the series. Although fused with the dentiferous process, they retain their
individual shape. The homology is also suggested because the dentiferous process
reaches dorsolingually the level of the dental gutter on which the bases of the
pleurodont teeth rest (fig. 4B, C).

The main maxillary cheek series comprises 14—15 teeth. They decrease in size
anteriorly and the 4—5 anteriormost teeth are tiny and completely fused (remnant of
the hatchling dentition? see Robinson, 1976). At least 3 and probably 5 tooth posi-
tions for the anterior pleurodont circa cylindrical teeth can be recognized. The
premaxilla has 4 perhaps 5 teeth.

The main mandibular cheek series comprises only circa 11 teeth. The degree
of fusion is subject to variability. The number of posterior teeth retaining their
independence ranges from 2 to 5. Anterior to the main cheek series, the number of
pleurodont cylindrical teeth is usually 6. A slight trace of a replacement pit on one
tooth suggests direct succesional type of tooth replacement occurring in this part of
the tooth row.

Priscagama sp.

Material. — ZPAL MgR-III/69, middle portion of right mandible. Coronoid,
posterior portion dentary, portion of splenial, prearaticular and supraangular pre-
served.

Stratigraphic and geographic range. — Barun Goyot Formation, late Cretaceous; Khulsan, Gobi Desert, Mongolia.

Measurements: See Table 2.

Description. — This specimen apparently differs from *Priscagama gobiensis* only in having a more robust mandibular ramus, a relatively taller coronoid with more accentuated muscular crests, and more widely spaced teeth. The differences may be either specific taxonomically, or be associated with the larger size of this Khulsan specimen, and therefore be ontogenetic. The posterior teeth are of the same shape as *P. gobiensis* but are proximally completely fused to the dentiferous process. They may represent the posterior pleurodont teeth of the cheek series which have separated during dentary growth and fused with the dentary in the same manner as have the anterior cheek teeth. Additional ontogenetic information is needed for all the species of the genus *Priscagama* in order to complete an analysis of these fossils.

Genus *Pleurodontagama* nov.

Type species: Pleurodontagama aenigmatodes sp. n. This is the only species of the genus.

Etymology: Pleurodont refers to the pleurodont type of tooth implantation and agama refers to the family Agamidae.

Stratigraphic and geographic range. — Red Beds of Khermeen Tsav (?late Santonian), Gobi Desert, Mongolia.

Diagnosis. — Differs from other priscagamid genera by irregular, semi-fused, pleurodont dentition, number of teeth, and proportions of the mandible. Maxilla has circa 18 tooth positions; premaxilla 2—4; and dentary 24. Precoronoid portion of mandible proportionately longer and more slender than in *Priscagama* and *Mimeo-*
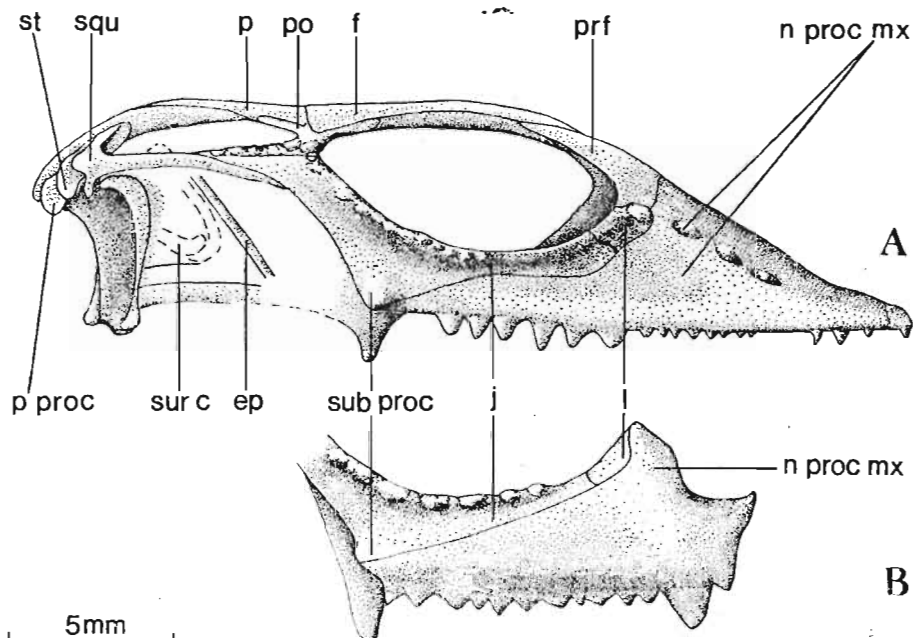

Fig. 3. A — *Priscagama gobiensis* gen. et sp. n. Reconstructed skull; right side view. B — *Mimeosaurus crassus* Gilmore. Maxillary portion of skull; right side view.

saurus. Pleudorontagama differs from *Mimeosaurus* by longer and flatter snout and more delicate skull bones.

Remarks. — *Pleurodontagama* is assigned to the Priscagaminae on the basis of skull and mandibular characters, which are identical with those of *Priscagama* except for some minor differences. Worth noticing is the extension of the splenial exactly the same as that in other priscagamid genera and the posterior mylohyoid foramen located within this bone. *Pleurodontagama* differs from *Priscagama* in having semi--pleurodont dentition, the longer and more slender mandible, the higher tooth number and ectopterygoid more oblique with respect to the maxilla. The differences of skull proportions and dentition when *Pleurodontagama* is compared with *Mimeosaurus* are more striking. The degree of these differences is believed to support generic status.

<div align="center">

Pleurodontagama aenigmatodes gen. et sp. n.

(pls. 15: 2; 18: 4; 19: 3, 4; figs. 4D; 5B)

</div>

Holotype: ZPAL MgR-III/35. Fairly complete skull with both mandibles. Dorsal dermocranial elements lacking. Pls. 15: 2; 18: 4; 19: 3, 4.

Type horizon: Red Beds of Khermeen Tsav.

Type locality: Khermeen Tsav, Gobi Desert, Mongolia.

Etymology: *ainigmatodes*, Greek for puzzling, inexplicable.

Diagnosis. — See generic diagnosis.

Material. — Holotype is only known specimen.

Measurements: See Tables 1 and 2.

Description. — Skull as a whole (pl. 15: 2): Subpentagonal in outline and relatively flat with its largest transverse dimension across the posterior part of orbital region. Orbits and supratemporal fenestra are large. Preserved parts of dermocranium bear nodule-like sculpturing.

Dermocranial elements: Premaxillary internarial process has a flat dorsal surface. Denticulate portion is 2X wider but may be damaged laterally. The ventral blade of the premaxilla is very short, perhaps separated from vomers by the maxillae. The frontals, known only from their impressions in the matrix, are constricted at the mid orbital level, but very wide at their parietal articulation.

The maxilla is shaped like a low isosceles triangle in lateral view. Its surface is moderately convex just above the teeth but becomes flattened dorsally. The premaxillary processes probably meet each other in the midline to separate the premaxilla and vomers. The posterior process of the maxilla extends posteriorly beneath the orbit to join the temporal process produced primarily by the jugal. This process lies just anterior to the frontoparietal suture. The maxilla contributes slightly more than does the jugal to the lateral surface of the infraorbital region. The triangular palatal process of the maxilla is produced directly below the prefrontal and lacrimal. It has an oblique articulation with the palatine. The maxilla borders the anterolateral half of the suborbital fenestra and is not excluded by the palatine and ectopterygoid. A very narrow, triangular ectopterygoid process of the maxilla is present at the level of the posteriormost tooth position.

The extension of the prefrontal on the dorsal surface of the skull is not known. Its orbital border strongly overhangs the orbit. It probably bore some tuberculated sculpture as documented by the roughness of the preserved part. The concave palatine process of the prefrontal forms a subhorizontal suture and the lateral border defines the medial border of the lacrimal foramen. Lacrimal duct is tiny. Lacrimal forms a small lozenge along the anteroventral margin of the orbit. Jugal tapers anteriorly to contact the lacrimal. Anterior half of its dorsal border is missing.

Temporal ramus has a series of nodules or tuberosities with the largest located on the infratemporal projection. Temporal ramus curves dorsoposteriorly and articulates broadly with the postorbital and with the anterior end of the squamosal.

The postorbital is a large triradiate bone. It lies in horizontal plane and is supported by the ascending rami of the jugal and ectopterygoid. The medial process is fork-shaped and articulates equally with the frontal and parietal. The small frontal process may represent a fused prefrontal. The posterior process extends along the anterior half of the supratemporal fossa and tapers posteriorly. The amount of its contact with the squamosal is equal to that of the jugal-postorbital contact. Postorbital has tuberal sculpturing along the anterior and lateral margins.

Quadrate body is arched; the proximal articulation faces posterodorsally and the distal ventrally. The tympanic crest is separated from the proximal condyle with a deep notch in which the squamosal peg fits. Its posterior surface is concave, particularly in the proximal part. Anterodorsal of the proximal part of the tympanic crest, a thick tubercle is the origin of the levator anguli oris muscle. Directly above the ventral condyle on its lateral surface lies another tubercle, probably connected with the mandibular joint capsule, which bears a rough pit for attachment of the collateral ligament. The ventral condyle is similunar in outline. The medial part is more robust than the lateral. A small medial conch is present. It extends anteromedial and bears a flattened facet for articulation with the pterygoid, just below the middle of the shaft. Below this facet and above the articular condyle is a tuber serving as a site of attachment for the medial collateral ligament of the mandibular joint.

The epipterygoid is long and slender. It ascends obliquely posterodorsally up to the part of the brain case directly superior to the anterior semicircular canal. It probably contacted the parietal.

Palatal complex: vomers are nearly flat plates rounded in outline, and articulate together on the midline. The surface of the vomers is angled obtusely with the anterior part of the palatines and produces a longitudinal concavity in the anterior palate. The vomers were probably separated from the premaxilla by the palatal extensions of the maxilla. The sutural conact with the palatines is very broad, transverse, and slightly interdigitated. Ventrally, the palatine has an extensive flat surface. The maxillary process is separated from the vomerine process by a very short and deeply concave palatine sulcus. The palatomaxillary suture is very loose with the maxilla overlapping the palatine ventrally. The vomerine processes do not fuse in the midline. The pterygopalatine contact and ectopterygopterygoid contact lie in a single obliquely directed line. The triangular anterior part of the pterygoid is nearly flat except for the thickened medial border which bears several palatal teeth. This part of the pterygoid extends posteriorly as a relatively narrow subrectangular shaft. This shaft is oriented along a line with the medial border of the pterygoid, but laterally develops the quadrate process. The posteromedial corner underlies the basipterygoid articulation and is excavated dorsomedially to accomodate the basipterygoid process. The quadrate process of the pterygoid is long, thin and deep blade which forms a circa 130 degree angle with the medial border of the anterior part of the pterygoid.

The ectopterygoid has a long process extending along the maxilla, but it does not exclude the maxilla from contributing to the border of the suborbital fenestra. A medial process of the ectopterygoid overlaps the pterygoid from the anteroventral surface and contributes an important part to the strongly protruding process for the pterygomandibularis muscle.

Brain case: The parabasisphenoid and basioccipital are completely fused. Very large basipterygoid processes project ventrolaterally with an angle of circa 80 degrees to each other. Their articular surfaces faces more laterally than anterolaterally. The

long sphenoccipital processes project ventrolaterally at about the same angle as do the basipterygoid processes but their distal ends are not laterally nor posteriorly bent, but instead project ventrally. Sharp ventrolateral crests extend from their tips to those of the basipterygoid processes. Each sphenoccipital process is laterally excavated for the occipital recess. The jugular recess is a broad, triangular furrow facing ventrally rather than laterally. It is bordered by a sharp prootic crest directed to the ventral corner of the paroccipital process. Directly anterior to the occipital recess, the brain case is swollen to include the ventral part of the labyrinth. Both the foramen magnum and the occipital condyle are large. The paroccipital processes project slightly above the horizontal plane. The posterior semicircular canals bulge from the surface of the paroccipital processes directly lateral and parallel to the margin of the foramen magnum. Two foramina in the type specimen are situated just medial to the left posterior semicircular canal adjacent to the ventral part of the foramen magnum. The upper is probably the vagal foramen and the lower is one of the two hypoglossal foramina.

The anterior semicircular canals are very distinct and produce the anterior borders of the brain case. The tiny alar process protrudes directly upwards. It is situated close to the processus ascendens of the supraoccipital. Together with the anterior semicircular canal it produces a flat vertical sheet of bone. Posterior to this sheet the brain case wall extends horizontally, corresponding with the plane of the horizontal semicircular canal. The brain case wall is, therefore, distinctly and acutely concave between the semicircular canals.

Mandible (pl. 19: 3, 4): The dentary portion of the mandible is straight. The postcoronoid ramus curves medially. This curvature is accentuated by the strong adductor crest extending on the lateral side of the supraangular from about the middepth of the precoronoid ramus to the lateral corner of the articular surface. The mandibular fossa is deep and a sharp medial vertical wall is not produced. The meckelian groove is posteriorly wide but tapers anteriorly. It is ventrally bordered by the dentary but turns to the ventral surface of the mandible at the symphysis. The dental gutter is deep and broad along the posterior portion of the tooth row. The labial surface of the dentary has circa 5 mental foramina.

The splenial is elongate and triangular in shape with a long acute anterior process extending 3/4 the length of the precoronoid mandible. Two small mylohyoid foramina are present in the central portion. A large inferior alveolar foramen is present in the anterior portion at the contact between the splenial and dentary. The angular is poorly preserved, and probably did not have foramina. The supraangular foramen is located at the posterior extremity of the adductor crest.

The coronoid is broadly triangular. It has a long broad anteromedial ramus and a ridged posteromedial ramus which does not extend to the ventral edge of the mandible. Labially, the coronoid has a broad process that overlaps the dentary and supraangular. The medioarticular process is a small process protruding anteromedially and connected by a short ridge with the retroarticular process. The length of the retroarticular process is not known. Its preserved proximal portion only suggests that it was ventrally flattened which corresponds with the ventral facing of the adjacent part of the mandible. The articular facet is bilobed, saddle-shaped, and has a distinct tubercle in the anteromedial part to which the supraangular contributes.

Dentition (pls. 18: 4; 19: 3, 4; figs. 4D, 5B): Two large pleurodont teeth are preserved in the premaxilla but the presence of two additional teeth in the missing lateral part of the premaxillary body can not be discounted. About four anterior maxillary teeth are typically pleurodont and enlarged relative to the main cheek series. The teeth of the latter are subequal in size and do not diminish anteriorly. There are circa 12—13 teeth in the left maxilla but only 8 posterior teeth preserved in the right.

The teeth of the dentary total 22 (fully exposed only in the left dentary) and are subequal in size. About 8 tall pointed anterior teeth make up a regular pleurodont series. Posterior to this series, there are 14 more closely spaced teeth. They are much more irregular in crown shape and orientation than the anterior enlarged series. The crowns retain their individual outlines down to the level of the dental gutter, rather than blending with the dentary, although the basal parts are ankylosed. Some of the teeth or groups of teeth are implanted more medial than the remaining tooth row. They are the 3rd and 8th teeth of the left upper cheek series, and the 11th through 15th and 22nd tooth of the left lower dentition. Among these, the 8th upper left cheek tooth and the 22nd left lower tooth seem to represent actual replacement teeth of the directly successional tooth replacement mode. The replacement pits are recognized in the 7th and perhaps the 10th teeth of the dentary series. However, the sucessional replacement does not seem to have proceeded in regular cycles. No part of the cheek series may be determined as hatchling dentition (Robinson, 1976) but the remains of the first and second teeth of the left upper cheek series are suggestive of producing a dentiferous process similiar to that in *Priscagama gobiensis*. In sum, the dentition of *Pleurodontagama* is very irregular and perhaps the result of pathology.
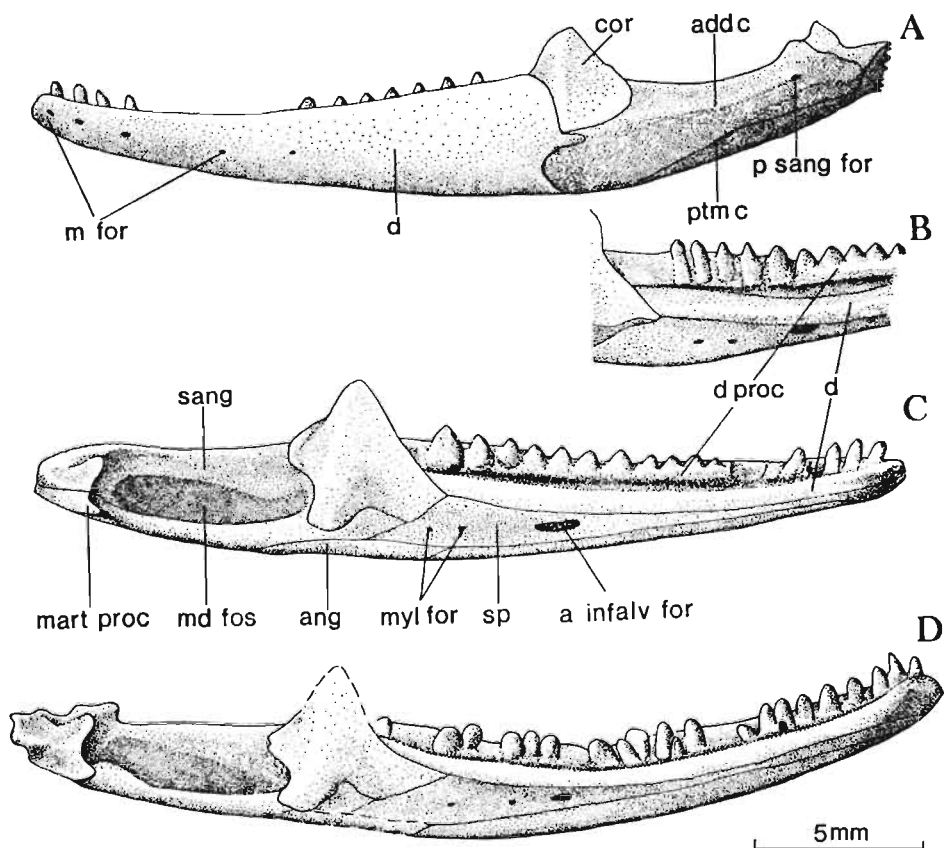

Fig. 4. *Priscagama gobiensis* gen. et sp. n. A — ZPAL MgR-III/32, Holotype; Mandible; labial view; B — ZPAL MgR-III/31; Mandible; lingual view; C — ZPAL MgR-III/32, Holotype; Mandible; lingual view; D — *Pleurodontagama aenigmatodes* gen. et sp. n. ZPAL MgR-III/35, Holotype. Mandible; lingual view.
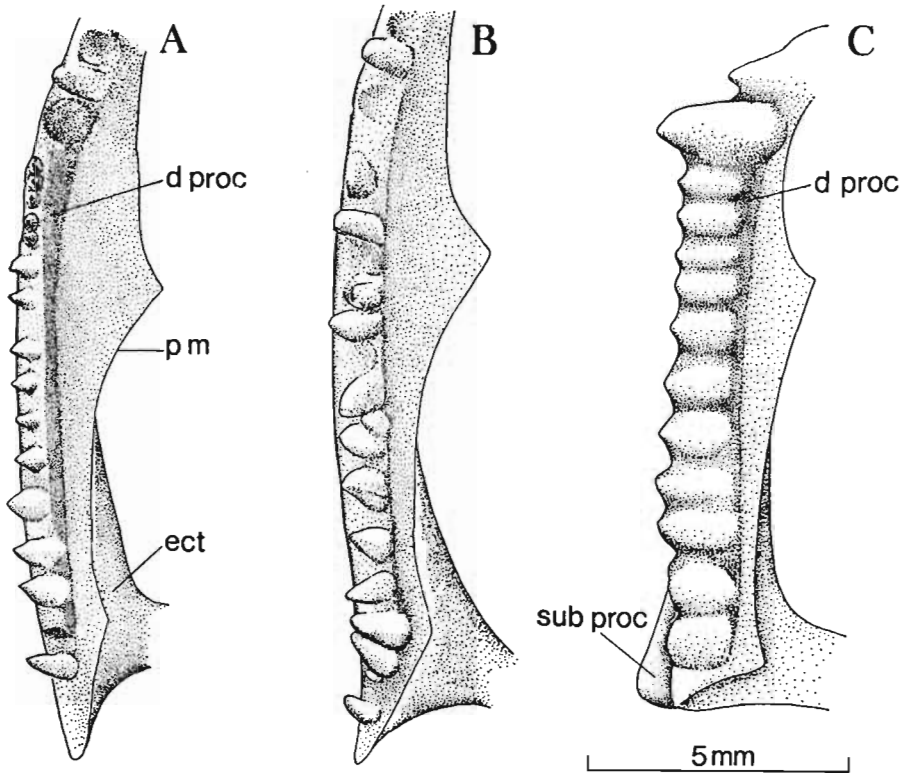
Fig. 5. Maxillary tooth row; lingual view; A — *Priscagama gobiensis* gen. et sp. n. Reconstruction based on ZPAL MgR-III/32; Holotype and ZPAL MgR-III/31; B — *Pleurodontagama aenigmatodes* gen. et sp. n. ZPAL MgR-III/35; C — *Mimeosaurus crassus* Gilmore; ZPAL MgR-II/40.

Genus *Mimeosaurus* Gilmore, 1943

Type species: *Mimeosaurus crassus* Gilmore, 1943.

Stratigraphic and geographic range. Known only from the type locality, Bajn Dzak, Gobi Desert, Mongolia and the type horizon, Djadochta Formation, Late Cretaceous.

Revised diagnosis. — Differs from *Priscagama* and *Pleurodontagama* in having more robust skull elements, shorter and steeper snout, proportionately deeper mandible and completely acrodont dentition. The high cylindrical teeth have triangular apices, are fused together and are strongly ankylosed to the jaw bones. They are homogeneously sized except for two or three anteriormost teeth.

Remarks. — The combination of acrodont dentition typical of the Agamidae and the primitive large splenial with two mylohyoid foramina and a large inferior alveolar foramen suggests assignment of this taxon to the Priscagaminae. *Mimeosaurus* also has a strongly developed adductor crest on the labial side of the mandible, a diagnostic characteristic shared with the priscagamids. Other important diagnostic characters, eg., amount of overlap of the coronoid on the labial side of the mandible, were not preserved. *Mimeosaurus* differs more from both *Priscagama* and *Pleurodontagama* than these two latter genera differ from each other.

Mimeosaurus crassus Gilmore, 1943
(pls. 17: 1—5; 18: 1, 2; figs. 3B; 5C)

Material. — AMNH 6655, Holotype, left maxilla, complete except for extreme anterior and posterior ends and tip of nasal process. Lower portion of jugal and most of ectopterygoid are attached. Nearly a complete series of 12 acrodont teeth are present but badly worn. ZPAL MgR-II/40, right maxilla, preserved nearly identically with holotype except for lacking the entire ascending part of the jugal. ZPAL MgR-II/73, middle portion of left mandible including the coronoid and posterior 2/3 part of dentary and splenial, and anterior portions of angular and supraangular.

Measurements: See Tables 1 and 2.

Description. — A major portion of the maxilla (pl. 17: 1—5; fig. 3B) contributes to the robust infraorbital region. Extremely short nasal process is hardly more than the anterior border of the orbit and the preorbital part is only a short premaxillary process. The maxilla contributes much more than the jugal to the lateral surface of the infraorbital region. Their suture runs obliquely from the lacrimal, posteroventrally to the infratemporal process. Along a vertical transect about the middle of the tooth row, the jugal contributes the upper 1/4 and maxilla the lower 3/4. The posterior end of the maxilla is a narrow infratemporal process which bears teeth. The lateral surface of the maxilla is convexly angled in a vertical transect, the line of angling extending between the infratemporal process and the base of the first maxillary tooth. It divides the surface at the level of the midheight of the infraorbital region (pl. 17: 1, 2) into two parts. The lower part, on nearly the same plane with the tooth row, is apparently the result of fusion of the basal parts of the teeth and the surrounding bony matrix.

The nasal process has a short base and a vertical anterior margin. These features together with the shortness of the premaxillary process suggest that the snout was short and steep. The ventral and posterior margins of the external nares suggest a vertically elliptical shape. A vertically oriented blunt ridge is on the nasal process.

A short palatomaxillary process is present but the palatine was not preserved. The edge is directed anteromedially and most likely the palatomaxillary suture was oriented similarly. This process lies within the anterior half of the orbit and attenuates just before this. The ectopterygoid process is tiny.

The jugal tapers acutely along the orbital border and contacts the small lacrimal. The preserved part of the jugal has 8 nodule-like tubercles extending along the orbital border and increasing in size posteriorly. A ninth much larger tubercle occurs at the posteroventral corner of the jugal just dorsal to the last maxillary tooth. The maxilla contributes slightly to this protuberance. The medial surface of the jugal is posteroventrally overlapped by the ectopterygoid but its upper part faces slightly dorsomedially. The ectopterygoid has a broad base, articulating primarily with the jugal and secondarily with the infratemporal process of the maxilla. The transverse ramus of the ectopterygoid lies at the level of the infratemporal process. The palatine and ectopterygoid almost meet along the medial wall of the maxilla to enclose the suborbital fenestra. The lacrimal boundaries are not distinct but the element is flat and moderate in size.

The mandible (pl. 18: 1, 2) is robust, short and deep, judging from the preserved part of the precoronoid and coronoid portions. Labial surface of the dentary is strongly convex. The convexity turns into the robust adductor crest beginning with the level of the coronoid. No dental gutter is produced but the medial wall of the dentary slopes steeply from the tooth bases down to the splenial. Its ventromedial part borders the splenial from below. The splenial is very long, extending from the

Table 1

Skull measurements

Cat. Nos. ZPAL MgR/	*Pleurodont-agama aeni-gmatodes*	*Priscagama gobiensis*						*Mimeo-saurus crassus*
	III-35	III-31	III-32	III-33	III-72	II-77	II-101	II-40
Premaxilla — basi-occipital condyle length	25.0							
Premaxilla — fronto-parietal suture length	18.0			12.0	13.4			
Skull width at post-parietals	16.8		16.8		12.2			
Skull width at jugals	17.8	16.5	18.2	11.5	12.0			
Skull width at pre-frontals	approx. 10.3	8.2	8.4	5.5	6.3	7.7		
Orbital opening length	8.4	8.1	7.4		6.4	7.0	9.4	
Orbital opening width			6.9	5.4	5.5	6.5		
Temporal fenestra length	approx. 6.9		7.5		4.2			
Temporal fenestra width			4.9		2.8			
Apex of prefrontal — premaxilla length (in projection) Width between proce-sses for pterygoideus muscles	9.9 10.3	9.1	9.6	5.9	6.6	9.5		
Width (maximum) across both palatines	5.9	5.7	6.2	4.0	3.7	4.8		
Skull depth at level of prefrontals	6.5	6.2	6.5	3.3	3.9	6.3		
Skull depth at level of parietals			8.3	6.9				
Frontal parasaggital length[1]			10.1	7.4	7.5	11.1	11.6	
Frontal width, anterior		4.1	3.8	2.5	3.0	3.5	4.0	
Frontal width, posterior	9.2		9.2		8.1		10.7	
Frontal width, orbital constriction	approx. 3.1		2.9	1.8	1.8	2.6	3.8	
Parietal parasaggital length			4.8		3.7		4.3	
Parietal width anteriorly	9.2		9.2		8.1		10.7	
Parietal width at crest constriction			3.4		2.3		2.8	

| Cat. Nos. ZPAL MgR/ | Pleurodont-agama aeni-gmatodes | Priscagama gobiensis | | | | | | Mime-osaurus crassus |
	III-35	III-31	III-32	III-33	III-72	II-77	II-101	II-40
Jugal, maximum horizon-tal length	8.0	7.8	7.8		5.8	6.8	10.0	
Jugal, maximum vertical length	6.2	6.6	6.2		4.5	6.8	6.2	
Maxilla, maximum length	16.0			10.5	11.3			approx 12.2
Maxilla, heigth nasal process			4.5	3.1	2.8	4.5		4.6
Suborbital fenestra, width	2.1	2.3	1.7	1.3	2.0	2.2		
Suborbital fenestra, length	4.6	4.5	4.4	3.3	3.0	4.3		
Vomer width (both halves)		3.5		2.2				
Vomer length		5.1		3.3				
Quadrate shaft length	4.9	5.1			4.0			
Quadrate width of condyle	2.3				1.4			

[1] to avoid the parietal foramen and frequently broken midline anterior process.
   L — left; R — right

level of the coronoid apex through the whole length of the preserved part of the ramus. In spite of the bad state of preservation, two small mylohyoid foramina and a large inferior alveolar foramen may be recognized. A robust triangular coronoid has its dorsal process broken off. Presence of the labial process overlapping the dentary can not be ascertained. The posterior coronoid ramus is strongly ridged, and does not reach the ventral margin of the mandible.

Dentition (pls. 17: 3, 5; 18: 2; fig. 5C): Maxillary teeth number is 12 or 13 and dentary teeth are 12. They are acrodont. The crowns are bluntly triangular labially and cylindrical lingually, and they are bilaterally compressed and lack supplementary cusps. They are about the same size and shape except for the anterior 2 or 3 maxillary teeth. The most anterior tooth is tiny and the next one or two are enlarged. Labially, the bases of the maxillary teeth are completely ankylosed with the maxilla, to the extent that they seem to add to its height. On the lingual side, cylindrical crowns of the main acrodont series of 10 teeth are fused together but lose their individuality only in the basal portion of the crowns ankylosed to and forming the dentiferous process. The latter makes up a slight furrow separating the distal parts of the crowns from the palatal shelf of the maxilla. The two or three anterior teeth are more triangular in outline and preserve their individuality down to the palatal shelf. Dentary teeth are implanted exactly in the same way as the maxillary teeth and are also fused lingually. No resorption pits or replacement teeth are present.

Table 2
Measurements of mandibles

	Pleurodontagama aenigmatodes III-35L	Priscagama sp. III-69R	Priscagama gobiensis III-31R	III-32L	III-72L	III-83R	Mimeosaurus crassus II-73L
Total length	27.6						
Total length to glenoid	26.2			23.6			
Length labial dentary	18.7			16.8	12.9		
Length alveolar dentary	16.8			14.0			
Length of splenial	11.4			11.0			
Coronoid length	2.3		3.0	3.0		2.5	3.0
Mandibular depth, maximum	3.1	4.0	3.5	3.8		3.4	4.3
Mandibular fossa length	6.0		5.0	5.6			
Mandibular fossa depth	2.2		2.5	2.4		2.0	
Mandibular height incl. coronoid	4.1	7.0	5.1			5.2	
Coronoid to articular length			6.0	6.4	4.8		

DISCUSSION

Three genera *Priscagama*, *Pleurodontagama* and *Mimeosaurus* consider-ed in the present paper, constitute a morphologically uniform and probably monophyletic group of lizards. They are agamoid lizards characterized by a tuberculate sculpturing of bone surface and a primitive long splenial. The agamoid nature is primarily understood as the acrodont type of dentition and skull proportions including a posteriorly shifted maxilla. The long unreduced splenial seems to exclude the group in question either from the Agamidae or from the Chamaeleonidae to which *Mimeosaurus* was first assigned (Gilmore 1943). Still, one important character, the structure of the brain-case wall, link priscagamids to the Agamidae, where-as none of the uniquely derived characters of the Chamaeleonidae is shared by the priscagamids. The acrodont dentition, and the tuberculate sculp-turing of bones, characters based on by Gilmore, are not unique to the Chamaeleonidae.

The main problem of the present paper is whether any of the charac-ters of the priscagamids shared with the family Agamidae could be con-sidered synapomorphic and, consequently, whether these two groups could be regarded as a monophyletic taxon. The second problem is what rank this taxon should be given and what is its relation to the remaining agamoid groups (chamaeleonids and uromasticids).

Although a detailed discussion of the morphocline polarities of the characters linking the priscagamids to the agamids is out of the scope of the present paper, some cursory examination suggests that four of them are uniquely derived for the taxon including both groups. They are as follows:

(1) Acrodont dentition. The mode of implantation, tooth replacement pattern of heterodonty and tooth form determine the priscagamids as acrodont lizards. Their cheek series consists of completely fused tiny teeth, probably corresponding to the hatchling dentition, of some bigger teeth fused to the hatchling series from behind and of some other, not com-pletely fused teeth added at the end of the series. Anterior to the main cheek series, the teeth are different size and different state of fusion, some of them may be big canine-like teeth.

It seems established (Edmund 1960, Cooper *et al.* 1970, Cooper *et al.* 1973), on the developmental data, that the acrodont tooth replacement has been derived from the continuous replacement which is regarded as plesiomorphic. The contribution of pleurodont teeth to the main cheek series is more significant in early phases of ontogeny of the acrodont dentition and decreases with increasing age. Corresponding to the early stage of ontogeny, the dentition of some, at least, priscagamid genera is regarded as representing the initial stage of development of the acrodont type of teeth in phylogeny. Great variability of the dentition, which oc-curred at the generic, and probably at the infrageneric level as well, is

not at all unexpected at the early stage of evolution of the agamoid stem of lizards. Variability and great contribution of pleurodont teeth determine the state of acrodont dentition regarded as autapomorphic for the agamoid stem of lizards.

(2) A posterior shift of the maxillary tooth row to underlay most of the orbit and to reach the level of the frontoparietal suture. The distribution of different positions of the maxilla relative to the rest of the skull within the Lacertilia suggests that the intermediate position of the maxilla, extending beneath the anterior part of the orbit, is primitive whereas both the position anterior to the orbit, characteristic of the Platynota, and the posterior position of the agamids, are derived. The drawback of this character is that it is probably easy to develop independently, as shown by (e.g.) *Crotaphytus*, which displays the extreme posterior position of the maxilla which is uncommon within the Iguanidae. Shifted to the posterior part of the orbit but hardly reaching the frontoparietal suture, the position of the maxillary tooth row in the priscagamids is here regarded as a less derived state (transitional between plesiomorphic and fully derived state) and autapomorphic for the agamoid stem. Associated with it is a vertical orientation of the process destined for the pterygoideus muscle and some other skull characters.

(3) Unique to the agamoid lizards, chamaeleonids and uromasticids included, is the union of the premaxillary processes of both maxillae in the midline to separate the premaxilla from the vomers.

(4) The brain case wall is deeply excavated between the semicircular canals (pl. 16: 3) in such a way that the prootic produces a broad shelf situated in the same plane as the horizontal semicircular canal, whereas the anterior semicircular canal along with a tiny alar process produce a sub--perpendicular wall. The latter meets the horizontal shelf at the skull region perforated by the epiotic foramen in all the agamids but in *Moloch* (Siebenrock 1895) and *Stelio tuberculata* (Moody 1980). The brain case wall is excavated but unperforated in *Uromastix* and *Leiolepis*. Instead, the brain case wall is usually oblique in other lizards and the prootic slopes ventrally, so as to be poorly exposed is dorsal aspect of the brain case. In the priscagamids the brain case wall is excavated and oriented exactly like the one in the agamids but lacks the epiotic foramen. The presence of this foramen, characteristic of the agamids, is unique among the lizards, which suggests that it is a derived character. It is hypothesised that the excavation of the brain case wall is autapomorphic in the agamids and makes up a predisposition to the perforation of this wall. The perforated and unperforated wall are just two different states of the same character — excavated brain case wall.

On the basis of the above synapomorphies the close relationship of the priscagamids and agamids seems to be established to the best of our present knowledge. The problem of systematic range of the monophyletic

taxon including the priscagamids and agamids is mainly an arbitrary one, but the relationships of the remaining agamoids, the uromasticids and chamaeleonids, are critical for the solution.

The uromasticids, recognized as a taxon of familial level by Moody (1980), fit perfectly well to the agamoid group by sharing all the above four synapomorphic characters (p. 72). Given the character complex of the priscagamids, the uromasticids appear to be more closely related to the Agamidae than they seemed to have been earlier, since they share some presumably derived agamid characters not yet developed in the priscagamids. They are as follows: reduced splenial, lack of the labial overlap of the coronoid on the dentary, and ventromedial limitation of the mandibular fossa by a sharp vertical lamina. Compared to the just listed features the characters discriminating the *Uromastix-Leiolepis* group from the agamids are of much lesser taxonomic significance. The most striking of them is the ventral concavity formed by the vomers. Other characters, such as the shape of the distal condyle of the quadrate, shape of the naris, pectoralis muscle with "pars cutaneous" are either not unique to the *Uromastix-Leiolepis* group or closely connected with an adaptation for a certain habitus. However, many other characters, though probably plesiomorphic, are listed by the author (Moody *l. c.*) which distinguish the *Uromastix* group from the other agamids. Regarded as a complex, they tend to support the existence of a monophyletic group including both genera, but they are not directly conclusive as to the taxonomic rank of this group. This matter will still be a subject to further studies of the junior author. For the time being we tentatively consider the *Uromastix* group as a part of the family Agamidae.

Chamaeleonidae share only three character states (p. 72: 1—3) of the above complex of four synapomorphjes. Their brain case wall shows none of the concavity (character state 4) said characteristic of the agamids, priscagamids and uromasticids. If not secondarily attained, which may not be entirely ruled out, this state of the brain case wall directly suggests that the chamaeleonids represent an early offshoot of the agamoid stem prior to the development of the brain case concavity, which appeared only in the common ancestor of the remaining agamoids. Conflicting distribution of a reduced splenial, which is shared by the chamaeleonids and the agamids (uromasticids included) but not by the priscagamids, makes it difficult to accept this suggestion. However, the independent reduction of the splenial is more probable than the independent development of the brain case concavity which would have occurred if the agamids were more closely related to the chamaeleonids than to the priscagamids. Some further doubts as to the closer connection of the Chamaeleonidae with the agamoid stem have also been raised by the results of Ethridge and De Queiroz (1982). These authors demonstrated that the epidermal mechanoreceptors of the chamaeleonids and the iguanid genera *Oplurus* and *Chala-*

rodon are very similar and quite different from agamids. This is to say that the exact systematic position of the chamaeleonids is not quite clear and this group is better to be provisionally kept aside from the definitely recognized agamoids.

We are, thus dealing with a very uniform agamoid group including primitive priscagamids, uromasticids and agamids and determined by four synapomorphies. Until new evidence comes, it seems more advisable to include all of them into the existing family Agamidae and to give them subfamilial status, instead of erecting a new taxon of suprafamilial level. This solution is accepted herein.

Demonstrated above, the relationships of the priscagamids to the family Agamidae directly imply the iguanian nature of this group of lizards. This makes us face the problem of what really the "iguanian nature" means and whether any of the features defining this nature could be regarded as synapomorphic for the infraorder Iguania.

The following complex of character states is considered characteristic of the Iguania on the basis of studies of both extant and fossil material. It contrasts with the states displayed by other lizard groups (Gekkota not fully considered).

(1) The sphenoccipital suture is shaped like an angle which opens widely posteriorly (see Borsuk-Białynicka 1984). It may be approximately transverse in some iguanians. In contrast this suture is trapezoidal in the Anguimorpha and Scincomorpha (Borsuk-Białynicka 1983, 1984).

(2) The pterygoids and palatines tend to produce broad and flat bone blades at the medial boundary of the suborbital foramina. They are relatively narrower in the Anguimorpha and Scincomorpha.

(3) The vomers are broad plates hardly narrowing or even growing broader posteriorly to contact the palatines instead of producing narrow processes to contact with the equally narrow vomerine processes of the palatines as it is the case in the Anguimorpha and Scincomorpha (still narrower in the Gekkota).

(4) The palate is bent ventrally concave (as in the over-retracted position of the kinetic skull apparatus, Borsuk-Białynicka, in press). The bending occurs at the level of the choanae, the vomers and the anterior part of the palatines making an obtuse angle with the posterior part of the palatine. In contrast, the vomers, palatines and pterygoids are situated almost in the same plane in the Anguimorpha and Scincomorpha.

(5) The long protrudent medioarticular process is usually present while being absent or not individualized in other lizard groups.

(6) The brain case is short without an ossified wall anterior to the anterior semicircular canal. The alar process is tiny and directed dorsally toward the parietals. Instead the Anguimorpha and Sincomorpha have basically a long, well developed alar process anterior to the anterior semicircular canal (Borsuk-Białynicka 1983, 1984).

(7) The broad triangular jugular recess faces ventrally rather than laterally in contrast to its oblique position in most of the Anguimorpha (Borsuk-Białynicka *l. c.*).

(8) The parietals are proportionately short, which is probably associated with having the parietal foramen located within the frontoparietal suture.

The evolution of large orbits in the Iguania may be the selective agent behind the characters (6) and (8). However, we cannot specify whether it has caused the development of these character states or prevented tham from being changed (but see Estes 1983: 23). The morphocline polarities have been proposed only for some of these characters (Borsuk-Białynicka 1983). On this basis the state of the sphenoccipital suture (1) is considered autapomorphic in the Iguania. The character states of the brain case (6) and (7) are considered plesiomorphic. It should be stressed that the structure of the priscagamids ties in well with the hypothesised morphoclines. Other than above three, the character states of the Iguania have not been determined in terms of their primitive and derived nature. Still, the perfect correspondence of the structure of the priscagamids with the whole character complex, supposed to be iguanian on the other data, supports iguanian nature of this complex. At the same time it suggests that more than one (1) of the contributing character states may prove to be autapomorphic in the Iguania.

The Iguanidae share some character states, apart from all the iguanian ones, with the priscagamids, which do not, however, falsify the position of the priscagamids close to the agamoid stem, since the characters shared are probably plesiomorphic (for the morphocline polarities see Moody 1980, 1982). They are as follows:

Relatively short dentary which does not reach posterior beyond the coronoid apex.

Overlap of the coronoid on the labial surface of the mandible.

Mandibular fossa broadly open medially instead of being delimited from the medial side by a vertical wall produced by the prearticular.

Pterygoid teeth present.

It may be, in our opinion, that the lack of the coronoid overlap on the labial surface of the mandible in the Agamidae results from the posterior shift of the dentary, the latter being associated with the similar posterior shift of the maxillary considered derived in the above discussion (p. 73). We are probably dealing with the derived complex of associated character states in the agamids and with the plesiomorphic state of this complex in the iguanids while dealing with a state less derived than in the agamids in the priscagamids. This morphocline polarity, hypothesised on the basis of our understanding of the biomechanical association of the particular skull parts, is supported by examination of character distributional data. The labial overlap of the coronoid on the mandible is in common to almost all lizards other than the agamids and chamaeleonids (the exceptions, such

as *Tiliqua* are probably secondary specializations). It may, thus, be regarded as plesiomorphic on the out — group criterium (Hecht 1976). The primitive nature of the pterygoid dentition is widely known, and thus, demands no special discussion, whereas the lingual limitation of the mandibular fossa by the vertical wall is unique to the agamids and, thus, the lack of the wall is probably plesiomorphic. So, none of the characters shared by the priscagamids and the iguanids indicates the existence of the ancestor common to both of them and not shared by other iguanians. The thesis about the agamoid nature of the priscagamids is, thus, indirectly supported.

In view of the systematic position of the priscagamids, accepted herein, the shortened splenial shared by the Iguanidae and the Agamidae should be considered as homoplastic. Further studies concerning the possible causes of the independent origin of this character state (or two similar but different character states) are strongly required and critical for the here accepted systematic concept.

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PRISCAGAMINAE, NOWA PODRODZINA AGAMIDÓW (SAURIA)
Z KREDY GÓRNEJ PUSTYNI GOBI

Streszczenie

Materiał opisany w niniejszej pracy, zebrany przez Polsko-Mongolską Ekspedycję paleontologiczną na pustynię Gobi w latach 1963—71, obejmuje siedem czaszek, w tym kilka prawie kompletnych okazów z żuchwami, oraz kilka fragmentów czaszek

i żuchw. Materiał ten był cytowany w literaturze pod nazwą *Mimeosaurus crassus* Gilmore 1943 (Moody 1980, Estes 1983). Jednak niniejsze opracowanie wykazało, że tylko dwa uzębione fragmenty szczęk, górnej i dolnej, można zaliczyć do *Mimeosaurus*. Pozostały materiał reprezentuje dwa nowe rodzaje i gatunki, *Priscagama gobiensis* i *Pleurodontagama aenigmatodes*, należące do nowej podrodziny jaszczurek agamidowych, Priscagaminae. *Mimeosaurus crassus* został zaliczony do tej samej podrodziny na podstawie niezredukowanego spleniale a więc cechy plezjomorficznej. Zaliczenie to, aczkolwiek nie całkiem pewne, jest jednak znacznie prawdopodobniejsze niż zaliczenie go do Chamaeleonidae przez Gilmore'a (1943), oparte na obecności uzębienia akrodontowego i guzowatego urzeźbienia powierzchni kości, które nie są cechami właściwymi wyłącznie kameleonom.

Opisany tu materiał pochodzi z dwóch stanowisk należących do dwóch różnych formacji górnej kredy. Bajn Dzak należy do formacji Dżadochta (? d. santon lub g. koniak), a Chermin Caw do formacji stanowiącej biostratygraficzny odpowiednik późnosantońskiej formacji Barun Gojot (Karczewska i Ziembińska-Tworzydło 1983). Formacje te były uważane za młodsze przez wcześniejszych autorów (Gradziński *et al.* 1977).

Nowa podrodzina Priscagaminae jest zdefiniowana przez zespół cech plezjomorficznych wyróżniający je zdecydowanie od reszty agamidów. W skład tego zespołu wchodzi: bardzo długie spleniale, w obrębie którego znajduje się tylny foramen mylohyoideum, znaczna zmienność sposobu osadzenia zębów, który waha się od subpleurodontowego do typowo akrodontowego; obecność uzębienia skrzydłowego; kość szczękowa nie sięgająca poziomu szwu czołowo-ciemieniowego; koronoid mający wargowy wyrostek nakładający się na kość zębową; brak foramen epioticum; brak ograniczenia dołu żuchwowego przez przyśrodkową, pionową ściankę kostną.

Następujące cechy łączące priskagamy ze znanymi dotąd przedstawicielami agamidów uznane zostały za synapomorficzne dla rodziny Agamidae: (1) Uzębienie akrodontowe określone przez sposób osadzenia i wymiany zębów oraz ich charakterystyczne zróżnicowanie wzdłuż szeregu zębów (przednie zęby pleurodontowe często ulegają przerostowi, całkowicie zlana seria zębów młodocianych i dorastające do nich od tyłu zęby większe o zmiennym stopniu zrostu ze szczękami i z sobą nawzajem, malejącym ku tyłowi szczęki); (2) Przesunięcie szczęki wraz z uzębieniem pod oczodół, w kierunku szwu czołowo-ciemieniowego lub poza poziom tego szwu; (3) Połączenie wyrostków przedszczękowych w linii środkowej, między kośćmi przedszczękowymi a lemieszami; (4) Zaklęśnięcie ściany puszki mózgowej między kanałami półkolistymi w ten sposób, że prooticum tworzy szeroką półkę w płaszczyźnie poziomego kanału półkolistego i niewielki wyrostek skrzydłowy. Zagłębienie to wydaje się predysponować ścianę puszki mózgowej do perforacji (for. epioticum), która jest cechą bardzo powszechną u agamidów.

Grupa *Uromastix-Leiolepis* wyodrębniona przez Moodiego (1980) w osobną rodzinę Uromasticidae dzieli z priskagamami i agamami wszystkie cztery wyżej wymienione synapomorfie, a ponadto dzieli z agamidami kilka cech pochodnych, których brak priskagamom. Są to: zredukowane spleniale, brak wargowego wyrostka koronoidu i ograniczenie dołu żuchwowego przez pionową blaszkę. Podtrzymanie rodzi-

nowej rangi grupy *Uromastix-Leiolepis* pociągnęłoby za sobą konieczność nadania takiej samej rangi priskagamom i stworzenie wspólnej dla trzech rodzin jednostki o randze nadrodzinowej. Dwa argumenty przemawiają przeciwko temu posunięciu: niejasne stanowisko kameleonów, które dzielą co najwyżej trzy z wymienionych synapomorfii oraz niewielkie znaczenie taksonomiczne, przy dużej liczbie, cech wyróżniających grupę *Uromastix-Leiolepis* spośród agamidów. Obie te sprawy wymagają wyjaśnienia zanim dojdzie do rozbicia tej, skądinąd jednolitej grupy jaką są agamidy i stworzenia taksonu wyższej rangi obejmującego lub wykluczającego kameleony.

Włączenie priskagam do agamidów oznaczające ich przynależność do Iguania pozwala na zweryfikowanie zespołu cech uznanego wcześniej (Borsuk-Białynicka 1983, 1984) za charakterystyczny dla Iguania i uzupełnienie go cechami nowymi. Są to: (1) Rozwartokątny kształt szwu klinowo-potylicznego; (2) Kości skrzydłowe i podniebienne tworzą szerokie i płaskie blaszki kostne w obrzeżeniu otworów podoczodołowych; (3) Lemiesze nie zwężają się w tylnej części; (4) Podniebienie załamane jest na poziomie otworów nosowych wewnętrznych w ten sposób, że lemiesze i przednia część kości podniebiennych tworzą kąt rozwarty z tylną częścią kości podniebiennych; (5) Zazwyczaj występuje długi, sterczący wyrostek stawowy wewnętrzny; (6) Puszka mózgowa jest krótka, przedni kanał półkolisty tworzy jej przednią krawędź, wyrostek skrzydłowy jest mały i skierowany ku górze; (7) Szeroki trójkątny recessus jugularis zwrócony jest dobrzusznie; (8) Kości ciemieniowe są stosunkowo krótkie, z czym przypuszczalnie związane jest położenie otworu ciemieniowego w obrębie szwu czołowo-potylicznego.

Przyjęcie hipotezy o pokrewieństwie priskagam z agamidami pociąga za sobą wniosek o homoplastycznym charakterze redukcji spleniale u Iguanidae i Agamidae, który może być przedmiotem dalszego testowania.

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EXPLANATIONS OF THE PLATES 14—19

Plate 14

1. Skull of *Priscagama gobiensis* gen et sp. n. ZPAL MgR-III/32. Holotype; dorsal view. Sterephotographs, ×3.
2. Skull of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/31; ventral view. Stereophotographs, ×3.

Plate 15

1. Skull of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/72; dorsal view. Stereophotographs, ×3.
2. Skull of *Pleurodontagama aenigmatodes* gen. et sp. n. ZPAL MgR-III/35. Holotype; dorsal view. Stereophotographs, ×3.

Plate 16

1. Skull of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/72; right side view. Stereophotographs, ×3.
2. Lacrimal region of skull of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/31; dorsal view. Stereophotographs, ×4.
3. Brain case of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/31; dorsal view. Stereophotographs, ×4.

Plate 17

1, 2, 5. Left maxillary portion of skull of *Mimeosaurus crassus* Gilmore AMNH 6655. Holotype. Stereophotographs, ×4.
1 Labial view; *2* Dorsal view; *5* Lingual view.

3, 4, 6. Right maxillary portion of skull of *Mimeosaurus crassus* Gilmore ZPAL MgR-III/40. Stereophotographs, ×4. *3* Lingual view; *4* Labial view; *6* Left maxillary tooth row of *Priscagama gobiensis* gen. et sp. n. Holotype. Stereophotographs, ×4. Lingual view.

Plate 18

1, 2. Fragment of left mandible of *Mimeosaurus crassus* Gilmore ZPAL MgR-III/73. Stereophotographs ×3. *1* Labial view. *2* Lingual view.
3. Right maxillary tooth row of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/31; lingual view. Stereophotographs, ×4.
4. Left maxillary tooth row of *Pleurodontagama aenigmatodes* gen. et sp. n. Holotype, ZPAL MgR-III/35; lingual view. Stereophotographs, ×4.

Plate 19

1, 2. Mandible of *Priscagama gobiensis* gen. et sp. n. ZPAL MgR-III/32. Holotype. Stereophotographs, ×3. *1* Lingual view. *2* Labal view.
Mandible of *Pleurodontagama aenigmatodes* gen. et sp. n. ZPAL MgR-III/35. Holotype. Stereophotographs, ×3. *3* Lingual view; *4* Labial view.